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BIOLOGICAL FLORA

International Biological Flora: *Tsuga canadensis**

No. 6

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Abstract

1. This account presents information on all aspects of the biology of *Tsuga canadensis* (L.) Carrière (Eastern Hemlock) that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *International Biological Flora*: distribution, habitat, communities, responses to biotic factors, responses to the environment, structure and physiology, phenology, floral and seed characters, herbivores and disease, history, conservation and management, and global heterogeneity.
2. *Tsuga canadensis* is a very shade-tolerant, long-lived and slow-growing canopy tree, native to eastern North America but widely planted in cool, humid parts of Europe as an ornamental. In its native range, it is commonly associated with *Betula lenta*, *B. alleghaniensis*, *Fagus grandifolia*, *Acer saccharum* and in the north *Pinus strobus*. Its distribution is mainly limited by lack of moisture; consequently, it grows best on moist soils, providing there is good drainage, but will also grow on rocky outcrops and steep eroding soils kept moist by seepage or a moist climate.
3. Reproduction is by seed; both pollination and seed dispersal are by wind. Seedling establishment is best on damp mineral soil or on rotting logs and stumps, which are warmer and moister than deep litter layers of the forest floor.
4. Eastern Hemlock has low value as a forest crop, but it is an important foundation species in the forest due to the habitats it offers directly and through its influence on the forest environment. However, Eastern Hemlock is in decline due to the introduced Woolly Hemlock Adelgid (*Adelges tsugae*; Hemiptera, Adelgidae) which kills developing buds, leading to extensive loss of needles and twigs, and death within 4–20 years. Cold weather can slow the progress of the pest, but global warming is acting against this. Chemical control and biological control using introduced beetles show some promise in isolated stands, but the prognosis is range-wide decline or extirpation.

KEYWORDS
communities, conservation, geographical and altitudinal distribution, germination, Hemlock Woolly Adelgid, herbivory, mycorrhiza, reproductive biology

*Nomenclature of vascular plants follows Royal Botanic Gardens, Kew: Plants of the World Online (POWO, 2025).

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Eastern Hemlock (Canadian Hemlock, Hemlock Spruce). Pinaceae. *Tsuga canadensis* (L.) Carrière (*Tsuga americana* (Mill.) Farwell, *Pinus canadensis* L., *P. americana* Du Roi, *P. mariana* Gaertn., *Abies americana* Miller, *A. canadensis* Mich., *A. pectinata* Poir., *A. curvifolia* Salisb., *Picea canadensis* (L.) Link) is a slow growing, long-lived evergreen tree forming a broad pyramidal, conic or tapering crown to 50 m. Dense, long slender horizontal lateral branches, irregularly whorled with pendulous branchlets; terminal shoot drooping. Crown typically covering two thirds of the stem; side branches retained even when killed by shade; long, straight stem up to 2 m diameter. Bark bright orange-brown with purple-brown scaly ridges when young, becoming purplish grey with lattice work of thick scaly ridges. Shoots pale brown or cream with dense, curly, pale orange pubescence, becoming dark grey or grey-brown in second year. Buds hidden by leaves, small, 1.5–2.5 mm long, broad conic to ovoid, red-brown. Leaves borne only on long shoots, 23–30 pairs, pectinate, those on upperside of shoots twisted at base with the lowerside facing uppermost. Individual leaves, dorsoventrally flattened, 0.96 × 0.15 cm, 0.04 cm thick, surface area *c*. 0.21–0.26 cm^2, broadest at base, tapering to obtuse apex from near base, minute teeth along each edge, distinctly petiolate, sweet lemony scent when crushed, falling to leave short brown pegs. Upper leaf surface with a central groove, lower surface with central green midrib containing a single resin canal, and two narrow white stomatiferous bands; stomata usually in four rows, guard cells sunken. Monoecious; male and female strobili borne in separate clusters on the same branch. Male strobili in leaf axils of 1-year-old shoots, occasionally 2–3-year-old shoots, rounded yellow clusters of spirally arranged 2-celled anthers. Female strobili borne singly, terminal on last year's lateral shoots, green, rounded scales longer than the bracts. Female cones mature in 1 year but may remain on tree into the second year; usually numerous, 1.3–2.5 × 1.0–1.5 cm, yellow-green when young, pale chestnut-brown when mature, ovoid, pendent, slender stalks, falling whole, *c*. 20 scales, rounded, obscurely toothed, 8–12 × 7–10 mm. Central scales seed bearing, bracts rarely exserted, scales opening to *c*. 45° when dry. Seeds 1.6 mm long with a slightly longer attached wing.

Tsuga contains 8–12 species globally, depending upon how many Asian species are recognised (Ellingson et al., 2019; Holman et al., 2017). Four species are native to North America, two on the east coast: the more widespread *Tsuga canadensis* and *T. caroliniana*, endemic to the southern Appalachians, which is contained within the southern native area of *T. canadensis* (Holman et al., 2017). *Tsuga caroliniana* is most closely related to Asian hemlocks and is taxonomically distinct from Eastern Hemlock, but both these east coast species lie within sister clades (Havill et al., 2008). Despite the close affinity of *T. caroliniana* to the Japanese *T. diversifolia*, the former is susceptible to Hemlock Woolly Adelgid, as is *T. canadensis*, while the latter is not (Havill & Montgomery, 2008).

Tsuga canadensis has been described as a tree of 'striking beauty' (Jenkins, 1946) and as such is the most widely variable and cultivated *Tsuga* species (Swartley, 1984). There are an estimated 280 named cultivars of dwarf, weeping, prostrate and variegated varieties, and more unnamed ones (Fordham, 1963; Swartley, 1984). One of the most interesting is *T. canadensis* 'Minuta'; very slow growing, reaching 45 × 55 cm after 40 years, discovered in 1935 in the Green Mountains of Vermont (Del Tredici, 1984, 2023).

Genetic diversity has been investigated by a number of authors. Using 19 allozyme markers present in 20 Eastern Hemlock populations across southeast United States, *Tsuga canadensis* was found to have a lower heterozygosity (0.072) than other North American hemlocks, including *T. mertensiana* (0.087) and *T. heterophylla* (0.142) in British Columbia (Ally et al., 2000; Potter et al., 2008; Wellman et al., 2003). Moreover, in the south of its native range, Eastern Hemlock was found to have considerably less genetic diversity than other conifers (mean of 0.176 across 103 allozymes in other Pinaceae species) while 57.9% of Eastern Hemlock loci were polymorphic, compared to 73% in the other Pinaceae species (Hamrick & Godt, 1996; Potter et al., 2008).

Eastern Hemlock is a long-lived (up to perhaps 700 years), slow growing (up to 250–300 years to reach maturity) and highly shade-tolerant conifer (Godman & Lancaster, 1990; Niinemets & Valladares, 2006) that is a foundation species of eastern North America (Ellison, 2014). It is the conifer counterpart to American Beech *Fagus grandifolia* in shade tolerance and longevity, and as shade tolerant as *Acer saccharum* (Foster, 2014). Despite being an abundant forest tree, Eastern Hemlock is now under threat of extirpation by the Hemlock Woolly Adelgid (HWA) *Adelges tsugae* Annand (Hemiptera, Adelgidae). Since the introduction of HWA from Japan more than 70 years ago (Havill et al., 2006), it has caused the widespread mortality and decline of Eastern Hemlock (Dharmadi et al., 2019; Ellison et al., 2018).

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

The northern limit of the contiguous native distribution of Eastern Hemlock (Figure 1) extends to northeast Minnesota, through northern upper Michigan, parts of northern Ontario, all of southern and central Ontario, southern Quebec and into the Maritime provinces. It continues southeastwards to the Atlantic seaboard, such as in Rhode Island (Brown et al., 1982). It extends westwards to Minnesota in the north and along the Appalachian Mountains in the south, south to northern Georgia and Alabama. The total range covers >10,000 km^2. The range of Eastern Hemlock completely encompasses the native range of *Tsuga caroliniana* in the Appalachians, which inhabits drier, rockier sites at higher altitude than Eastern Hemlock.

Outlying populations of Eastern Hemlock are known from southern Michigan and western Ohio, with scattered islands in southern Indiana (Ellingson et al., 2019; Godman & Lancaster, 1990; Hotchkiss et al., 1976) and central Alabama, mostly in sheltered ravines with streams (Hart & Shankman, 2005; Oosting & Hess, 1956). In addition, isolated stands of Eastern Hemlock occur in Indiana, Kentucky, Wisconsin and Ohio as glacial relicts on steep slopes (Black & Mack, 1976; Friesner & Polzger, 1932, 1933; Goder, 1955). Although

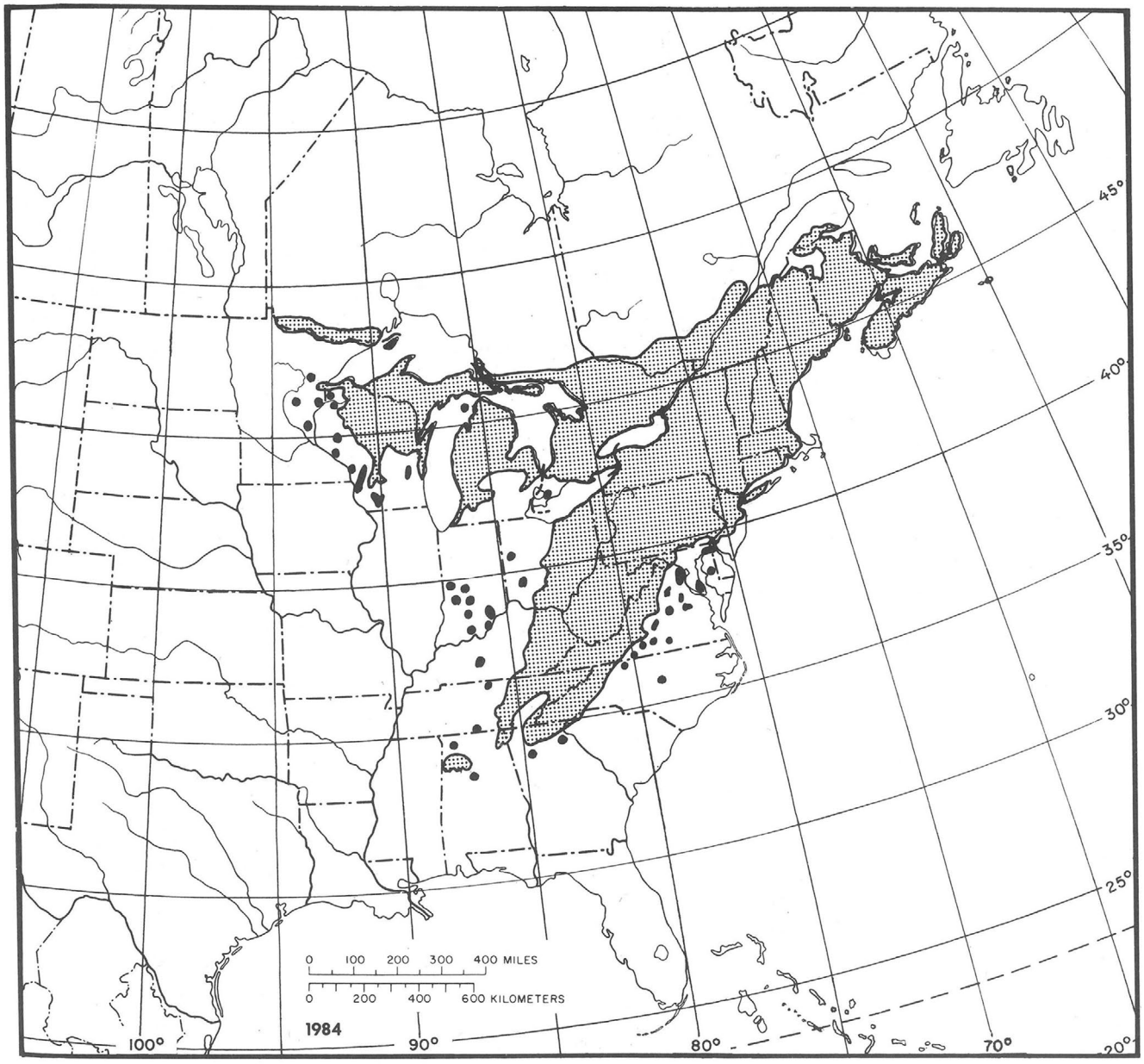


FIGURE 1 Native distribution of *Tsuga canadensis* in eastern North America. This map, taken from Godman and Lancaster (1990), includes its presence in eastern Ontario and northern Minnesota. These areas are omitted from the other common map from Little Jr. (1971).

Eastern Hemlock is widespread in Canada, it covers <4% of the total forest area (Emilson et al., 2018).

Eastern Hemlock is a neophyte in Britain, introduced in 1736 and planted throughout in parks and small-scale plantations (Stace, 2019). It is also widely planted in suitable climatic areas around the world, particularly Germany, Norway and Poland (POWO, 2025).

In the north of its native range, Eastern Hemlock grows from near sea level to 730 m. Further south in the Adirondack Mountains, New York and into Pennsylvania, it is found between 300 and 910 m, and in the southern Appalachians it grows between 610 and 1520 m. Furthest south in Georgia and Alabama, it is not found below 240 m, and up to 1840 m (Brisbin, 1970; Frothingham, 1915; Godman & Lancaster, 1990; Narayanaraj et al., 2010; Schmitt & Slack, 1990).

2 | HABITAT

2.1 | Climatic and topographical limitations

In its native range, hemlock is restricted to cool, humid sites. Although Eastern Hemlock can survive temperatures as low as −20 to −30°C (Sakai & Larcher, 1987), in northern areas, the mean January temperature is −12°C and the July temperature is 16°C (Godman & Lancaster, 1990). Further south, it grows where temperatures commonly range from −10 to 20°C (Dunckel et al., 2017; Lepage, 2003) and in more maritime areas, the mean January temperature can be as high as 3.3°C and the July temperature 21.6°C (Ford et al., 2012). Winter temperature may become limiting near the northern end of

Eastern Hemlock's range (Tardiff et al., 2001) but in central Ontario, Eastern Hemlock is found mainly on western and northern slopes (Kavanagh & Kellman, 1986) suggesting otherwise. The frost-free period is less than 80 days at the northern range limits and nearly 200 days in the eastern and southern portions of the range (Godman & Lancaster, 1990).

Eastern Hemlock does not tolerate long periods of drought (Section 5.3) and moisture is often the limiting factor in establishment and growth. Annual precipitation in the form of rain, snow and fog varies from less than 740 mm in heavy snowfall areas of the north to more than 1270 mm further south, with about half falling in the summer, and Eastern Hemlock will cope with up to 4500 mm (Dunckel et al., 2017; Godman & Lancaster, 1990; Lepage, 2003). Near the Atlantic coast and in the southern Appalachians, where growth is highest, mean January temperature can be as high as 6°C, with annual precipitation of >1520 mm. The southern disjunct populations in Alabama are limited to areas where evaporation is reduced, such as in ravines with streams where the humidity is higher (Godman & Lancaster, 1990).

In New England, Kessell (1979) identified two apparent sympatric ecotypes across the range: the 'high-response' Eastern Hemlock prefers mesic sites, has a high radial growth rate and is highly sensitive to moisture but not to temperature; the other, the 'low-response' ecotype, also prefers mesic sites but is most common on subxeric slopes, has a slow radial growth rate and is highly sensitive to temperature but not to moisture. The differences appeared to be genetic with intermediates between the two extremes, and the two ecotypes may have originated allopatrically. Kessell concluded that under moist conditions, the high-response ecotype dominated, but under drier conditions, the low-response type had a competitive advantage, the advantages being sufficient to maintain the two ecotypes within the same range.

In the north of its range, Eastern Hemlock grows on gentle to steep slopes (Anderson & Gordon, 1994) of any aspect, although Rogers (1978) found 67% of Eastern Hemlock stands faced west to northeast. Similarly, in southern New England, over 70% of 237 stands were on slopes facing from west to northeast, and most were located on ridgetops, steep hillsides or narrow valleys (Orwig et al., 2002, 2012). In upland areas within its native range, Eastern Hemlock grows on cool, moist north- and east-facing slopes, the sides of ravines and along streams (Godman & Lancaster, 1990; Hotchkiss et al., 1976). At the south end of its range, it is restricted to cool, moist slopes facing north and east (Hart & Shankman, 2005; Oosting & Hess, 1956). Narayanaraj et al. (2010) found that Eastern Hemlock is most abundant on gentle slopes (<20%) in the southern Appalachia at 25 stems/ha, declining to zero on slopes over 70%.

2.2 | Substratum

Eastern Hemlock is at its best on moist to very moist soils with a constant supply of soil moisture but also good drainage, ranging from sandy loam to clay loam, high in organic matter, including stream edges but avoiding extremely wet or swampy areas and very dry soils (Parker et al., 2023). In the Lake States, hemlock grows on upland sandy loams, loamy sands and silt loams, often with an abundance of glacial or fluvial material, sometimes with a subsurface pan (Frelich et al., 1993). In Canada and the northeastern States, soils tend to be shallow loams and silt loams, often over granite, gneiss and slate bedrock producing steep, eroding soils kept moist by seepage or a moist climate (Rogers, 1978), or sandy loams when mixed with *Pinus strobus*. In southern New England, Eastern Hemlock grows on soils formed from glacial deposits of gneiss, schist and granite, and primarily inceptisols and entisols (Orwig et al., 2002, 2012). Eastern Hemlock will grow on limestone soils if not too dry (Frothingham, 1915) and can thrive on very shallow soils.

Organic matter levels can be high (Boettcher & Kalisz, 1990) since Eastern Hemlock needles are slower to decompose compared to other co-occurring trees (Cobb, 2010; Cobb et al., 2006) creating a characteristically spongy organic layer. This also tends to make the soil typically highly acidic and podzolic (typically pH 3.6–4.4 but can be up to 6.6) than under co-occurring tree species (Catovsky & Bazzaz, 2002; Finzi et al., 1998; Godman & Lancaster, 1990; Kizlinski et al., 2002; Orwig et al., 2008; Rogers, 1978; Sangster et al., 2009). In southern New England, organic matter depths averaged 3.7–5 cm with a maximum of 15 cm and a mean organic C:N of 26 (Orwig et al., 2002, 2012). On sites in Massachusetts where Eastern Hemlock forest was removed by logging 25–30 years prior and replaced with *Betula lenta* regeneration, the soil organic matter depth was significantly deeper in hemlock (4–6 cm) versus birch forest (1.4–2.5 cm) (Fassler et al., 2019; Zukswert et al., 2014).

Soils are also usually nutrient poor, and carbon flux (Ford et al., 2012; Hadley et al., 2008; Nuckolls et al., 2009; Savage & Davidson, 2001) and nutrient cycling (Jenkins et al., 1999; Orwig et al., 2008, 2013; Stadler et al., 2005) are much slower in Eastern Hemlock stands than in areas dominated either by hardwoods or other conifers (Ellison, 2014). Bigelow and Canham (2002) recorded Eastern Hemlock growing with *Quercus rubra*, *Fagus grandifolia* and *Acer rubrum* on soils where the total content of exchangeable Ca^{2+}, Mg^{2+} and K^{+} was low and Al^{3+} was high. In Kentucky, these concentrations were Ca 6.3–9.4 g/kg, Mg 0.6–1.1 g/kg, K 1.6–2.0 g/kg, P 0.8–1.1 g/kg and mineralisable N was 19.5–22.1 g/kg with a forest floor mass of 1474–2240 g/m^2 (Boettcher & Kalisz, 1990). Annual soil respiration rates on moist sites within Eastern Hemlock–hardwood stands were measured at 0.41–0.81 kg C m^{-2} $year^{-1}$, the variation being between years (Savage & Davidson, 2001). Similarly, low rates of 0.3 kg C m^{-2} per growing season day were maintained across years in healthy hemlock stands (Orwig et al., 2013). When compared to mature birch stands, respiration rates were significantly lower in Eastern Hemlock stands (Ignace et al., 2018).

3 | COMMUNITIES

Eastern Hemlock is a typical late-successional dominant tree in old-growth communities (Orwig et al., 2001; D'Amato et al., 2006). Even

where it is not the tallest or most abundant tree, it acts as a foundation species that creates and defines the community (Ellison, 2014; Foster, 2014) altering the quantity and quality of light, temperature and moisture levels below the canopy, creating conditions favourable for other species (Ellison et al., 2005; Hadley, 2000b; Rankin & Tramer, 2002a, 2002b; Section 11.1). In the southern Appalachian Mountains, in the mixed conifer-hardwood forests of New England and along riparian corridors throughout its entire range, Eastern Hemlock can form >50% of the total basal area in a stand (Rogers, 1980). It is dominant in over 85% of known old-growth stands in southern New England and commonly grows with Sweet Birch *Betula lenta*, Yellow Birch *B. alleghaniensis*, American Beech *Fagus grandifolia* and Red Spruce *Picea rubens* (D'Amato et al., 2008). Eastern Hemlock occurs in 29 forest community types as described by the Society of American Foresters (Eyre, 1980) and is a major component of four forest communities (Table 1). The following information is taken from Ellingson et al. (2019), Eyre (1980), Godman and Lancaster (1990), Fike (1999), Kincaid (2007) and Krapfl et al. (2012).

The White Pine–Hemlock community (Type 22) is dominated by both conifers, with *Pinus strobus* commonest on the driest sites and in large canopy gaps, and *Tsuga canadensis* on wetter sites, although they can and do co-exist (Figure 2). *Acer rubrum* is the most common and widespread associate throughout this community, and in the north, it is associated with *Betula papyrifera*, *B. alleghaniensis*, *B. populifolia*, *B. lenta*, *Quercus rubra*, *Fagus grandifolia*, *Acer saccharum*, *Picea rubens*, *Fraxinus americana* and *Abies balsamea*. In the south, these species are replaced by *Quercus alba* and *Betula lenta*, and to a lesser extent, *Prunus serotina* and *Quercus montana*. Representative shrubs include *Rhododendron maximum*, *Viburnum lantanoides*, *V. acerifolium* and *Hamamelis virginiana*. The herbaceous layer tends to be sparse but typically includes *Maianthemum canadense*, *Mitchella repens*, *Lycopodium* spp., *Gaultheria procumbens*, *Medeola virginiana* and the ferns *Thelypteris noveboracensis* and *Polystichum acrostichoides*.

The White pine-Hemlock community is commonest on wet sites. In northern areas of the Canadian Shield, it is thus found on steep ridges with some pan formation impeding drainage. Further south in New England, it is on moderately well-drained slopes or closer to water courses if the soil is well-drained without pan formation. In the south, it occurs sporadically along the Appalachians where it is restricted to stream bottoms and north-facing slopes at higher altitudes of 600–1000 m. In the south, White pine-Hemlock is often transitional between the Red Spruce-Fraser Fir (Type 34) community at higher elevations and a purer White Pine community below. However, with time, *P. strobus* tends to die out and the community transitions towards pure Hemlock (Type 23) with many of the associates above but including *Tilia americana*.

On drier soils, but still with a build-up of surface organic matter, particularly in Canada and New England, *Betula alleghaniensis* can be almost as common as Eastern Hemlock forming the Hemlock-Yellow Birch community (Type 24; Figure 3) or Hemlock (white pine)-northern hardwood forest. *Pinus strobus* is common among the Eastern Hemlock, but the conifers form no more than 25% of the canopy cover. Hardwood species form a greater part of the forest than in Type 22, particularly *Betula alleghaniensis* but also *Fagus grandifolia*, *Acer saccharum*, *A. rubrum* and *Betula lenta*. In studies of Type 24 in southern New England, over 80% of 237 forests also contained *Betula lenta*, *Quercus rubra* and *Acer rubrum* (Orwig et al., 2002, 2012). *Rhododendron maximum* may be locally abundant in the shrub layer mixed with *Mitchella repens*, *Gaultheria procumbens*, *Hamamelis virginiana*, *Acer pensylvanicum* and various *Viburnum* species. The herbaceous layer is generally sparse with a northern affinity, similar to Type 22 with the addition of *Lysimachia borealis* (formerly *Trientalis borealis*), *Lycopodium lucidulum*, *Maianthemum canadense*, *Dennstaedtia punctilobula* and *Clintonia borealis* (Orwig et al., 2012). Old-growth stands are characterised by *Aralia nudicaulis*, *Ctenitis vilis* (=*Dryopteris intermedia*) and *Hydrangea arborescens* (=*Viburnum alnifolium*); *Lycopodium lucidulum*, *Polypodium virginianum* and *Polystichum acrostichoides* are common (D'Amato et al., 2009). A diverse bryophyte layer is often present.

Yellow-Poplar-Eastern Hemlock (Type 58) is concentrated on the fertile lower slopes in the Piedmont plateau region and west into Pennsylvania. It is characterised by the presence of *Liriodendron tulipifera* in the canopy and up to 25% canopy cover of Eastern Hemlock. Conifers such as *Pinus strobus* may form a subcanopy or occur as a relict supracanopy. *Quercus rubra* is usually present, often dominant/codominant, most often with *Acer rubrum*, *Quercus velutina*, *Q. alba*, *Carya tomentosa*, *Betula lenta*, *Fraxinus americana* and *Fagus grandifolia*. Shrubs and small trees include *Viburnum acerifolium*, *Rhododendron periclymenoides*, *Amelanchier laevis*, *A. arborea*, *Carpinus caroliniana*, *Ostrya virginiana*, *Hamamelis virginiana* and *Lindera benzoin*. The herbaceous layer is highly variable but characteristically includes *Maianthemum canadense* (particularly in the shade of Eastern Hemlock), *Arisaema triphyllum*, *Symphyotrichum lateriflorum* (=*Aster divaricatus*) and *Podophyllum peltatum*, along with a diverse range of ferns including *Dryopteris marginalis*, *Botrychium virginianum* and *Polystichum acrostichoides*.

Tsuga canadensis is also found as a frequent but not abundant component of seven other communities and as a minor component of 18 others (Table 1) including riparian forests at the south of its range, where the understorey is often dominated by *Rhododendron maximum* (Krapfl et al., 2011).

It is important to note that human disturbance has altered communities throughout eastern North America to the extent that the current cultural landscape is not representative of pre-European communities (see Section 10).

4 | RESPONSE TO BIOTIC FACTORS

Eastern Hemlock is one of the most shade-tolerant of all co-occurring species, approached only by *Fagus grandifolia* and *Acer saccharum*, surviving in <5% full sunlight (Baker, 1949) for as long as 400 years (Godman & Lancaster, 1990). Survival of Eastern Hemlock, and other shade-tolerant trees, is attributed to comparatively high levels of stored non-structural carbohydrates and the capacity to

TABLE 1 Forest communities in which *Tsuga canadensis* is associated, using the Society of American Foresters Forest Types from Eyre (1980).

Type	Community	Defining species
Tsuga canadensis a major (dominant) component		
22	White Pine-Hemlock	*Pinus strobus*, *Tsuga canadensis*
23	Eastern Hemlock	*Tsuga canadensis*
24	Hemlock-Yellow Birch	*Tsuga heterophylla*, *Betula alleghaniensis*
58	Yellow-Poplar-Eastern Hemlock	*Liriodendron tulipifera*, *Tsuga canadensis*
Tsuga canadensis frequent but uncommon		
20	White Pine-Northern Red Oak-Red Maple	*Pinus strobus*, *Quercus rubra*, *Acer rubrum*
21	Eastern White Pine	*Pinus strobus*
30	Red Spruce-Yellow Birch	*Picea rubens*, *Betula alleghaniensis*
31	Red Spruce-Sugar Maple-Beech	*Picea rubens*, *Acer saccharum*, *Fagus grandifolia*
32	Red Spruce	*Picea rubens*
33	Red Spruce-Balsam Fir	*Picea rubens*, *Abies balsamea*
34	Red Spruce-Fraser Fir	*Picea rubens*, *Abies fraseri*
Tsuga canadensis a minor component but not always present or abundant		
5	Balsam Fir	*Abies balsamea*
18	Paper Birch	*Betula papyrifera*
19	Pin Cherry	*Prunus pensylvanica*
25	Sugar Maple-Beech-Yellow Birch	*Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*
26	Sugar Maple-Basswood	*Acer saccharum*, *Tilia americana*
27	Sugar Maple	*Acer saccharum*
28	Black Cherry-Maple	*Prunus serotina*, *Acer* spp.
35	Paper Birch-Red Spruce-Balsam Fir	*Betula papyrifera*, *Picea rubens*, *Abies balsamea*
37	Northern White-Cedar	*Thuja occidentalis*
39	Black Ash-American Elm-Red Maple	*Fraxinus nigra*, *Ulmus americana*, *Acer rubrum*
44	Chestnut Oak	*Quercus montana*
52	White Oak-Black Oak-Northern Red Oak	*Quercus alba*, *Q. velutina*, *Q. rubra*
53	White Oak	*Quercus alba*
57	Yellow-Poplar	*Liriodendron tulipifera*
59	Yellow-Poplar-White Oak-Northern Red Oak	*Liriodendron tulipifera*, *Quercus alba*, *Q. rubra*
60	Beech-Sugar Maple	*Fagus grandifolia*, *Acer saccharum*
97	Atlantic White-Cedar	*Chamaecyparis thyoides*
108	Red Maple	*Acer rubrum*

replace tissues lost to herbivory or damage (Kobe, 1997; Parker et al., 2023). It also casts a dense shade (Figure 4); light transmission below a closed Eastern Hemlock canopy can be as low as 1–2% full sunlight (Thomas et al., 2021). Catovsky and Bazzaz (2000, 2002) pointed out that low light levels and low nitrogen levels, which are typical conditions beneath Eastern Hemlock stands, favour its own seedlings to the near exclusion of other species. In its own shade, Eastern Hemlock can exist as seedlings and saplings, dominating the understorey (Kelty, 1986; Marshall, 1927; Runkle, 1998), showing slow growth but tolerating long periods of suppression. For example, Stearns (1951) found saplings of 3.8 cm diameter that were 53 years old and a tree 68.6 cm diameter that was 370 years old. Tubbs (1977) also recorded that saplings 5–8 cm diameter could be as old as 100 years. A sapling at Harvard Forest, Massachusetts that was less than a metre tall was found to be 85 years old (N. Pederson and D. Orwig, unpublished data).



FIGURE 2 White pine-Hemlock community, dominated here by *Pinus strobus* which is commonest on the driest sites while *Tsuga canadensis* dominates on the wetter sites. Photograph from Harvard Forest by D.A. Orwig.



FIGURE 3 On drier soils, *Betula alleghaniensis* can be almost as common as *Tsuga canadensis*, forming the Hemlock-Yellow Birch community. Photograph from Harvard Forest by D.A. Orwig.

In the deep shade cast by Eastern Hemlock, especially on thin or nutrient-poor soils, even shade-tolerant trees, forbs and graminoids will usually be suppressed (Farnsworth et al., 2012; Kobe, 1996). On deeper and richer soils, however, Eastern Hemlock is not as competitive and tends to be co-dominant (Rogers, 1978) creating a more open canopy. Part of this is due to the negative effect of *Acer*



FIGURE 4 *Tsuga canadensis* casts dense shade down to as little as 1%–2% of full sunlight. Photograph from Harvard Forest by D.A. Orwig.

saccharum litter in reducing Eastern Hemlock establishment (Witt & Webster, 2010). In the southern Appalachians, a closed canopy of Eastern Hemlock suppresses the growth of *Rhododendron maximum*, but the removal of hemlock leads to a higher growth rate of the rhododendron (×2.6) and this in turn may suppress tree regeneration (Ford et al., 2012).

Although shade-tolerant, Eastern Hemlock will respond to release with increased diameter and height growth (Godman & Lancaster, 1990; Lorimer & Frelich, 1994). In the full sun of large gaps in the canopy, it shows faster stem radial growth than either *Fagus grandifolia* or *Acer saccharum*, though not as fast as *Betula alleghaniensis* or *Aesculus flava* (Barden, 1983; Pacala et al., 1995). Extension growth of Eastern Hemlock seedlings may reach >60 cm/year, but height growth slows rapidly as the leading shoot tends to lose dominance due to faster growing competitors (Swartley, 1984). *Quercus rubra*, *Acer rubrum* and *Betula lenta* can grow 2–3 times faster in height than Eastern Hemlock in full sun (Foster, 2014). Sapling growth rate is thus slower, measured at 8–14 cm/year, but similar to competing northern hardwoods, and so they all tend to close gaps at similar rates (Runkle, 1998). However, in the low light levels of smaller gaps, Eastern Hemlock grows the slowest of those species, but survives for longer than all competitors except *F. grandifolia* (Pacala et al., 1996). Modelling by Pacala et al. (1996) indicates that over the next millennium, northern hardwood forests would be dominated by a mix of Eastern Hemlock and *F. grandifolia*, with *Betula alleghaniensis* in gaps.

In the Appalachians, Runkle (1998) noted that Eastern Hemlock was the only tree species that decreased in relative density in disturbed sites while increasing in undisturbed sites. This is partly due to Eastern Hemlock seed production being variable between years (Section 8.3), so establishment after disturbance is less reliable than species that regularly produce large numbers of seeds, such as *A. saccharum*. Moreover, seedlings of *A. saccharum*, *F. grandifolia* and *Picea rubens* have deeper root systems than hemlock and so are more successful in the drier substrates of gaps; they are also not as palatable to browsers and can more readily sprout after browsing. Eastern Hemlock thus responds to canopy gap formation primarily by growth of its large, previously suppressed stems rather than by an increase in density. Indeed, Kenefic and Seymour (1999) noted that in Maine, 80% of Eastern Hemlock saplings originated beneath the canopy of mixed conifers rather than in gaps, much higher than in competing species such as *P. rubens* (51%). In southern New England, Kelty (1986) found that in a large gap created by wind-throw, Eastern Hemlock saplings were readily overgrown by hardwoods and could only maintain an overstorey position if they were at least 3 m tall at the time of disturbance.

Eastern Hemlock can steadily grow through overtopping hardwoods, but the terminal shoots are vulnerable to breakage by abrasion against the hardwood branches (Kelty, 1986) helping maintain the dominance of the hardwoods. Once it reaches the top of the canopy, however, growth in diameter and volume is relatively rapid (Frothingham, 1915) but often too slow to be commercially useful (Section 10.1). Growth of >6.4 cm diameter per decade is possible following release from competition (Godman & Lancaster, 1990).

Eastern Hemlock is susceptible to browsing at all stages of its life cycle, especially by white-tailed deer *Odocoileus virginianus* (Zimmermann) and moose *Alces alces* (L.) which remove the



FIGURE 5 The Hemlock Woolly Adelgid (*Adelges tsugae*; Hemiptera, Adelgidae) forms extensive colonies on *Tsuga canadensis* branches (a), causing significant thinning of the crown (b) and eventual death (c). Photographs from Harvard Forest by D.A. Orwig.

apical buds and most of the needles (Mladenoff & Stearns, 1993; Rogers, 1978; Vasiliauskas & Aarssen, 2000). White-tailed deer readily browse Eastern Hemlock (Cook & Williams, 2011), although it has been ranked seventh in winter food preference in Pennsylvania. In some regions, patches of Eastern Hemlock regeneration have been eliminated following heavy browsing in years when deer populations are high. Although deer have been blamed for the absence of Eastern Hemlock in many localities, in Ontario, no regeneration was found even in fenced areas, suggesting other limiting factors (Euler & Thurston, 1980). Moose may also play an important role; a study in Ontario found that moose browsing caused 60% mortality of Eastern Hemlock, and seedlings may be browsed for up to 30 years before the leaders are out of reach (Vasiliauskas & Aarssen, 2000).

Browsing particularly limits the establishment and survival of seedlings and young trees under 1 m tall (Rooney, 2001; Runkle, 2005; Weckel et al., 2006; Witt & Webster, 2010). This is partly due to the palatability of Eastern Hemlock (Section 9.1) but also due to deer being attracted to Eastern Hemlock-dominated stands in winter due to less wind and reduced extreme cold temperatures and snow depth (Euler & Thurston, 1980). In a 400-ha wind-throw area in northwest Pennsylvania, Eastern Hemlock seedling density was seen to be initially high (*c*. 3.8 seedlings/0.5 m^2 plot) but deer browsing and a drought in 1988 caused heavy mortality such that by 1991 there were <0.5 seedlings/0.5 m^2 plot (Peterson & Pickett, 1995). By contrast, seedling densities of *Betula alleghaniensis*, *Fagus grandifolia* and *Acer pensylvanicum* were all much higher, and it seemed that the combination of browsing and drought was stopping the succession to Eastern Hemlock. Similarly, in Northern Wisconsin and Michigan, white-tailed deer reduced the estimated half-lives of seedlings from 35.2 years in exclusion plots to 15.0 years when browsed. Moreover, the time taken to grow above 2 m, and thus be able to escape browsing, was 33.4 and 77.7 years for protected versus unprotected juveniles, respectively (Alverson et al., 2024). There is an interesting interaction between deer browsing in areas of canopy disturbance by the Hemlock Woolly Adelgid (HWA). The greater amount of light reaching the ground under HWA disturbance increases the positive effects of removing deer herbivory in allowing seedlings to establish

and grow. However, due to its high shade tolerance, Eastern Hemlock seedling performance was least improved by HWA disturbance compared to five hardwood species tested (Eschtruth & Battles, 2008).

Eastern Hemlock is more severely damaged by browsing than *Acer saccharum* since the maple resprouts more readily than hemlock and grows quickly to above browsing height (Anderson & Loucks, 1979). Frelich and Lorimer (1985) noted that in Michigan, deer browsing was the main factor leading to a change in dominance from Eastern Hemlock to *Acer saccharum* and they suggested that in less than 150 years, Eastern Hemlock will be only a minor component within former hemlock forests. Grittinger (2009) identified the same shift in Wisconsin. Severe winters that reduce deer populations might allow a window for Eastern Hemlock regeneration, but a study in Michigan found that the large seedling bank of maples meant that they prospered over hemlock during reductions in browsing pressure (Parikh & Webster, 2019). However, Eastern Hemlock seedlings can be protected from deer browsing by *Abies balsamea*. Borgmann et al. (1999) found that Eastern Hemlock seedlings in Wisconsin were three times as dense within patches of fir than outside (1.97 ± 0.28 [SE, $n = 11$] seedlings/m^2 within; 0.69 ± 0.12/m^2 outside) and twice as tall (189.7 ± 5.6 cm within; 97.5 ± 6.0 cm outside). This was presumed to be due to the fir acting as a visual or physical barrier to the deer. Large boulders and wind-felled trees can also form a similar barrier, as well as the latter creating soil mounds suitable for seedlings (Section 8.4; Carson et al., 2005; Krueger & Peterson, 2006).

While hemlock has not historically been valued highly as a timber species (Section 10.1), it is valued for habitat and aesthetics. As summarised in Goerlich and Nyland (2000) and Mroz and Martin (1995), silviculture practices to promote hemlock regeneration typically involve removing a portion of the overstorey such as with two-cut shelterwood with soil scarification, light selection harvests and stand thinning to approximately 80% of residual crown cover, and mechanical scarification with bulldozer and rock rake. However, white-tailed deer browsing is a major limiting factor following silvicultural treatments in many areas (Anderson & Gordon, 1994). Successful regeneration of Eastern Hemlock can be enhanced with a reliable source of seed and suitable conditions for germination, especially adequate soil moisture.

4.1 | Hemlock Woolly Adelgid (HWA)

The process of infestation by HWA (*Adelges tsugae*; Hemiptera, Adelgidae), leading to feeding on Eastern Hemlock twigs by successive generations of HWA (Figure 5a) and progressive needle loss and tree decline, is a chronic process lasting years to decades (see Section 9.1.1). As Eastern Hemlock canopies deteriorate, elevated needle loss occurs (Figure 5b; Knoepp et al., 2011) and the ratio of new to old foliage declines (Stadler et al., 2005) because the tree does not produce new buds or foliage after infestation. Progressive needle loss occurs from lower and interior portions of tree crowns upwards and outwards (Orwig et al., 2002) increased by loss of strength and flexibility of twigs and needles (Soltis et al., 2014). Long-term feeding can result in trees with branches retaining only tufts of needles at the branch ends.

Persistent HWA feeding results in a series of structural and compositional changes to individual trees, which alters microenvironmental conditions and eventually impacts ecosystem function in the forest (Section 11.1).

Although tree death (Figure 5c) and decline continue over broad areas, initial predictions of complete mortality of *T. canadensis* and *T. caroliniana* have not yet been realised (Preisser et al., 2014). In the south of its range, the spread of HWA leads to death of Eastern Hemlock within 4 to 7 years of infestation due to mild winters and a long growing season (McClure, 1991) while in colder, northern regions mortality may not occur for over 20 years (Eschtruth et al., 2013; Foster, 2014; Orwig et al., 2012). The extent of canopy thinning and mortality in these stands has ranged from 0% to 99%, and mortality appears to be higher in understory canopy trees. Within 44 stands in southwest Virginia, the mean time to tree death resulting from HWA was just over 11 years (McAvoy et al., 2025). In the southern Appalachians, Eastern Hemlock decline was more rapid in some locations, with hemlock mortality reaching >98% in less than a decade (Ford et al., 2012; Fraterrigo et al., 2018). In addition, the understorey shrub *Rhododendron maximum* is often the species that gains in importance with the loss of hemlock along riparian forests in the region (Ford et al., 2012; Krapfl et al., 2011; Martin & Goebel, 2013; Webster et al., 2012) which in some cases inhibits seedling establishment (Dharmadi et al., 2019). In the Delaware River Water Gap of Pennsylvania and New Jersey, Eastern Hemlock mortality rates varied between 10% and 60% after 20 years of HWA infestation (Eschtruth et al., 2013). In a survey of riparian forests along the east coast of the USA, half of the forests were infested with HWA and southern sites had over 50% of their hemlocks in severe decline (Evans et al., 2011; Williams et al., 2016).

After dying, trees usually remain standing for 8–10 years, accompanied by fine twig and branch loss, large branch loss and eventual toppling to the ground. Since Eastern Hemlock has an affinity for riparian habitats, HWA-induced mortality often leads to large increases in woody inputs to streams (Costigan et al., 2015; Evans et al., 2011, 2012). Observations from over 200 Eastern Hemlock stands in southern New England document that hemlock is often replaced with deciduous hardwood species such as *Betula lenta*, *Acer rubrum* and *Quercus* species over a few decades (Orwig et al., 2002, 2012).

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

Eastern Hemlock tends to regenerate, though not prosper, in small openings where one or more trees have died or been wind-thrown, so dispersion can be related to disturbance patterns (Frelich, 2002; Runkle, 1998). However, seedling establishment can be high in

closed stands which tend to be aggregated, becoming more so with increasing abundance (Kincaid, 2012), attributable to seedlings establishing and surviving preferentially on rotting stems, stumps and soil mounds (Section 8.4). Indeed, modelling of forest development in Connecticut suggests clumping of individual species within the transition of northern hardwoods to dominance by Eastern Hemlock and *Fagus grandifolia* (Pacala et al., 1996).

Mean seedling density in the Great Lakes region was found to vary between years and to be spatially variable. In 109 stands scattered across *c*. 20,000 km^2, 13% of stands had no seedlings and 66% of stands had >100 seedlings/ha (Rooney & Waller, 1998). Seedling numbers across all stands in the Great Lakes region varied from 0 to 20,400 seedlings/ha, with a mean density of 840 seedlings/ha (Rooney & Waller, 1998), reaching as high as 70,000/ha in Wisconsin (Nelson, 1997) and 400,000/ha at the north of its range (Rogers, 1978). Sapling density can remain high, reaching 260/ha in the north and averaging 314–450 stems/ha in southern New England, where Eastern Hemlock was the most abundant sapling (Orwig et al., 2002, 2012; Rogers, 1978). Certainly, on sandy, infertile soil, the stem density of Eastern Hemlock exceeds that of other shade-tolerant trees such as *Acer saccharum*. Northern hardwood and hemlock stands can contain 40–100 standing dead stems/ha, even in second-growth areas (Runkle, 1998).

At the south end of its range, in pure Eastern Hemlock stands in the southern Appalachians, seedling density was seen to vary from zero to 2041 seedlings/ha (Kincaid, 2012). Density of saplings (<5 cm dbh) in the Appalachians was also variable, reaching up to 2109 saplings/ha (Kincaid, 2012).

5.2 | Performance in various habitats

The response of Eastern Hemlock to shade is covered in Section 4. It was noted in Section 2.1 that Eastern Hemlock density declines with increase in slope in the Southern Appalachians. Basal area was also found to decline linearly with slope, reducing from 4.4 m^2/ha on gentle slopes (<20%) to 1.3 m^2/ha on 40% slopes (Narayanaraj et al., 2010). The performance of Eastern Hemlock was also found to decline exponentially away from streams in these southern forests. Density was as high as 27 stems/ha next to a stream, declining to <5 stems/ha >100 m away. Similarly, basal area of Eastern Hemlock was >5 m^2/ha at the streamside, declining to <1 m^2/ha by 100 m away (Narayanaraj et al., 2010). The relationship between increase in wood volume in the trunk and leaf area is well documented (Seymour & Kenefic, 2002). Old-growth stands of Eastern Hemlock are structurally more complex than secondary stands: the former have been found to have larger overstorey trees and greater volumes of downed coarse woody debris (135.2 vs. 33.2 m^3/ha) and snags (21.2 vs. 10.7 m^3/ha; D'Amato et al., 2008).

Radial growth of shade-suppressed seedlings of Eastern Hemlock can be as little as 0.042 to 0.142 mm/year, with 10-year means for radial growth ranging from 0.05 to 0.75 mm/year (Friesner & Polzger, 1932). In an early study of over 300 hemlock trees, the mean increase in trunk diameter for the 40-year period prior to suppression release was 2.5 cm, and 14 cm for the 40-year period after release (Marshall, 1927). In full sunlight, annual ring widths of 2–3 mm are normal in the first few decades (Abrams et al., 2000; Black et al., 2008) but thereafter tend to be similar throughout its life span at <0.5 to 1 mm/year due to competition with surrounding trees, until it declines significantly in older trees. However, in optimum growing conditions, growth can be significantly faster, particularly on high nitrate soils (Bigelow & Canham, 2002); Abrams and Orwig (1996) found dramatic growth changes with annual ring widths in Pennsylvania that were <1 mm/year before release and up to 8.8 mm/year after release.

Since radial growth of Eastern Hemlock is sensitive to soil moisture (Cook & Cole, 1991), tree-ring chronologies have been used in climate and stream flow reconstructions throughout eastern North America (Maxwell et al., 2017; Rayback et al., 2020). However, the relationship between annual increment and environmental conditions may be more nuanced in different parts of its range. Certainly, in southwestern Quebec, annual increment was found to be correlated to annual precipitation but also related to temperature, and notably positively correlated to winter temperature, and negatively correlated with temperatures during early summer (May) of the current year and with temperatures during the late summer (July–August) of the previous year (high summer temperatures potentially leading to water shortage). Relatedly across a region stretching from Wisconsin to New England, radial growth was negatively associated with June and July temperature and positively associated with March temperature (Cook & Cole, 1991). Radial growth was also positively correlated with precipitation of the current and previous year and negatively correlated with snow amount in March (Cook & Cole, 1991; Dye & Woods, 2019; Tardiff et al., 2001). At the southern end of its range in Alabama, Hart et al. (2010) found a significant positive correlation between radial growth and monthly minimum temperature for September and October of the current year, and with monthly total precipitation for September of the previous year (the driest time of year) and May of the current year. Significant negative relationships between radial growth and August temperature of the previous year were also found. August is usually the warmest month in the region, and the high temperatures may act to slow carbon fixation.

In southern Quebec, Eastern Hemlock near a rock quarry were exposed to a maximum dust fall rate at ground level of 1690 g dust m^{-2} 30 $days^{-1}$ in 2004 and 1310 g dust m^{-2} 30 $days^{-1}$ in 2005. In severe deposition areas, ≥5 cm of dust was visible on the ground. Mean radial growth was reduced by 43% compared to growth before the quarry started, and radial growth responded more weakly to precipitation and more strongly to summer temperatures in the previous year (Farahat et al., 2016).

Long dendrochronological series for Eastern Hemlock have been constructed in southern Quebec spanning the historical colonisation period from 1524 to 1982 (Delwaide & Filion, 1999) and northern Michigan, with the longest from 1708 to 2015, extending older chronologies by 25 years (Dye & Woods, 2019).

In Upper Michigan, Frelich and Lorimer (1991) observed that in mixed Eastern Hemlock-Sugar Maple that mean canopy mortality was estimated at 5.7% to 6.9% per decade, giving a mean canopy residence time of 145–175 years. Similarly, in the Appalachians, Runkle (1998) found average mortality rates of 6.3% per decade. In contrast, old-growth hemlock in the Huron mountains of Michigan had mortality rates of 0.3%/year and a canopy residence time of 357 years (Woods, 2000).

5.3 | Effect of frost, drought, fire, etc.

Eastern Hemlock is resistant to cold as low as −20 to −60°C (Hepting, 1971; Sakai & Larcher, 1987) and its late bud-opening in spring greatly reduces the risk of damage by spring frosts (Hepting, 1971). However, Eastern Hemlock is still susceptible to winter injury by photoinhibition (Boyce et al., 2003). Eastern Hemlock is normally undamaged by freezing rain and ice due to its flexible and drooping branches (Hough, 1960; Irland, 2000; Seischab et al., 1993). After a severe ice-storm in Québec, Duguay et al. (2001) recorded that Eastern Hemlock was the least damaged species, with just 5%–9% of trees with >50% of canopy damaged, compared to 17%–46% of trees in nine hardwood species. However, the hardwood species can resprout and recover dominance more rapidly than the non-sprouting Eastern Hemlock. Indeed, Lafon (2004) predicted that ice storms in the Adirondack Mountains would favour *Acer saccharum* dominance due to their faster height growth and recovery compared to Eastern Hemlock. While Eastern Hemlock is resistant to mechanical injury from ice storms, it is more susceptible to physiological effects like water stress and subsequent foliar loss due to cuticular damage in the needles after ice loading (Boyce et al., 2003).

Due to its shallow root depth, it has been thought that Eastern Hemlock should be especially susceptible to drought, reducing growth and increasing mortality (Secrest et al., 1941). However, in Connecticut, the probability of mortality and poor growth was found not to be linked to soil moisture in Eastern Hemlock, *Quercus rubra* and *Pinus strobus*, although there was a link for many hardwood species. The effect of drought is more nuanced since Eastern Hemlock has been shown to grow better in shade than *P. strobus* but be less tolerant of low soil moisture than the pine: On a xeric site with a mean soil moisture of 24.15% (range 13.6%–35.7%), 30% of Eastern Hemlock individuals were dead, while on a mesic site (mean soil moisture 37.3%; range 20.4%–64.6%), 11% were dead (Caspersen & Hobe, 2001).

The shallow root system makes Eastern Hemlock vulnerable to wind-throw (Willis & Coffman, 1975). Wind-throw can occur on shallow soils with exceptional wind, especially if the stand has been opened by felling (Godman & Lancaster, 1990) or where trees have established on logs or stumps which encourage the development of relatively weak stilted root systems (Hough, 1960). Exceptionally strong winds make the problem worse. In northwest Pennsylvania after a strong tornado in 1985, Peterson and Pickett (1991) found that of 630 trees sampled in a 400 ha area where 99% of the trees had fallen, *c*. 70% of Eastern Hemlock snapped while *c*. 30% uprooted. At least 16 hurricanes have affected rural Massachusetts since 1635 (McLachlan et al., 2000). In 1938, a major hurricane in Massachusetts resulted in up to 75% of trees being wind-thrown or, to a lesser degree, broken across the area of damage (Foster, 1988; Foster & Boose, 1992). Despite high losses in exceptional winds, Eastern Hemlock can be less susceptible to damage by the wind compared to other conifers such as natural stands of *Pinus strobus* and plantations of *P. strobus*, *P. resinosa* and *Picea abies*, and to hardwood species (Foster & Boose, 1992). This is partially attributable to Eastern Hemlock being largely below the canopy rather than canopy dominants in these stands, shielding them to some extent from the wind (Foster, 1988).

The 1938 Massachusetts hurricane changed the nature of the forest since it is now dominated by moderately shade-tolerant sprouting species such as *Acer rubrum*, *Betula lenta* and *Quercus rubra* (McLachlan et al., 2000). However, Eastern Hemlock and *Acer saccharum* can recover well in local areas after severe storms; Sass et al. (2018) followed stands damaged by the 1938 hurricane and found that over the next 78 years, Eastern Hemlock remained dominant with significantly increased amounts of *A. saccharum*. This was largely a result of a large seedling and sapling bank of the two species that established prior to the wind disturbance (Lafon, 2004; Sass et al., 2018). However, seedling establishment after windstorms can be significantly reduced by excessive coarse woody debris (CWD) and the persistence of damaged and dying trees. After the 1938 Massachusetts hurricane, the majority of CWD was Eastern Hemlock and *Pinus strobus* which decays slowly and so was unlikely to act as nurse logs in the short term (Section 8.4), impeding rather than helping regeneration (Sass et al., 2018).

As a late-successional species, Eastern Hemlock is readily damaged by fire. Its shallow roots are at risk from ground fires burning into soil organic matter, and even an intense surface fire may kill the roots or damage them, leaving them susceptible to pests and pathogens (Rogers, 1978). Severe crown fires are inevitably fatal (Frothingham, 1915), aided by the retention of branches to the ground acting as ladder fuels carrying surface fires into the canopy. This undoubtedly restricts the range of Eastern Hemlock in warmer, drier and more fire-prone areas; certainly, the southern extent of Eastern Hemlock in Wisconsin appears to be limited by fire (Goder, 1955). Nevertheless, the bark can be 0.8–1.3 cm thick in trees 15 cm in diameter, and in old trees, the bark at the base of the stem can be 5–8 cm thick (Frothingham, 1915), offering a degree of resistance to low-intensity surface fires.

Seedling establishment after fire is variable. Mature Eastern Hemlock trees can sometimes survive low-intensity fires while much of the competing vegetation is killed, facilitating high regeneration from seed (Payette et al., 2015; Rogers, 1978; Varner et al., 2015). But this also requires extensive exposure of mineral soil, either due to organic matter burning away or mechanical scarification (Becker et al., 1996). After a stand-replacing fire in Wisconsin, Murray et al. (2012) noted that regeneration over 3 years was highest in fire

breaks scraped down to the mineral soil and lowest on the burnt areas, attributed to competing vegetation and drying of the residual soil organic matter. Poor establishment of Eastern Hemlock leads to a change in dominance towards early successional *Betula papyrifera* and *Populus tremuloides* (Frelich & Reich, 1995) and Eastern Hemlock density may take over 500 years to recover (Foster, 2014).

Surface fires which char organic matter increase the pH over the first month after fire by 2 pH units, reaching a maximum of *c*. pH 7.0, accompanied by an increase in ammonium ions for the first 2 weeks (Mroz et al., 1980) but these do not appear to affect germination or early seedling survival.

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Eastern Hemlock is a large tree commonly reaching a diameter at breast height of 0.4 m at 200 years and 0.89–1.02 m diameter and >30 m height by 400 years (Godman & Lancaster, 1990); these authors also describe a notable tree of 1.93 m dbh and 53.3 m in height as being among the largest recorded. Long-term data on height and girth have been collected by The Eastern Native Tree Society (American Forests, 2011). They have measured 75 hemlocks over 48.5 m tall, the largest being 173.1' ft. (52.8 m). Sadly, only one of these trees is currently alive, kept so by diligent chemical treatment against HWA (American Forests, 2011; Section 11.2).

The wood is comparatively dense, 0.38–0.45 g/cm^3, and is similar to *Pinus strobus* (0.34 g/cm^3) but, at its densest, not much less than *Acer saccharum* at 0.56 g/cm^3 (Nowak, 2021). Nevertheless, the wood has comparatively few uses (Section 10.1), especially since wind can cause separation between growth rings known as 'shakes', which particularly affects the base of the stem, making it unsuitable for timber (Frothingham, 1915). When growing in deep shade, Eastern Hemlock may have partial or missing rings at the base of the stem. Godman and Lancaster (1990) describe a suppressed tree that had 10–40 missing rings over a 120-year period.

Hemlocks are renowned for a plagiotropic leader that initially droops below the horizontal and then straightens during the growing season. However, the leader is frequently replaced by growth from a lateral branch (Hibbs, 1981), observed by Ewers and Zimmermann (1984) to occur a mean of 6.7 times in 10 years. The mass of bole, branches and needles was found to be linked to stem diameter by log–log linear relationships, given by Santee and Monk (1981). Bark forms *c*. 19% of the stem volume and varies little with the size of the tree (Frothingham, 1915). The bark is also relatively stable; Winget and Kozlowski (1964) found that winter shrinkage in stem diameter, attributable mostly to changes in bark thickness with hydration and thermal contraction, was low in Eastern Hemlock, comparable to *Acer saccharum* but less than that in *Tilia americana* and *Betula alleghaniensis*. This stability may help reduce the incidence of frost cracks. Traumatic resin canals are produced in the xylem upon wounding (Bannan, 1934). Cellular development of the apical growth is described by Mottier (1892) and growth rates of tracheid cells through the growing season by Skene (1972).

Canopy development has a high degree of plasticity since shoots under 6 cm long tend to be proleptic but monopodial, forming the canopy framework, while longer shoots can produce new sylleptic shoots, creating second-order shoots in the same season (Powell, 1991). Powell (1992) observed that as shoot length increased from 8 to 10 cm, leaf size increased and the number of leaves per unit length of shoot decreased. Acropetally along shoots, lamina length and leaf width decreased, relative petiole length increased, apices became more pointed and leaf margins bore more teeth. From the top of the shoot round to the underside, leaf size and the number of marginal teeth in the proximal halves of leaves increased. Most leaves produced in a season are formed during the growth season (i.e. not preformed), a comparatively rare trait in gymnosperms, seen in *Ginkgo*, *Larix* and *Picea* when young (Powell, 1991). Leaves contain small amounts of silica (0.14%–0.16% dry mass), smaller than those of other conifers tested in New York State (Klein & Geis, 1978). Details of the morphology of the leaf interior and secondary xylem are given by Gambles and Dengler (1974) and Grozdits and Ifju (1984).

Mean life expectancy of leaves on lateral branches ranged from 2.48 ± 0.30 (SD) years in open grown trees to 3.35 ± 0.36 years in shaded trees, although some individual needles can last for up to 7 years (Whitney, 1982). Stomatal density is comparatively low at 96.0/mm^2, each with a mean guard cell length of 48.5 µm (Barwise et al., 2024). Gambles and Dengler (1974) noted that on leaves collected in winter, *c*. 95% of stomata were occluded with a continuous layer of rod-like wax particles, forming a plug which may act to reduce transpiration.

Eastern Hemlock roots are slow growing at first. First-year seedlings may grow only 25–38 mm in height with roots extending less than 13 mm into the soil (Godman & Lancaster, 1990), hence the requirement for moist regeneration sites (Section 8.5). After reaching a height of 1–2 m, the root system on most soils has grown deep enough to be largely unaffected by surface drying. The root system, however, remains shallow and wide spreading, the depth depending upon depth of soil and water-table, being deeper on better drained sites where they can penetrate 'to some depth' (Frothingham, 1915; Rogers, 1978). The shallow root system makes trees susceptible to wind-throw, (Section 5.3) especially when exposed through timber cutting or by planting in open sites. Fine root density (<2 mm diameter) was measured in Connecticut stands at <8 cm/cm^3, less than half that of *Acer saccharum* but fine-root length per area of forest floor of Eastern Hemlock at 43.6 cm/cm^2 was significantly higher than the 16.2 cm/cm^2 measured for *A. saccharum* (Dijkstra & Smits, 2002).

6.2 | Mycorrhiza

Predominantly ectomycorrhizal (Averill & Hawkes, 2016). Eastern Hemlock is known to associate with at least 75 ectomycorrhizal fungal species, making it one of the most diverse fungal communities in temperate forests (Baird, Stokes, Wood-Jones, Alexander,

et al., 2014). However, Godbold et al. (1997) found that Eastern Hemlock growing in Massachusetts had 18% of the root lengths examined colonised by arbuscular mycorrhizal fungi, which significantly increased to 24% under elevated CO_2 (700 ppm) for 27–35 weeks.

In North Carolina, Baird, Stokes, Wood-Jones, Alexander, et al. (2014) identified the commonest ectomycorrhizal fungal partners to be *Russula fragrantissima* Romagn. (22.0% of trees sampled), *Amanita citrina* (Schaeff.) Pers. (17.1%), *Austroboletus gracilis* (Peck) Wolfe (14.6%), *Laccaria laccata* (Scop.) Cooke (9.8%), *Russula russuloides* (Peck) Sacc. (9.8%) and *Amanita cinereopannosa* Bas. (2.4%)—all Basidiomycota. Other taxa reported as mycorrhizal fungi on Eastern Hemlock include *Cenococcum graniforme* Fr. (Ascomycota, Mytilinidiales), *Suillus granulatus* (L.) Roussel and *Paxillus involutus* (Batsch) Fr. (Basidiomycota, Boletales), *Lactarius tabidus* Fr. and *Russula pectinatoides* Peck (Basidiomycota, Russulales) (Amoia, 2017; Trappe, 1962).

In a mixed hardwood-conifer forest in Connecticut, Booth (2004) found that 23% of seedlings planted into the forest floor survived over a year while 50%–63% survived if root competition from surrounding trees and mycorrhizal connections were prevented. Allowing access to mycorrhizal fungi but not root competition resulted in the survival of 73% of seedlings, indicating the negative importance of root competition compared to the positive effects of mycorrhizal connections in seedling survival.

6.3 | Perennation: Reproduction

Phanerophyte. Reproduction is almost wholly by seeds, although, rarely, vegetative spread has been observed from branches held to the ground and subsequently layering (Godman & Lancaster, 1990; Hough, 1960). Del Tredici and Orwig (2017) recorded 12 trees, each with 5–20 layered branches growing on the upper slopes of Wachusett Mountain, Massachusetts. New stems were 7–17 m tall and several of these had produced second-generation layers. Layering is likely to be restricted to open-grown trees that maintain live lower branches for a long period and under conditions that pin lower branches to the ground by fallen debris. Certainly, stem cuttings are readily rooted (Ellingson et al., 2019; Hough, 1960). Stumps do not sprout (Peterson & Pickett, 1991), although they have been recorded as maintaining annual increments for at least 69 years, presumably due to being connected by root grafts to living trees (Davidson, 1963; Davidson & Davis, 1964).

First seeds are produced when 20–30 years old when trees are 4–9 m tall but occasionally from 15 to 50 years old; shading delays seed production (Bonner & Karrfalt, 2008). Cones are produced almost every year with larger seed crops every 2–3 years, slightly more frequently than in other *Tsuga* species (Bonner & Karrfalt, 2008; Frothingham, 1915; Olson et al., 1959) and trees are reported to produce good cone crops for more than 450 years (Godman & Lancaster, 1990).

Eastern Hemlock is a long-lived late-successional species. In the south of its range in North Carolina, the maximum age is *c.* 550 years (Black et al., 2008). Similarly, in the Great Lakes region to the north, Lorimer et al. (2001) found the mean age at death of Eastern Hemlock in hemlock-hardwood forest was 328 years old, with a maximum age of 513 years, suggesting that 'old-growth' probably occurs after the stand is 180–250 years old. In the main part of its range, Eastern Hemlock can take 250–300 years to reach maturity and is suggested to live for up to 800 years (Godman & Lancaster, 1990; Jenkins, 1946), but the oldest specimen so far found was a tree in northwest Pennsylvania that was 657 years old (David Orwig, unpublished data). This maximum age is thus similar to that of *Quercus alba* (a deciduous tree co-occurring with Eastern Hemlock—Section 3) but shorter than the maximum age of *Pinus ponderosa* (800 years; a late-successional species) or *Pseudotsuga menziesii* (1000 years; an early to mid-successional species) (Black et al., 2008).

6.4 | Chromosomes

$2n = 24$ (Farjon, 1990), although Gavrilov and Butorina (2005) found extrachromosomal elements of DNA outside of the chromosomes in some cells of specimens in southeast Russia.

6.5 | Physiological data

6.5.1 | Shade

In Massachusetts, maximum rates of photosynthesis have been measured at 15 $\mu mol\, m^{-2}\, s^{-1}$ in Eastern Hemlock, compared to 25 $\mu mol\, m^{-2}\, s^{-1}$ in a *Quercus rubra* stand (Hadley et al., 2008). Carbon fixation begins up to 2 months before deciduous species in the same area and *c.* one third of the annual carbon fixation in Eastern Hemlock occurs in the spring and autumn (Catovsky et al., 2002) rather than the summer when hemlock is in competition with deciduous species in full leaf (Hadley, 2000b; Hadley et al., 2008).

In a stand in Massachusetts where Eastern Hemlock made up 83% of the above-ground biomass, carbon flux was controlled from April to September by light flux; but in early spring, daily minimum air temperature was a strong limiting factor, and below 0°C, carbon fixation was greatly reduced and ceased at −5°C (Hadley & Schedlbauer, 2002). Under high light, net photosynthesis was measured at 2.5 $\mu mol\, m^{-2}\, s^{-1}$ when minimum air temperature the previous day was 7°C in mid-March, and reached a maximum at relatively low temperatures of 11 and 18°C but did not change significantly between 15 and 30°C (Adams & Loucks, 1971; Hadley, 2000a, 2000b). In the autumn, temperature again becomes important, and Hadley (2000a) found that when minimum air temperature during the previous 24 h dropped to −2°C, photosynthesis averaged *c.* 5 $\mu mol\, m^{-2}\, s^{-1}$ but fell to about 1 $\mu mol\, m^{-2}\, s^{-1}$ at −8°C. In an Eastern Hemlock stand with *c.* 14% of the canopy trees being deciduous, Hadley (2000b) noted that daily maximum air temperature was

3–4°C lower than above the canopy in July through September, but only 1–2°C lower from October through June.

At 22°C, the light compensation point of Eastern Hemlock foliage occurred at a photon flux density of *c*. 10 μmol $m^{-2} s^{-1}$ and light saturation at *c*. 350 μmol $m^{-2} s^{-1}$ or <20% full sunlight (Hadley, 2000b). As photon flux density is typically <20 μmol $m^{-2} s^{-1}$ (*c*. 1% full sunlight) below the canopy, rising to >200 μmol $m^{-2} s^{-1}$ for <1.2% of daylight hours in July to September, Eastern Hemlock seedlings and saplings are likely to survive but grow slowly, adding as little as 1.0 mm radial growth per year (Caspersen & Hobe, 2001). Since light saturation occurs at a comparatively low light level, when shaded saplings are exposed to high light, as in the creation of a canopy gap, Eastern Hemlock depends strongly on the production of new foliage, which may take several years of growth to achieve (Mohammed & Parker, 1999).

Root respiration of 8-month-old seedlings reached a maximum of 1.59 mg O_2 $g^{-1} h^{-1}$ (dry mass), similar to the dark respiration of shoots (Szaniawski & Adams, 1974). The oxygen concentration of sapwood was found to be *c*. 18% under the bark, declining to *c*. 6% while the cambium was active and constant at *c*. 6% through the sapwood to the transition to heartwood (Spicer & Holbrook, 2005). Sapwood tissue respiration was unaffected by a drop in oxygen from 15% to 5%, and respiration per live cell was uniform across the sapwood; this is similar to other conifers, but respiration tends to decline with depth below the bark in deciduous hardwoods (Spicer & Holbrook, 2007).

6.5.2 | Water relations

Although the survival of Eastern Hemlock is somewhat sensitive to drought (Section 5.3), carbon fixation is generally insensitive to drought. Field grown seedlings were found by Adams and Loucks (1971) to decrease photosynthesis sharply only when soil became very dry (soil moisture 15%). Light and temperature have a more important effect on photosynthesis.

In North Carolina, Eastern Hemlocks growing in riparian areas were found to have a maximum transpiration rate of 178–186 kg H_2O $tree^{-1} day^{-1}$ in trees with a mean diameter of 57 cm, 57 kg $tree^{-1} day^{-1}$ in trees with a mean diameter of 32 cm and 7–17 kg $tree^{-1} day^{-1}$ in the smallest trees of 9.5–10.6 cm diameter (Ford & Vose, 2007). This equates to a maximum transpiration rate of 1.34, 1.05 and 1.03 mmol m^{-2} of needles s^{-1} for the three size classes, respectively. Transpiration rates per tree of Eastern Hemlock have been measured at less than half that of *Quercus rubra*, *Betula lenta* and *Acer rubrum* but are similar to that of *Acer saccharum* (Catovsky et al., 2002; Daley et al., 2007; Davis, 2008; Eickmeier et al., 1975; Hadley et al., 2008).

Water loss varies seasonally. In the mild winter temperatures of the Appalachians, 50% of transpiration in an Eastern Hemlock stand can occur in winter (9.1 mm/year) and spring (25.9 mm/year; Ford & Vose, 2007). Transpiration loss can also be higher during the summer in southern regions due to higher temperatures, calculated in the southern Appalachians to be 5136 kg H_2O/year compared to 1531 kg H_2O/year in the northeast (Catovsky et al., 2002; Ford & Vose, 2007).

Leaf specific conductivity (LSC: hydraulic conductivity per gram dry mass of supplied needles) in a 19-year-old Eastern Hemlock was measured to be highest in the trunk (297 μL $h^{-1} g^{-1}$) and lower at branch junctions (12 μL $h^{-1} g^{-1}$) than in first and second-order branches (29–56 μL $h^{-1} g^{-1}$), a similar ratio to that found in many trees, designed to equalise the availability of water to each needle (Ewers & Zimmermann, 1984). Similarly, LSC steadily decreased vertically up the trunk, until it was 52 μL $h^{-1} g^{-1}$ at the top, such that LSC values near the tip of the leader were only slightly greater than those of adjacent branches, allowing needles at the top of the tree to compete for water with those lower down (Ewers & Zimmermann, 1984). The supply of water to leaves (defined as the xylem transverse sectional area per gram dry mass of supported needles) followed a similar pattern, reducing from 3 mm^2/g at the trunk base to as little as 0.8 mm^2/g in second order branches, but increased up the trunk and along branches as tracheid diameters became wider, varying from 4.4 μm diameter at the bottom of the trunk compared to 17 μm at the top (Ewers & Zimmermann, 1984). The mechanics of water bulk flow through Eastern Hemlock shoots is discussed by Tyree et al. (1975) and Tyree and Yang (1990).

Water use by different tree species varies through the year. In mixed forest at Harvard Forest, Massachusetts, maximum transpiration rates in midsummer were twice as high in *Betula lenta* as Eastern Hemlock ($100 \times 10^{-6} \pm 2.8 \times 10^{-5}$ mm/s and $58 \times 10^{-6} \pm 1.3 \times 10^{-5}$ mm/s per projected crown area, respectively; SE, $n = 8$) but in late summer just before leaf abscission, maximum rates were almost equal and that of birch declined progressively as leaves fell (Daley et al., 2007). Water use efficiency of Eastern Hemlock is thus high compared to co-occurring species. For example, Davis (2008) measured mean sap flux density in North Carolina at *c*. 12–15 g H_2O m^{-2} sapwood s^{-1} in Eastern Hemlock which was similar to that of *Rhododendron maximum* (13–15 g $m^{-2} s^{-1}$) but lower than *c*. 42–43 g $m^{-2} s^{-1}$ in *Betula lenta* and 25–32 g $m^{-2} s^{-1}$ in *Acer rubrum*. Hadley et al. (2008) estimated that water use by the *Quercus rubra* forest reached 4 mm/day, compared to a maximum of 2 mm/day in Eastern Hemlock. As a result, the anticipated extirpation of Eastern Hemlock could potentially increase whole-forest water loss and carbon gain by 2–4-fold, provided nitrogen and water are not limiting (Catovsky et al., 2002; Daley et al., 2007).

Whole-tree hydraulic resistance (R) of Eastern Hemlock varied from 0.091 h MPa/kg in the largest tree (47.8 cm diameter) to 5.70 h MPa/kg in the smallest measured (5.4 cm diameter). R was higher in *Betula lenta*, varying from 0.096 h MPa/kg in the largest tree (27.4 cm) to 7.00 h MPa/kg in the smallest (4.5 cm). Time constants for sap flow (the inertia of sap flow) ranged from 9.4 to 24.8 min in Eastern Hemlock trees compared with 5.9 to 10.5 min in *Betula lenta*. It was concluded that in Eastern Hemlock there is a greater time lag between transpiration and absorption of water from the soil (Daley et al., 2008). Thus, if birch were to become more common in a forest, it would result in more rapid depletion of soil water.

6.5.3 | Mineral nutrition

In northern Wisconsin, Eastern Hemlock forms almost monotypic stands (90% of basal area) on cliffs with thin organic soils where litter decomposes slowly, creating deep acidic humus (Finzi et al., 1998; Lovett et al., 2004; Rogers, 1978) often with low N mineralisation (29 kg ha^{-1} year^{-1} compared to 26–84 kg ha^{-1} year^{-1} in other surrounding woodland communities), low nitrification (6 kg ha^{-1} year^{-1} compared to 2.5–98 kg ha^{-1} year^{-1} in other communities) and low P content (110 kg ha^{-1} compared to 2000–6400 kg ha^{-1}) (Pastor et al., 1984). Nevertheless, annual production reaches 5.3 Mg ha^{-1} year^{-1} compared to 4.1–9.5 Mg ha^{-1} year^{-1} in other communities. Annual litter fall was measured at 0.45 Mg ha^{-1} year^{-1} and of low-quality containing 1.3% N and 0.11% P, although a comparatively high amount of nitrogen given the low mineralisation (Pastor et al., 1984).

6.6 | Biochemical data

The essential oil of Eastern Hemlock needles is dominated by monoterpenes. Up to 94 different terpenes have been recorded, 23 of them at concentrations higher than 0.1% of the total oil content (Craft & Setzer, 2017; Lagalante et al., 2006; Lagalante & Montgomery, 2003). The commonest are bornyl acetate (24%–39% of total oil content), α-pinene (5%–24%), camphene (3%–13%), manool (7%) limonene (6%–7%), piperitone (4%–8%), tricyclene (4.5%), α-humulene (4.4%) and β-caryophyllene (3.4%) (Craft & Setzer, 2017; Kılıç & Kocak, 2014). Other terpenes include phellandrine, terpinene, cymene, cubebene, terpinene, sabinene, ocimene, terpinolene, linalool, borneol, piperitone, myrcene, phellandrene, thujone, sabinyl acetate, isobornyl acetate and geranyl acetate (Broeckling & Salom, 2003; Kılıç & Kocak, 2014; McClure & Hare, 1984; Shaw, 1951).

Several studies have identified α-pinene, camphene, and isobornyl acetate as the most effective in conferring resistance to defoliators and sapsuckers, including the Hemlock Woolly Adelgid—HWA (Lagalante et al., 2006, 2007; Lagalante & Montgomery, 2003). Ingwell et al. (2009) noted no significant differences in terpene concentrations between Eastern Hemlocks that were resistant to HWA and those that were not. However, HWA-infested trees released higher amounts of volatile monoterpenes from the branch tips but with lower concentrations of α-pinene; 57% of volatiles from affected foliage compared to 66% from unaffected foliage (Broeckling & Salom, 2003).

There are also differences in feeding preferences for old and new needles by several defoliating insects (Section 9.1). New needles generally have smaller concentrations of chemical defences than 1-year-old foliage. Kinahan, Rigsby, et al. (2020) found that in new needles, concentrations of α-pinene, camphene, isobornyl acetate and diterpene rose to levels similar to older foliage within a month of budbreak, while lignin concentrations took till July, and soluble phenolic and condensed tannin concentrations in new foliage remained low through the first growing season and only approached that of older needles in December.

7 | PHENOLOGY

Bud dormancy is normally broken by brief chilling (<5°C for 5–15 weeks) but growth will occur without it given short nights of ≤4 h darkness (Olson et al., 1959; Olson & Nienstaedt, 1957). After chilling, buds open in the first half of May and lateral branches appear in the middle of June, growing perhaps 2–3 cm in the first year. Reproductive buds are initiated the summer before opening (Olson et al., 1959). Male strobili are visible in late April to early July, and pollen is shed around 2 weeks after vegetative bud burst (Godman & Lancaster, 1990). The female gametophyte forms in early May within the strobilus, and the two ovules per cone scale are exposed to the air and pollen in the second week of May (Olson et al., 1959). Fertilisation is complete 6 weeks after pollination (Godman & Lancaster, 1990; Olson et al., 1959). Female strobili give rise to cones the same year, ripening in August–early September with seed release by early- to mid-October. Seed dispersal occurs in the autumn and early winter; although some seeds are retained through the winter, these are usually sterile. Cones remain on the tree until the following year. Seeds germinate the spring after falling from cones, from March to the beginning of July (Godman & Lancaster, 1990). Winter buds begin to form in mid-September (Frothingham, 1915).

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Wind pollinated. Self-compatibility appears to be high; in trials using bags over flowers to control pollination on up to 12 trees, Bentz et al. (2002) germinated 553 self-pollinated seeds compared to 1992 cross-pollinated seeds. Abundant pollen is produced. Ibe (1983) measured up to 550 pollen grains/cm^2 of soil surface area under a parent tree, and this tailed off beyond the edge of the crown to <200 grains/cm^2 by 100 m from the parent (29% of the pollen per unit area at the base of the tree).

8.2 | Hybrids

Tsuga canadensis and *T. caroliniana* are partially sympatric, but naturally occurring hybrids have not been documented (Holman et al., 2017). This is supported by substantial differences in chloroplast polymorphisms between the two species (Wang et al., 1997). Hybridisation has been artificially attempted between *T. canadensis* and Asian species resistant to the Hemlock Woolly Adelgid, including *T. diversifolia*, *T. chinensis* and *T. sieboldii*, but was difficult to achieve (Bentz et al., 2002). *Tsuga caroliniana* is more closely related to Asian

Tsuga species than *T. canadensis*, which undoubtedly explains why *T. caroliniana* hybridises more easily with Asian *Tsuga* species than *T. canadensis* (Bentz et al., 2002). Recently, two adelgid-resistant hybrids, *T. chinensis*×*T. caroliniana* 'Traveler', and *T. caroliniana*×*T. chinensis* 'Crossroad', were introduced to the horticultural trade for landscape settings (Bentz et al., 2023).

8.3 | Seed production and dispersal

The cones of Eastern Hemlock at 13–19 mm long are the smallest in the genus, which typically range from 13 to 80 mm (Godman & Lancaster, 1990). The total number of scales per cone increases with cone volume, but the proportion of fertile scales was seen to be independent of cone size (Turgeon et al., 2004). Each cone can carry 25–31 ovules; although mature cones usually contain 2–8 seeds, presumed to be limited by pollination (Godman & Lancaster, 1990; Jetton et al., 2013; Thomas et al., 2021; Turgeon et al., 2004); fewest at the southern end of its range in the southern Appalachians (Jetton et al., 2013). Godman and Lancaster (1990) reported that 35.2 L (1 bushel) of cones weigh *c.* 15.4 kg, and yield from 0.64 to 0.68 kg of seed, so 1 kg of cones (*c.* 2 L) contains 42–44 g of seeds. In mixed hemlock-hardwood stands in Michigan, seed traps under Eastern Hemlock produced 39.7 ± 39.4 (SE, $n = 33$) seeds m^2/year (McEuen & Curran, 2004).

The number of cleaned seeds per kg ranges from 56,250 to 163,290 (Godman & Lancaster, 1990) and individual seed mass varies from 1.1 to 1.7 mg (Frothingham, 1915; McEuen & Curran, 2004) with seeds being usually larger in eastern and southern regions (Godman & Lancaster, 1990). Seeds of Eastern Hemlock are slightly larger than those of *Tsuga heterophylla* but smaller than those of *T. caroliniana* and *T. mertensiana* (Godman & Lancaster, 1990).

The winged seeds are wind-dispersed, which begins in September and continues through the winter. Most seeds fall within a tree height but can secondarily move by being blown over crusted snow (Godman & Lancaster, 1990). Seeds typically disperse 30 m, half that of their hardwood competitors (Foster, 2014). McEuen and Curran (2004) found that open ground of 300–500 m was sufficient to prevent seed dispersal between stands.

8.4 | Viability of seeds: Germination

Germination of mature seed under optimum ex situ conditions is variable—(0)15%–70% (Jetton et al., 2013; Olson et al., 1959)—but is commonly around 25% in the field (Mladenoff & Stearns, 1993). Fresh Eastern Hemlock seeds were found by Pence (1991) to be tolerant of storage in liquid nitrogen since germination after stratification was as high as for non-frozen seeds (28% and 36%, respectively). By contrast, Olson et al. (1959) found that seeds that have been stratified and were beginning to germinate were readily damaged by drying; 60% were found to be unviable after just 2 h of drying, with 80% loss of viability after 6 h.

Eastern Hemlock shows partial dormancy and stratification for 60–70 days at 1–5°C improves germination (Godman & Lancaster, 1990; Olson et al., 1959). Germination is reduced by up to 50% without stratification and takes longer; *c.* 4 weeks for maximum germination compared to 2 weeks after stratification (Stearns & Olson, 1958). Daylight for 8–12 h at 17–22°C can compensate for a lack of stratification, but germination levels are still lower (Olson et al., 1959; Stearns & Olson, 1958). In the north of Eastern Hemlock's range, stratification needs are readily met through winter under field conditions, and spring germination is not delayed. However, seeds of southern origin respond more to light than northern seeds (Olson et al., 1959; Stearns & Olson, 1958), perhaps due to higher winter temperatures.

Stratification in dilute sulphuric acid followed by germination on saturated mats watered at the same pH as used in stratification resulted in the germination of Eastern Hemlock being unaffected between pH 5.6 and 3.0 (35.7%–37.7%) but significantly lower at pH 2.4 (4.3%). However, *Acer rubrum*, *A. saccharum* and *Betula alleghaniensis* showed no germination at pH 2.4, and only *Pinus strobus* showed increasing germination with more acidic treatments (Raynal et al., 1982).

Germination occurs between 7 and 27°C; although, under laboratory conditions, a constant 17°C is optimal, similar to the co-occurring *Betula alleghaniensis* (Godman & Lancaster, 1990; Olson et al., 1959). Under field conditions, Eastern Hemlock needs 45–60 days of warm conditions for germination to peak; warmer conditions than are typically found under a mature hemlock canopy. Seeds which have begun germination, and seedlings, are highly susceptible to drying. Olson et al. (1959) noted visible shrinkage of the root within 10 min of exposure to air at 40% relative humidity and a further shrinkage to 25% of their original diameter within an hour.

It is generally considered that Eastern Hemlock has no persistent soil seed bank (Marquis, 1975). However, some seeds can persist in the soil for several years, mainly in the top 10 cm of organic matter, but this is minor compared to annual seed fall (Mladenoff, 1990; Sullivan & Ellison, 2006). Catovsky and Bazzaz (2000) noted seedling emergence of 12/m^2 from the soil seed bank and Farnsworth et al. (2012) found a mean of 3.3 emerging seedlings/m^2—far fewer than *Betula lenta* (26/m^2) and *B. papyrifera* but more than *Pinus strobus* and *Populus grandidentata* (<1/m^2).

Germination and seedling establishment are rare on deep litter layers, whether from conifers or hardwoods (Friesner & Polzger, 1932; Rooney & Waller, 1998; Witt & Webster, 2010), due to the high probability of drying damage to the shallow roots (Marx & Walters, 2008). Grant and Hart (1961) recorded 30% mortality of Eastern Hemlock seedlings between June and November where there was <25% of the plot area covered by undisturbed hardwood litter and 54% where cover was >25%. Moreover, deep litter is also a refuge for pathogenic fungi that infect seeds buried in the soil (Godman & Lancaster, 1990; O'Hanlon-Manners & Kotanen, 2004). Fungicide has been seen to improve germination of seeds buried in organic soil but not in seeds inserted into rotting logs (O'Hanlon-Manners & Kotanen, 2004). Moreover, fungicide applied to seeds

prior to burial in soil in an Eastern Hemlock stand increased germination from 38% in unprotected seeds to 63% in fungicide-protected seeds. Germination of Eastern Hemlock seeds buried under *Acer saccharum* was unaffected by fungicide application, suggesting a build-up of host-specific pathogens beneath Eastern Hemlock (Kotanen, 2007).

Deep litter, particularly from hardwoods, may prevent the slow-growing hypocotyl (Olson et al., 1959) from buried Eastern Hemlock seeds (which have little stored food) from emerging (Olson et al., 1959; Rogers, 1978). Subsequent growth of seedlings that manage to establish on deep litter is usually reduced due to low availability of nutrients, particularly nitrogen. However, growth of more nutrient-demanding hardwoods is even more affected and may favour the slow but steady growth of Eastern Hemlock (Pastor et al., 1984).

Seedling establishment is most successful on damp mineral soil or coarse woody debris such as rotting logs or stumps that are warm and retain moisture, especially when moss-covered (Frothingham, 1915; Marx & Walters, 2008; Mladenoff & Stearns, 1993; Rogers, 1978; Rooney & Waller, 1998; Witt & Webster, 2010). *Pinus strobus*, which forms a large component of many communities following fire (Section 3), makes a significant contribution to the woody debris since, along with Eastern Hemlock logs, it rots slowly, which helps Eastern Hemlock establish long after hardwood logs have rotted away, leading to dominance by Eastern Hemlock, *Fagus grandifolia*, *Acer rubrum* and *Betula lenta* (D'Amato et al., 2017). Success is not affected by nitrogen supply from different species of woody substrate (Marx & Walters, 2006).

Even on these moist microhabitats, prolonged drought can result in mortality by desiccation of Eastern Hemlock's shallow roots (Coffman, 1978; Mladenoff & Stearns, 1993). Unsurprisingly, there is a positive correlation between seedling survival and rainfall on well-drained sites, but a negative correlation with summer temperatures (Cook & Cole, 1991; Hart et al., 2010; Tardiff et al., 2001). Parshall (1995) also found a correlation between drought and growth release of Eastern Hemlock, with seedlings showing an increase in growth 3–4 years after drought in northern Michigan.

Seedling establishment is higher in small openings that reduce excessive shading yet prevents the soil from drying too quickly (Jordan & Sharpe, 1967). As such, Eastern Hemlock regeneration is aided by single treefall events that disturb the soil and create a small canopy opening (Mladenoff & Stearns, 1993). Regeneration is also favoured under the lighter shade of hardwoods, with or without pines, upon moist organic matter (Frothingham, 1915). Stems of young Eastern Hemlock seedlings are susceptible to sunscald in large gaps (Mladenoff & Stearns, 1993). Growth of saplings of different tree species in canopy gaps is covered in Section 4.

Seedling survival is just as dependent on microhabitat as establishment. In Upper Michigan, establishment and survival of Eastern Hemlock was found to be higher on Eastern Hemlock logs: established seedlings per metre square on Eastern Hemlock 0.42 seedlings/m^2; *Betula* wood 0.21/m^2, *Acer* wood 0.08/m^2 and soil 0.01/m^2. Moreover, Eastern Hemlock wood supported seedlings as old as 13 years, while on quicker rotting *Acer* wood, seedlings >3 years old were rare (Marx & Walters, 2008). Nevertheless, seedling mortality can be very high. In Indiana, studies found that 88.3% of Eastern Hemlock seedlings died during their first year (Friesner & Polzger, 1932) and at the end of 10 years of cumulative establishment, only 13.9% of all seedlings were still living (Friesner & Polzger, 1944). Seedling survival can be reduced by progressive canopy closure, drought, browsing (Section 4) and competition from herbs and shrubs (Thomas et al., 2021). In the southern Appalachians, Kincaid (2012) found a negative relationship between sapling density and the cover of *Rhododendron maximum*.

8.5 | Seedling morphology

Germination is epigeal (Figure 6). The radicle grows at 2–3 mm per day for several days after which the hypocotyl starts to grow, reaching its full length of 2–3 cm within 1–3 weeks, and it then begins to straighten (Olson et al., 1959). Root growth is slow and they may reach 2–4 cm below the surface after 1 month and 6–10 cm after 3 months. The first needles above the cotyledons appear in threes giving 3, 6 or 9 needles in apparent whorls, although the grouping in threes becomes less apparent over the growing season (Olson et al., 1959). Seedlings this size are easily buried in leaf litter from *Acer saccharum* and other deciduous trees. Seedlings form a slender taproot during the first year which is lost in the development of the lateral roots. First-year seedlings may grow just 2.5–3.8 cm in height with roots extending <1.3 cm into the soil. Second-year seedlings reach a depth that tends to remain moist and then growth speeds up. Seedlings 'are fully established' when 0.9–1.5 m tall and can cope with shade being removed without mortality (Godman &

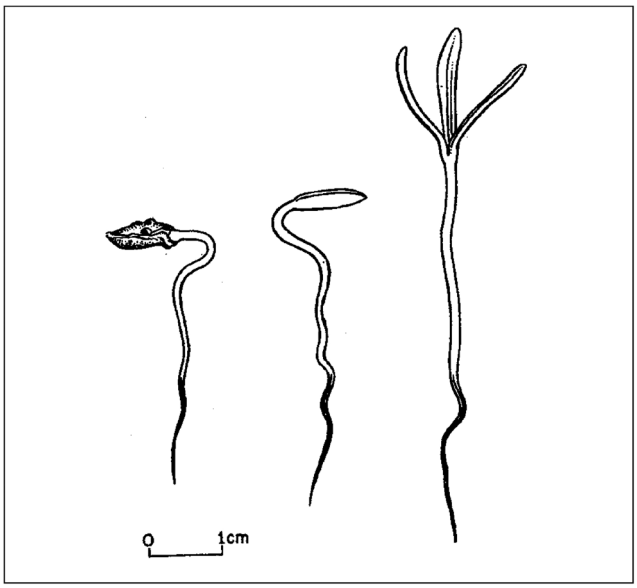


FIGURE 6 Seedlings of *Tsuga canadensis* at 2, 4 and 7 days after germination. From: Bonner and Karrfalt (2008).

Lancaster, 1990) and, indeed, the high degree of plasticity to switch from shade to sun plant in both young and old trees is highly unusual in forest trees (Foster, 2014).

Once established, hemlock seedlings grow slowly for the first 10 or 15 years; with adequate light and limited competition, later growth is more rapid (described in Section 4). Hemlock is highly tolerant of shade, but saplings, small trees and even mature trees respond quickly to the opening of the canopy with increased growth (Mladenoff & Stearns, 1993).

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

Insects and Arachnida recorded on Eastern Hemlock in its native range are given in Table 2. Buck (2004) lists 280 insects found within the crown of Eastern Hemlock in the Great Smoky Mountains National Park, Tennessee. Similarly, Dilling et al. (2007) identified 243 insect species associated with Eastern Hemlock in the same area; of these, 33.5% were transient, 25.5% were scavengers and 22.2% predators compared to just 5.1% that were herbivorous, almost completely opposite to the pattern in studies of other conifers.

Of the insects recorded on Eastern Hemlock, larvae of the native Hemlock Borer *Phaenops fulvoguttata* (Harris) (fomerly *Melanophila fulvoguttata* [Harris]) (Coleoptera, Buprestidae) are particularly damaging, often attacking stressed or injured trees (Balch, 1935) particularly those weakened by HWA (Souto & Shields, 2000). Outbreaks of the Hemlock Looper *Lambdina fiscellaria* (Lepidoptera, Geometridae) can be quite damaging but are infrequent (e.g. Trial Jr & Devine, 1994). In the mixed oak forests of New York State in 1981, Eastern Hemlock saplings were killed by severe defoliation by Spongy Moth larvae *Lymantria dispar* (Lepidoptera, Erebidae) (Lovett et al., 2006). However, many insects associated with Eastern Hemlock are relatively benign. For example, Elongate Hemlock Scale *Fiorinia externa* (Hemiptera, Diapididae), introduced from Japan over a century ago, has migrated north and commonly co-occurs with HWA in many forests (Preisser et al., 2008). However, it appears to have little impact on the regeneration of Eastern Hemlock (Preisser et al., 2011) or trigger defensive reactions to infestation (Radville et al., 2011), and widespread tree mortality resulting from this insect has never been documented (Venette et al., 2024). This scale insect also has a number of native insect predators (Lynch, 2006). Psocoptera form a large component of insect diversity on Eastern Hemlock, acting primarily as consumers of microepiphytes as well as acting as a food source for predators. A total of 44 Psocopterans (of >300 species North America species) have been found on Eastern Hemlock in the southern Appalachians (Coots et al., 2012a, 2012b). Snyder et al. (2002) noted that 8% of invertebrate taxa in forests of northeast Pennsylvania and west New Jersey were strongly associated with Eastern Hemlock; streams draining hemlock stands had significantly more taxa than those draining mixed hardwood stands but had fewer rare species.

The main insects exploiting Eastern Hemlock seeds are *Leptoglossus occidentalis* (Hemiptera, Coreidae), *Megastigmus hoffmeyeri* (Hymenoptera, Torymidae) and the Spruce Budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae) (de Groot et al., 1994; Milliron, 1949). However, in Ontario, the first record of *Eupithecia mutata* (Lepidoptera: Geometridae) larvae attacking Eastern Hemlock seeds was noted by Turgeon et al. (2004). They found larvae in up to 21% of cones, which destroyed >90% of the filled seeds within each cone. In the same study, *Megastigmus hoffmeyeri* larvae had relatively little impact on seed production: larvae were found in 9%–40% of cones, but the proportion of seeds destroyed ranged from just 1.1% to 6.1% (Turgeon et al., 2004).

Both the sistens and progrediens generations of HWA (Section 9.1.1) were found to feed preferentially on leaf cushion tissue of mature Eastern Hemlock needles (Lagalante et al., 2006). Higher terpenoid content of Eastern Hemlock needles has also been associated with reduced fecundity of Elongate Hemlock Scale *Fiorinia externa* (Hemiptera, Diaspididae), also introduced from Japan (McClure & Hare, 1984). The Hemlock Looper *Lambdina fiscellaria*, a defoliator of Eastern Hemlock, also has preferences for different aged needles (Carroll, 1999); early instar larvae feed on expanding needles and older larvae move to feed on older foliage. Indeed, 55% of larvae fed an exclusive diet of new foliage survived, whereas when larvae were fed exclusively on 1- or 2-year-old foliage, only 5% and 0% survived, respectively (Carroll, 1999). Larvae given access to both new and old foliage survived better and were heavier than those restricted to new foliage.

Eastern Hemlock is browsed by white-tailed deer *Odocoileus virginianus* (Zimmermann) and moose *Alces alces* (L.), described in Section 4. Snowshoe hares *Lepus americanus* Erxleben (Alverson et al., 2019) and New England cottontails *Sylvilagus transitionalis* (Bangs) are also common browsers of Eastern Hemlock. Small mammals, including White-footed Mice *Peromyscus leucopus* (Rafinesque), Meadow Voles *Microtus pennsylvanicus* (Ord) and Southern Red-backed Voles *Clethrionomys gapperi* (Vigors), feed on seeds and small seedlings (Abbott, 1962). Porcupines *Erethizon dorsatum* (L.) are usually a minor issue for Eastern Hemlock but gnaw the bark on larger trees, causing serious wounds and occasional death of stems (Brander, 1973). Birds are generally limited in their feeding on Eastern Hemlock, although the Yellow-bellied Sapsucker *Sphyrapicus varius* (L.) regularly drills holes in Eastern Hemlock and has been associated with ring shake (Section 6.1) in some areas (Jorgensen & Lecznar, 1964).

9.1.1 | Hemlock Woolly Adelgid (HWA)

The Hemlock Woolly Adelgid, *Adelges tsugae* Annand (Hemiptera, Adelgidae), is a serious pest of Eastern Hemlock in eastern North America, first found and identified in 1951 but likely introduced from Japan decades earlier on ornamental hemlocks, possibly *Tsuga diversifolia* or *T. sieboldii* (Foster, 2014; Havill et al., 2006; Parker et al., 2023; Stoetzel, 2002). Free from natural predation and well

TABLE 2 Insects and Arachnida recorded directly on *Tsuga canadensis* in eastern North America.

Species classification	Ecological notes	Source
INSECTA		
Hymenoptera		
Torymidae		
Megastigmus hoffmeyeri Walley	Larvae; seeds	12
Hemiptera		
Adelgidae		
Adelges tsugae Annand	Hemlock Woolly Adelgid; serious pest	1
Aphrophoridae		
Aphrophora parallela (Say)	Spittlebug on a range of conifers	3
Coreidae		
Leptoglossus occidentalis Heidemann	Larvae; seeds	17
Diaspididae		
Ceroplastes ceriferus (Fabricius)	Scale of leaves; native to southern Asia	11
Aspidiotus cryptomeriae Kuwana	Native to Japan, scale of evergreen leaves	3
Dynaspidiotus tsugae (Marlatt)	Native to Japan, serious scale pest of Eastern Hemlock	2, 13
Fiorinia externa Ferris	Native to Japan, serious scale pest of Eastern Hemlock; range of conifers	2, 4, 8, 13, 16
Hemiberlesia ithacae (Ferris)	Hemlock Scale; Eastern Hemlock preferred host; fatal defoliation	1
Tsugaspidiotus tsugae (Marlatt)	Serious scale pest, range of conifers	8
Pentatomidae		
Halyomorpha halys Stål	All stages found on Eastern Hemlock; introduced	11
Coleoptera		
Buprestidae		
Phaenops fulvoguttata (Harris) [=*Melanophila fulvoguttata* (Harris)]	Hemlock Borer; formerly the most important economic pest	1
Lepidoptera		
Erebidae		
Dasychira plagiata Walker	Larvae; eastern North America; conifers	14
Lymantria dispar (L.)	Spongy Moth; kills understory trees	1, 14
Orgyia antiqua subsp. *nova* Fitch.	Conifers; common in Europe on deciduous shrubs	14
Orgyia leucostigma subsp. *intermedia* Fitch	Larvae; deciduous trees, conifers	14
Gelechiidae		
Coleotechnites apicitripunctella (Clemens)	Leaf mining larvae; hemlock	3, 14
Coleotechnites macleodi (Freeman)	Leaf mining larvae; hemlock	14
Zanclognatha cruralis (Guenée)	Southern Canada to Texas	14
Geometridae		
Campaea perlata Guenée	Larvae; looper moth	14
Caripeta divisata Walker	Conifers, North America	14
Cladara limitaria (Walker)	*Kalmia angustifolia*, conifers; North America	14
Ectropis crepuscularia (Denis & Schiffermüller)	Polyphagous larvae	14
Eufidonia notataria (Walker)	Larvae; range of conifers	3
Eupithecia lariciata (Freyer)	Larvae; North America; mainly *Larix*	14
Eupithecia mutata Pearsall	Larvae; seeds	12
Eupithecia palpata Packard	Conifers, mostly Canada	14

TABLE 2 (Continued)

Species classification	Ecological notes	Source
Hydriomena divisaria (Walker)	Eastern North America; mainly *Abies balsamea*, *Picea*, *Pinus*	14
Lambdina fervidaria athasaria (Walker)	Larvae; *Abies balsamea*, *Picea*, Eastern Hemlock	14
Lambdina fiscellaria Guenée	Hemlock Looper; larvae	1
Macaria fissinotata Walker	Larvae; North America	14
Macaria signaria (Hübner)	Larvae; North America to Japan; mainly on *Picea abies*, *Larix sibirica*	14
Nemoria mimosaria (Guenée)	Larvae; deciduous shrubs and trees, conifers	14
Nepytia canosaria Walker	Larvae; *Abies balsamea*, *Picea*, Eastern Hemlock; Eastern North America	14
Pero morrisonaria (H. Edwards)	Widespread North America	14
Protoboarmia porcelaria (Guenée)	Conifers, eastern North America	14
Tetracis cachexiata Guenée	Trees, widespread in North America	14
Lasiocampidae		
Tolype laricis (Fitch)	Mostly on *Larix*	14
Noctuidae		
Elaphria versicolor Grote	NE North America; conifers	14
Feralia jocosa Guenée	Northern North America; mainly on *Pinus*	14
Lithophane innominata Smith	Woodlands of North America; polyphagous on trees	14
Morrisonia confusa Hübner	Larvae; mostly deciduous trees	14
Morrisonia latex Guenée	Larvae; mostly deciduous trees	14
Panthea acronyctoides (Walker)	North America; conifers	14
Syngrapha abstrusa Eichlin & Cunningham	Larvae; primarily on *Picea engelmannii*, *Picea glauca*, *Pinus banksiana*	14
Syngrapha rectangula (Kirby)	Boreal and montane forests; mainly on *Tsuga heterophylla*	14
Xestia badicollis Grote	North America; conifers	14
Torticidae		
Acleris variana (Fernald)	NE North America; mainly on *Abies balsamea*, *Picea glauca*	14
Amorbia humerosana Clemens	Eastern North America; polyphagous on trees	14
Argyrotaenia occultana Freeman	Webbing larvae; North America; conifers	14
Choristoneura fumiferana (Clemens)	Spruce Budworm; uses Eastern Hemlock as a secondary host	1
Clepsis persicana (Fitch)	North America; polyphagous on trees	14
Eucosma tocullionana (Heinrich)	Larvae on cones; range of conifers	3
Pscoptera		
Caeciliusidae		
Valenzuela flavidus (Stevens)	Mostly broadleaf trees, lower canopy only	5, 6
Valenzuela pinicola (Banks)	Lower canopy only, foliage	5, 6
Xanthocaecilius quillayute (Chapman)	Evergreen trees	6
Xanthocaecilius sommermanae (Mockford)	Lower canopy only, mostly broadleaf trees	5, 6
Dasydemellidae		
Teliapsocus conterminus (Walsh)	Upper canopy only, foliage	5, 6
Ectopsocidae		
Ectopsocopsis cryptomeriae (Enderlein)	Hanging dead leaves	5, 6
Ectopsocus meridionalis Ribaga	Lower canopy only; dead leaves	5, 6

(Continues)

TABLE 2 (Continued)

Species classification	Ecological notes	Source
Lachesillidae		
Anomopsocus amabilis (Walsh)	Hanging dead leaves	6
Lachesilla anna Sommerman	Dead leaves	6
Lachesilla contraforcepeta Chapman	Lower canopy only, foliage	5, 6
Lachesilla corona Chapman	Dead leaves	6
Lachesilla forcepeta Chapman	Foliage	6
Lachesilla major Chapman	Dead leaves	6
Lachesilla pedicularia (L.)	Foliage	6
Lachesilla rufa (Walsh)	Lower canopy only, bark	5, 6
Lepidopsocidae		
Echmepteryx hageni (Packard)	Bark	5, 6
Mespsocidae		
Mesopsocus unipunctatus (Müller)	Variety of trees	6
Myopsocidae		
Lichenomima lugens (Hagen)	Shaded trunks	6
Peripsocidae		
Peripsocus alboguttatus (Dalman)	Lower canopy only, various conifers	5, 6
Peripsocus maculosus Mockford	Lower canopy only, foliage and branches	5, 6
Peripsocus madidus (Hagen)	Lower canopy only, mostly conifers	5, 6
Peripsocus stagnivagus Chapman	Trunk and branches	6
Peripsocus subfasciatus (Rambur)	Lower canopy only, variety of trees	5, 6
Philotarsidae		
Aaroniella badonneli (Danks)	Variety of trees and shrubs	6
Aaroniella maculosa (Aaron)	Forest trees on moist soils	5, 6
Psocidae		
Blaste opposita (Banks)	Branches	5, 6
Blaste quieta (Hagen)	Lower canopy only, branches	5, 6
Blastopsocus lithinus (Chapman)	Upper canopy only, trunk and branches	5, 6
Cerastipsocus venosus (Burmeister)	Lower canopy only, trunk and branches	5, 6
Hyalopsocus floridanus (Banks)	Trunk and branches	6
Indiopsocus infumatus (Banks)	Dead branches	6
Loensia moesta (Hagen)	Trunk and branches	6
Metylophorus novaescotiae (Walker)	Lower canopy only, branches	5, 6
Metylophorus purus (Walsh)	Middle of canopy only, trunk and branches	5, 6
Psocus leidyi Aaron	Middle of canopy only, trunk and branches	5, 6
Ptycta polluta (Walsh)	Middle of canopy only, branches	5, 6
Trichadenotecnum alexanderae Sommerman	Middle of canopy only, bark	5, 6
Trichadenotecnum castum Betz	Lower canopy only, trunk and branches	5, 6
Trichadenotecnum merum Betz	Trunk and branches	6
Trichadenotecnum quaesitum (Chapman)	Upper canopy only, branches	5,6
Trichadenotecnum *slossonae* (Banks)	Branches	6
Stenopsocidae		
Graphopsocus cruciatus (L.)	Upper canopy only	5, 6
ARACHNIDA		
Amaurobiidae		
LiCallioplus pantoplus (Bishop & Crosby)		7
Coras aerialis Muma		7

TABLE 2 (Continued)

Species classification	Ecological notes	Source
Wadotes calcaratus (Keyserling)		7
Wadotes dixiensis Chamberlin		7
Wadotes hybridus (Emerton)		7
Wadotes tennesseensis Gertsch		7
Antodiaetidae		
Antrodiaetus unicolor (Hentz)		7
Anyphaenidae		
Hibana gracilis (Hentz)		10
Araneidae		
Acanthepeira stellata (Walckenaer)		10
Araneus gemmoides Chamberlin & Ivie		10
Araneus miniatus (Walckenaer)		10
Araniella displicata (Hentz)		10
Larinioides patagiatus (Clerck)		10
Mangora maculata (Keyserling)		10
Mangora placida (Hentz)		10
Marpissa formosa (Banks)		10
Mecynogea lemniscata (Walckenaer)		10
Micrathena mitrata (Hentz)		10
Mimetus puritanus Chamberlin		10
Neoscona arabesca (Walckenaer)		7
Rabidosa rabida (Walckenaer)		10
Anyphaenidae		
Anyphaena fraterna (Banks)		10
Anyphaena pectorosa L. Koch		10
Clubionidae		
Elaver excepta (L. Koch)		10
Corinnidae		
Castianeira cingulata (C. L. Koch)		10
Scotinella redempta (Gertsch)		7
Cybaeidae		
Cybaeus patritus Bishop & Crosby		7
Dictynidae		
Cicurina breviaria Bishop & Crosby		7
Cicurina arcuata (Keyserling)		7
Gnaphosidae		
Drassyllus fallens Chamberlin		7
Leptonetidae		
Leptoneta gertschi (Barrows)		7
Linyphiidae		
Bathyphantes bishopi Ivie		7
Ceraticelus fissiceps (O.P.-Cambridge)		10
Ceratinopsis interpres (O.P.-Cambridge)		10
Eperigone maculata (Banks)		7
Frontinella pyramitela (Walckenaer)		10

(Continues)

TABLE 2 (Continued)

Species classification	Ecological notes	Source
Lepthyphantes zebra (Emerton)		7
Pityohyphantes costatus (Hentz)		10
Pocadicnemis americana Millidge		7
Walckenaeria minuta (Emerton)		7
Walckenaeria brevicornis (Emerton)		7
Walckenaeria pallida (Emerton)		7
Lycosidae		
Pirata montanus Emerton		7
Nesticidae		
Nesticus tennesseensis (Petrunkevitch)		7
Philodromidae		
Philodromus marxi Keyserling		10
Philodromus rufus Walckenaer		10
Phytopidae		
Nalepella neotsuga n.sp.	Rust Mite	9
Pisauridae		
Dolomedes tenebrosus (Hentz)		7, 10
Salticidae		
Habrocestum parvulum (Banks)		7
Habrocestum pulex (Hentz)		7
Neon nelli Peckham & Peckham		10
Pelegrina flaviceps (Kaston)		10
Pelegrina peckhamorum (Kaston)		10
Theridiidae		
Argyrodes elevatus Taczanowski		10
Enoplognatha ovata (Clerck)		10
Episinus amoenus Banks		10
Euryopis funebris (Hentz)		10
Phoroncidia americana (Emerton)		10
Theridion differens Emerton		10
Theridion murarium Emerton		10
Theridion frondeum Hentz		10
Thymoites unimaculatus (Emerton)		10
Theridiosomatidae		
Theridiosoma gemmosum (L. Koch)		10
Tetragnathidae		
Leucauge venusta (Walckenaer)		7, 10
Thomisidae		
Xysticus ferox (Hentz)		10
Xysticus triguttatus Keyserling		10
Trachelidae		
Trachelas tranquillus (Hentz)		10
Uloboridae		
Hyptiotes cavatus (Hentz)		10
Uloborus diversus Marx		10

TABLE 2 (Continued)

Species classification	Ecological notes	Source
Uloborus glomosus (Walckenaer)		10
Tetragnatha laboriosa Hentz		10
Tetragnatha versicolor Walckenaer		10
Acarina		
Eriophyidae		
Nalepella tsugifoliae Keifer	Hemlock Rust Mite; conifers especially hemlocks	15
Tetranychidae		
Oligonychus ununguis (Jacobi)	Spruce Spider Mite; global	15

Sources: 1. Godman and Lancaster (1990); 2. McClure (1986); 3. USDA (1985); 4. Lambdin et al. (2007); 5. Coots et al. (2012a); 6. Coots et al. (2012b); 7. Jetton et al. (2009); 8. McClure and Fergione (1977); 9. Domes (2003); 10. Mallis and Rieske (2011); 11. Thomas et al. (2021); 12. Turgeon et al. (2004); 13. McClure and Hare (1984); 14. Maier et al. (2004); 15. Munck et al. (2018); 16. Preisser et al. (2011); and 17. de Groot et al. (1994).

adapted to the climate except in extreme cold locations (Parker et al., 1998, 1999), HWA has rapidly spread to 22 states and two Canadian provinces (Ontario and Nova Scotia), largely transported by wind and birds (MacQuarrie et al., 2025; McClure, 1990; Russo et al., 2019). This aphid-like insect, *c.* 1.5 mm long, is holocyclic with two generations a year comprised of parthenogenetic asexual reproduction on Eastern Hemlock and a sexual generation on a *Picea* species (Havill & Foottit, 2007). Adults settle on hemlock twigs and produce a 'wool-like' protective material, rich in waxes that provide both physical and chemical protection (Jones et al., 2012). HWA feed on all sizes and ages of hemlock by inserting a long feeding tube or stylet into the twigs preferentially at the base of the needles at the leaf cushion and accessing starches stored in the xylem ray parenchyma cells (Ayayee et al., 2014; Young et al., 1995). Infestation of HWA is often a chronic process lasting from 4 to 20 years from infestation to tree death (McClure, 1991; Orwig et al., 2012; see Section 4.1).

The precise mechanisms leading to adelgid-induced hemlock mortality remain elusive, but HWA feeding leads to a variety of physiological and anatomical responses, including induced changes in the volatile content of resin in both plantations and natural forests (Pezet et al., 2013; Pezet & Elkinton, 2014). Compared to Eastern Hemlock without HWA, infested trees exhibit altered xylem anatomy (Huggett et al., 2018), increased water stress and false-ring formation (Domec et al., 2013; Gonda-King et al., 2012, 2014), altered amino acid concentrations (Gómez et al., 2012), higher foliar nitrogen (Schaeffer, Soltis, et al., 2017; Stadler et al., 2005) and hypersensitive plant defence increases in hydrogen peroxide and salicylic acid (Radville et al., 2011; Rigsby et al., 2019, 2020; Schaeffer et al., 2018). In addition, HWA feeding leads to reduced photosynthesis (Gonda-King et al., 2014; Nelson et al., 2014; Rubino et al., 2015), basal area increment (Livingston et al., 2017; Nuckolls et al., 2009; Walker et al., 2014), starch reserves (Wilson et al., 2018), branch growth (Miller-Pierce et al., 2010), fine root production (Nuckolls et al., 2009), ectomycorrhizal colonisation (Schaeffer, Wilson, et al., 2017; Vendettuoli et al., 2015) and root bacterial abundance (Vendettuoli et al., 2015). Eventually, years of HWA feeding lead to a depletion of resources and accelerated host decline (Wilson et al., 2018). HWA also reduces regeneration of Eastern Hemlock within affected stands (Preisser et al., 2011).

9.2 | Plant parasites

Eastern Hemlock is comparatively resistant to stem decaying fungi (Hepting, 1971; Table 3). However, *Tyromyces borealis* (Fr.) Imazeki (Basidiomycota, Polyporales) attacks the heartwood of Eastern Hemlock (Hepting, 1971). *Pholiota adiposa* (Batsch) P. Kumm. (Basidiomycota, Agaricales) also affects dead wood (Hepting, 1971). *Stereum sanguinolentum* (Alb. & Schwein.) Fr. (Basidiomycota, Russulales) forms brown rot not only on dead wood, particularly in spruces and Douglas-fir but also Eastern Hemlock; *Porodaedalea pini* (Brot.) Murrill (=*Phellinus pini* (Brot.) Bondartsev & Singer) causes red ring rot of heartwood, while the Hemlock Varnish Shelf *Ganoderma tsugae* Murrill (Basidiomycota, Polyporales) is the most common decomposer of stumps and old logs (Godman & Lancaster, 1990).

Baird, Stokes, Wood-Jones, Watson, et al. (2014) isolated 124 fungal taxa across 23 genera from Eastern Hemlock roots in North Carolina, including mycorrhizal and saprobic taxa. The most common genera were mostly ectomycorrhizal Basidiomycota: *Piloderma* (Atheliales) in 8.2% of sequenced fungal samples, *Russula* (Russulales) 6.8%, *Tomentella* (Thelephorales) 4.0% and *Clavulina* (Cantharellales) 2.9%. *Meliniomyces* (Ascomycota, Heliotales) were also common in 3.4% of samples. Ninety-seven of the taxa identified occurred at <1% of relative abundance. The most frequent Ascomycota species were *Meliniomyces variabilis* Hambleton & Sigler sp. nov. (Heliotales) in 22.6% of samples, *Cladophialophora chaetospira* (Grove) Crous & Arzanlou (Chaetothyriales) 16.1% and *Phialocephala fortinii* C.J.K. Wang & H.E. Wilcox (Heliotales) 9.7%.

Several epiphytes have been identified on Eastern Hemlock. However, in the Adirondacks of New York, Eastern Hemlock had fewer lichen species (12) than did deciduous trees (23–31), while

TABLE 3 Fungi (by phylum and order) associated with *Tsuga canadensis*.

Species classification	Ecological notes	Source
Ascomycota		
Capnodiales		
Dimerosporium tsugae Dearn	Sooty mould on needles	3
Diaporthales		
Sirococcus tsugae Castl., D. F. Farr & Stanosz	Common on conifers; recorded on Eastern Hemlock in Maine in 2009 and Georgia in 2010	4, 7
Heliotales		
Fabrella tsugae (Farl.) Kirschst.	Needle blight of hemlocks	1
Rhizothyrium abietis Naumov	Needles; normally on *Abies balsamea*	6
Xylariales		
Rosellinia herpotrichioides Hepting & Davidson	Needle browning on lower branches	2, 3
Basidiomycota		
Agaricales		
Armillaria calvescens Bérubé & Dessur.	Rare on Eastern Hemlock	5
Armillaria gallica Marxm. & Romagn.	Common on Eastern Hemlock	5
Armillaria gemina Bérubé & Dessur.	Rare on Eastern Hemlock and other conifers	5
Armillaria mellea (Vahl) P. Kumm.	Rarely kills Eastern Hemlock	1, 5
Armillaria ostoyae (Romagnesi) Herink	Very common on Eastern Hemlock	5
Hymenochaetales		
Fomitiporia robusta (P. Karst.) Fiasson & Niemelä	White rot	3
Porodaedalea pini (Brot.) Murrill	Common in conifers; sapwood and heartwood rot	3
Polyporales		
Phaeolus schweinitzii (Fr.) Pat.	Rarely kills Eastern Hemlock	1
Postia balsamea (Peck) Jülich	Rarely kills Eastern Hemlock	1
Pucciniales		
Melampsora abietis-canadensis C.A. Ludw.	Rust of needles	1
Melampsora farlowii (Arth.) Davis	Rust of needles, twigs, cones	1
Naohidemyces vaccinii (Alb. & Schwein.) S. Sato, Katsuya & Y. Hirats	Hemlock Blueberry Rust; causes early needle drop	1, 7
Pucciniastrum hydrangeae (Magn.) Arth.	Rust of needles	3
Russulales		
Heterobasidion annosum (Fr.) Bref.	Rarely kills Eastern Hemlock	1

Sources: 1. Godman and Lancaster (1990); 2. Hepting and Davidson (1937); 3. Hepting (1971); 4. Stanosz et al. (2011); 5. Brazee and Wick (2011); 6. Darker (1965); and 7. Munck et al. (2018).

numbers increased southwards and had doubled on all trees at the Southern Blue Ridge, North Carolina location (Schmitt & Slack, 1990). Two lichens (Ascomycota, Lecanorales) were common to both areas: *Parmelia squarrosa* Hale and *Usnocetraria oakesiana* (Tuck.) M.J.Lai & J.C.Wei (=*Tuckermannopsis oakesiana* (Tuck.) Hale). Epiphytic bryophytes were also lowest on Eastern Hemlock compared to co-occurring trees, attributed to the acidic bark, decreasing from 13 species in the north to 8 in the south. The mosses *Dicranum montanum* Hedw. (Bryophyta, Dicranales) and *Hypnum pallescens* (Hedw.) P.Beauv. (Hypnales) were found on most hemlocks in both regions, and the liverwort *Bazzania trilobata* (L.) Gray (Marchantiophyta, Jungermanniales) was also common, especially on larger trees (Schmitt & Slack, 1990).

Everhart et al. (2008) recorded 17 species of Myxomycetes on the bark of Eastern Hemlock at the southern end of the Appalachians, which was intermediate in number compared to other woody plants investigated (10–38 species of Myxomycete) despite Eastern Hemlock bark being the most acidic (pH 4.1). Only *Cribraria minutissima* Schwein. (Mycetozoa, Cribrariales) and *Paradiacheopsis acanthodes* (Alexop.) Nann.-Bremek. [=*Comatricha acanthodes* Alexop.] (Stemonitidales) were restricted to Eastern Hemlock.

9.3 | Plant diseases

Several species of *Armillaria* (Basidiomycota, Agaricales; Table 3) are frequently associated with Eastern Hemlock, but none are known to cause significant decay or mortality (Hepting, 1971). The most damaging pathogen on Eastern Hemlock is *Sirococcus tsugae* Castl., D.F. Farr & Stanosz (Ascomycota, Diaporthales), the most widely distributed and frequently observed pathogen in Maine (Munck et al., 2018). In Georgia, as many as 70% of shoots have been seen to be infected; shoots from the previous year lose needles, and in the spring and summer, current year shoots become infected showing dead and dying needles (Stanosz et al., 2011). *Sirococcus tsugae* was first reported in western North America on *Tsuga heterophylla*, *T. mertensiana*, *Cedrus atlantica* and *C. deodara*, but has now reached Eastern Hemlock (Rossman et al., 2008). It has also been introduced into Europe, being recorded in the United Kingdom, Belgium and Germany from 2014 (Butin et al., 2015; Pérez-Sierra et al., 2015; Schmitz et al., 2018) where it causes aesthetic disfigurement but low mortality of *Cedrus atlantica* and a number of other conifers, including *Tsuga* species.

Pathogenic rusts (Basiomycota, Pucciniales) attacking Eastern Hemlock were identified in the early 20th century, including *Peridermium* sp., *Melampsora farlowii* (Arthur) Davis (=*Necium farlowii* Davis), and *Melampsora abietis-canadensis* (Farl.) Ludw. (=*Caeoma abietis-canadensis* Farl.) on needles and *Peridermium fructigenum* Arthur on cones and twigs (Spaulding, 1911).

10 | HISTORY

The fossil record of *Tsuga*, including lignified wood, leaves, seeds, pollen and seed cones, indicates that the genus was widely distributed across North America and Eurasia from the Late Cretaceous to the late Tertiary (Kirchheimer, 1934; Lepage, 2003; Wang et al., 2015) leading to a current disjunct distribution in North America and Asia and the appearance of *T. canadensis* in the Oligocene (Havill et al., 2008).

Eastern Hemlock was an important tree in the early Holocene; *Tsuga* pollen reached 10%–40% of total pollen counts along the eastern seaboard of North America (McAndrews & King, 1976). A small number of Pleistocene glacial refuges have been suggested in the southeast United States, with subsequent postglacial movement into the northeast and the Great Lakes region (Davis, 1983; Potter et al., 2012). Eastern Hemlock was one of the last tree species to migrate into the western Great Lakes region, extending its range across Michigan *c*. 7000–5400 years BP and into Wisconsin, and then expanded rapidly in the region from *c*. 6500 to 5500 years BP at a time of increasing precipitation and winter temperature, followed by a sudden decline within the last 1000 years (Calcote, 2003; Davis et al., 1986; Maenza-Gmelch, 1997; Parshall, 2002). Eastern Hemlock colonised a 50 000 km^2 area of northern Michigan between 6000 and 5000 years ago, extending its range northwards at a mean rate of 20–25 km per century, along with *Fagus grandifolia* (Davis, 1989).

Palynological data show that Eastern Hemlock underwent several short-duration declines in the Holocene *c*. 9500–6000 years BP, followed by a particularly significant decline in the mid-Holocene, *c*. 5500 years BP that was synchronous across eastern North America. (Smyth et al., 2015; Zhao et al., 2010). The first decline is attributed to the effects of drought on this moisture-sensitive tree (Fuller, 1998; Oswald & Foster, 2011) and the main decline was caused by a combination of insect-driven defoliation (which is likely to have been exacerbated by the stress of climatic change), decreasing winter temperature, precipitation lower than it is currently and localised reductions in water-table depth (Bennett & Fuller, 2002; Booth et al., 2012; Calcote, 2003; Foster et al., 2006; Haas & McAndrews, 2000). In a number of areas, there is a strong link between Eastern Hemlock decline and the remains of hemlock needles with chewing damage typical of the Hemlock Looper *Lambdina fiscellaria* (Lepidoptera, Geometridae) and head capsules of the Looper and the Spruce Budworm *Choristoneura fumiferana* (Lepidoptera, Torticidae) (Bhiry & Filion, 1996). However, *L. fiscellaria* remains are not universally found to match hemlock decline in pollen records (Oswald et al., 2017), suggesting a combination of causes. Pollen records in northern Michigan indicate that the boundaries between patches of different communities have changed little since their formation about 3200 years ago (Davis et al., 1993).

Following the main decline, hemlock recovered to its maximum extent after 300–1200 years in the north and at higher elevations as July temperature and precipitation increased (Calcote, 2003; Foster & Zebryk, 1993; Parshall, 2002). At the same time, small, scattered populations of Eastern Hemlock extended west beyond the previous range during wetter periods (Parshall, 2002). Further south, however, pollen records are characterised by a stair-step pattern of progressive decline (Foster et al., 2006; Oswald & Foster, 2011).

In pre-settlement times, fire-sensitive species such as Eastern Hemlock and *Picea rubens* were commonest in low, moist areas, and *Quercus rubra* and *Castanea dentata* dominated the drier exposed areas (Cogbill et al., 2002; Foster & Zebryk, 1993; Hall et al., 2002; Parshall & Foster, 2002; Whitney, 1990), although this would have been affected to some degree by land management by Native American populations (McLachlan et al., 2000). Agricultural expansion due to European settlement around 1700, which resulted in >80% open land in central New England in the early 1800s (Foster, 1992), led to a decline in Eastern Hemlock and other major tree genera such as *Pinus*, *Quercus* and *Fagus* (Maenza-Gmelch, 1997; Thompson et al., 2013). But following agricultural abandonment from the mid-1800s, losses of *Castanea dentata* from chestnut blight from 1910, extensive timber extraction and periodic drought, the forest canopy became dominated by Eastern Hemlock and a variety of hardwood species (Ellison et al., 2014; Foster et al., 1992; Whitney, 1990). Eastern Hemlock increased in frequency and abundance; basal area increasing >400% over the 60 years since 1934–1935, stem density increasing from 13 to 71 stems/ha, especially near streams, in the Southern Appalachians, and to >1100 stems/ha in Massachusetts (Elliott & Swank, 2008; McLachlan et al., 2000). However, the forest structure is still very different from the pre-settlement forest, with many formerly common species, such as *Acer saccharum*, *Fagus grandifolia* and *Castanea dentata* less common than they were (Ellison et al., 2014; Foster et al., 1992; Thompson et al., 2013). Moreover, due to extensive browsing by white-tailed deer (Section 4) quick-growing, shade-intolerant sprouting species, such as *Prunus serotina* and *Acer rubrum*, have expanded (Whitney, 1990). Some old-growth stands still exist, restricted usually to steep, inaccessible places, aided by the low value of their timber (Section 10.1).

The name 'hemlock' comes from leaves and branches resembling the European poisonous Hemlock *Conium maculatum* (Jenkins, 1946); hence, it was called Hemlock-spruce then Hemlock. *Tsuga* is derived from the Japanese words for 'tree' and 'mother'.

10.1 | Uses

Eastern Hemlock wood has historically had limited market value due to several deficiencies including brittleness, proneness to swelling, abundant ring-shakes (the lengthwise separation of wood between and parallel to annual growth layers), low resistance to decay and a tendency to split radially when drying (Baumgras et al., 2000; Brown & Sendak, 2006; Scheffer & Morrell, 1998; Wilson, 1962). Indeed, Eastern Hemlock timber is 'inferior… in almost every aspect' to *Tsuga heterophylla* (Swartley, 1984). It is, however, used for pulpwood, although the short fibres limit this to newsprint rather than premium products (Foster, 2014). Other low-grade uses include fences, pallets, studs, boards, railway sleepers, post and beam house frames, firewood and landscape timbers and mulch (Frothingham, 1915; Gardner & Diebel, 1995; Hough, 1960; Rogers, 1978). There is growing interest in Eastern Hemlock being used in cross-laminated timber construction (Kaboli et al., 2020).

Native people in eastern Canada have used the twigs and bark of Eastern Hemlock to make a medicinal tea and, with the needles, as a source of vitamin C. Resin is also used for topical ailments (Arnason et al., 1981). The Micmac people have been recorded as using the bark for dye, and grating and eating the inner bark as a famine food (Speck & Dexter, 1951). Eastern Hemlock bark was extensively used for tanning leather due to it having 7%–12% naturally occurring tannins (Ellingson et al., 2019; Garr & Éwe, 1920; Rogers, 1978). By 1879, hemlock bark was used more for tanning than oak and chestnut combined (McMartin, 1992). Needles have been collected for use as soft animal bedding (Foster, 2014).

Acetone extracts of cones have antioxidant and antibacterial properties against strains of *Staphylococcus aureus* Rosenbach (Bacillota, Caryophanales) and *Escherichia coli* (Migula) (Pseudomonadota, Enterobacterales), attributed to kaempferol glycosides, particularly kaempferol-O-rutinoside (Hofmann et al., 2021). Oil extracts have been used as an antiseptic (Garr & Éwe, 1920) and the terpenes act as anti-inflammatories and have traditionally been used to treat rheumatism (Craft & Setzer, 2017).

Described as an attractive tree, Eastern Hemlock has been widely planted, but with the growing impact of HWA, it may be replaced in urban landscapes by the resistant *Tsuga chinensis* (Dampier et al., 2015; Harper & Weston, 2016). Eastern Hemlock bark is still widely used as landscape mulch (Howard et al., 2000).

11 | CONSERVATION AND MANAGEMENT

Eastern Hemlock was globally classified as Near Threatened in 2011, having moved from Least Concern in 1998, including in the United States and Canada (Farjon, 2013; WCS Canada, 2023), primarily due to the threat of HWA but made more complex by other issues. For example, in Minnesota, Eastern Hemlock has formed small disjunct populations for at least 1200 years but is currently listed as Endangered (Minnesota Department of Natural Resources, 2013). It has always been climatically limited here but has declined further because of fire, logging, poor regeneration and browsing predation to the extent that in 2008 there were <50 mature trees of natural origin (i.e. not planted) together with scattered saplings and seedlings (Smith, 2008).

An allozyme study by Zabinski (1992) found little genetic variation across the range of Eastern Hemlock, and an analysis of chloroplast DNA restriction fragment length polymorphisms (Wang et al., 1997) detected little differentiation among populations. Since Eastern Hemlock is an out-crossing, wind-pollinated tree with small seeds (Young & Young, 1992), it is likely to be an efficient disperser of genes within and between stands. However, disjunct populations of Eastern Hemlock are generally less genetically diverse than main-range populations, but some are more genetically differentiated or contain unique alleles (Potter et al., 2012). This suggests that ex situ conservation seed collections of Eastern Hemlock should be concentrated to the east of the southern Appalachians and in the high-elevation populations of the southernmost Appalachians in North Carolina, South Carolina and Tennessee where genetic diversity is greatest (Potter et al., 2008). In situ conservation efforts, particularly of small, disjunct populations, should concentrate on stopping an influx of planted trees which would dilute the genetic makeup of the original populations (Ellingson et al., 2018). These authors have identified eight microsatellite markers that may help identify indigenous individuals which can be propagated.

11.1 | Consequences of Eastern Hemlock loss

As a result of canopy thinning, primarily caused by HWA, more light reaches the forest floor (Ford et al., 2012; Orwig & Foster, 1998) and soil temperature increases (Cobb et al., 2006; Lustenhouwer et al., 2012; Orwig et al., 2008). These changes, combined with reduced water uptake by declining trees, lead to enhanced soil organic matter decomposition (Cobb et al., 2006; Fraterrigo et al., 2018; Ignace et al., 2018), increased nitrogen cycling and availability (Jenkins et al., 1999; Orwig et al., 2008, 2013; Yorks et al., 2003) and reduced soil respiration (Nuckolls et al., 2009). The presence of HWA itself can also affect the flow of nutrients from tree crowns to the soil. Adult adelgids secrete a protective waxy covering that is rich in C and N (Cobb & Orwig, 2008) and may deter other insects from feeding on it (Jones et al., 2012). The wax provides energy to fuel increased populations of bacteria, yeast and fungi, which then enhance the nutrient content of precipitation passing through infested canopies and falling to the soil (Stadler et al., 2005, 2006).

Long-term ecosystem consequences of hemlock loss include reduced carbon uptake initially and then a rapid increase and eventually higher uptake than intact hemlock stands over subsequent decades as early successional hardwood species replace hemlock (Albani et al., 2010; Crowley et al., 2016; Finzi et al., 2014; Krebs et al., 2017; Raymer et al., 2013). However, these studies also forecast an overall net loss of ecosystem carbon content after a century or more because it takes 20–40 years for the hardwood regrowth to reach the same standing crop that HWA removed and

the loss of hemlock growth that would have occurred during that time. In terms of carbon flux, individual declining Hemlock stands could transition from being carbon sinks to carbon sources depending on the timing and composition of replacement tree species (Ellison et al., 2018).

The new environment created by the loss of Eastern Hemlock is suitable for the establishment of tree seedlings and also ideal habitat for light-demanding herbs like *Carex* spp., shrubs such as *Rubus* spp. and a myriad of invasive species like Oriental Bittersweet *Celastrus orbiculatus*, Wineberry *Rubus phoenicolasius*, Japanese Barberry *Berberis thunbergii*, Japanese Stiltgrass *Microstegium vimineum* and Tree of Heaven *Ailanthus altissima* (Kizlinski et al., 2002; Small et al., 2005). Understorey species diversity, cover and richness often increase significantly with the loss of Eastern Hemlock (Eschtruth et al., 2013; Ford et al., 2012; Ingwell et al., 2012; Orwig et al., 2013).

Eastern Hemlock stands hold a unique assemblage of associated fauna, particular birds, arthropods and salamanders (Dilling et al., 2007; Mallis & Rieske, 2011; Mathewson, 2009; Rohr et al., 2009; Sackett et al., 2011; Tingley et al., 2002). Yamasaki et al. (2000) list 96 birds and 47 mammal species associated with Eastern Hemlock forests in northeast USA, of which 8 birds and 10 mammal species are strongly associated with Eastern Hemlock. The loss of this tree, particularly old-growth stands, will adversely affect many mammalian and bird species (Godman & Lancaster, 1990).

Due to its conical-shaped evergreen crown, Eastern Hemlock serves as important habitat for a variety of bird species (Benzinger, 1994), including many that are significantly more abundant in Eastern Hemlock than in hardwood forests. Species with the strongest affinity for Eastern Hemlock include Black-throated Green Warbler *Setophaga virens* (Gmelin), Blackburnian Warbler *D. fusca* (Müller), Acadian Flycatcher *Empidonax virescens* (Vieillot) and Solitary or Blue-headed Vireo *Vireo solitarius* (Wilson) (Benzinger, 1994; Howe & Mossman, 1995; Keller, 2004; Mitchell, 1999; Tingley et al., 2002). Observations show that several other species are strongly associated with Eastern Hemlock, including American Goshawk *Astur atricapillus* (Wilson, A.), Winter Wren *Troglodytes hiemalis* Vieillot, Black-throated Blue Warbler *Setophaga caerulescens* (Gmelin), Northern Parula *Setophaga americana* (L.), Red-breasted Nuthatch *Sitta canadensis* (L.) and Hermit Thrush *Catharus guttatus* (Pallas).

As hemlocks begin to decline due to HWA, avian changes occur rapidly. For example, there were 70% fewer breeding pairs of Acadian Flycatchers in riparian forests heavily infested with HWA in the Appalachian Mountains (Allen et al., 2009) and over a span of 16 years as Eastern Hemlock declined in Pennsylvania, the occupancy of Black-throated Green Warbler declined by 30% (Toenies et al., 2018). But it is not all losses. The abundance of Eastern Wood-pewee *Contopus virens* (L.), Brown-headed Cowbird *Molothrus ater* (Boddaert), Tufted Titmouse *Baeolophus bicolor* (L.), White-breasted Nuthatch *Sitta carolinensis* Latham, Red-eyed Vireo *Vireo olivaceus* (L.), Hooded Warbler *Wilsonia citrina* (Boddaert), due to the development of a dense hardwood understorey, and several woodpecker species was highest in forests with >60% Eastern Hemlock mortality in Connecticut (Tingley et al., 2002). In addition, Eastern Wood-pewee, Great-crested Flycatcher *Myiarchus crinitus* (L.) and Wood Thrush *Hylocichla mustelina* (Gmelin) benefitted from the increased number of dead hemlocks in Pennsylvania for the same reasons (Becker et al., 2008).

The Eastern Red-backed Salamander *Plethodon cinereus* Green was found to be equally abundant in Eastern Hemlock and mixed deciduous stands (Mathewson, 2009) but Cox et al. (2022) noted more than five times the relative density of several salamander species in stands in Tennessee treated with insecticides to control the demise of hemlock from HWA. Following the loss of Eastern Hemlock by HWA, the relative abundance of *P. cinerus* and Eastern Red-spotted Newts *Notophthalmus viridescens* (Rafinesque) is predicted to be significantly lower (Ochs & Siddig, 2017; Siddig et al., 2016).

Specialist communities of aquatic invertebrates and fish inhabit streams that flow through Eastern Hemlock stands would also be affected (Adkins & Rieske, 2015a, 2015b; Siderhurst et al., 2010; Snyder et al., 2002). Fish species such as the brook trout *Salvelinus fontinalis* (Mitchill) are likely to be negatively affected, at least in the short term due to the loss of thermal and water-level stability (Ford & Vose, 2007; Siderhurst et al., 2010). There would also be a loss of aquatic invertebrate and fish populations compared to mixed-hardwood forests (Snyder et al., 2002), although it is likely that a number of these communities may be unaffected (Sackett et al., 2011).

In addition to the compositional changes of streams associated with the loss of hemlock is the change in hydrological processes. It was found in New England that the first years of infestations and tree decline led to an increase in water yield as the trees took up less water (Kim et al., 2017). In the southern Appalachians, the opposite was true in riparian forests as Eastern Hemlock was replaced by species that utilised more water and subsequently resulted in lower yield (Brantley et al., 2015). The timing and magnitude of changes will depend on location, the composition and function of replacement species (Ellison et al., 2005).

With loss of Eastern Hemlock, there is also a loss of fungal and bacterial species (Fassler et al., 2019). Declining health of Eastern Hemlock was seen to reduce ectomycorrhizal colonisation by as much as 67% (Caruso & Horton, 2021; Vendettuoli et al., 2015). However, the diversity of higher plants may increase due to higher light levels, certainly in riparian areas (Martin & Goebel, 2013).

11.2 | Control of Hemlock Woolly Adelgid (HWA)

Eastern Hemlock has exhibited little or no resistance to HWA in natural populations (McClure, 1987) but the search continues for resistant trees and populations (Ingwell & Preisser, 2011; Kinahan, Grandstaff, et al., 2020). However, continued infestation is likely to cause a range-wide decline or elimination of this ecologically, culturally and economically important tree species. Cold temperatures are the only factor that can cause widespread mortality of HWA over broad areas. Laboratory studies show that HWA survival

significantly drops at temperatures below −25°C with no survival below−35°C (Parker et al., 1999; Skinner et al., 2003). However, cold hardiness of HWA has been found to vary significantly among populations with those further north adapting to survive colder temperatures (Lombardo & Elkinton, 2017). Moreover, cold hardiness has been found to vary from place to place and from year to year and indeed on the shorter-term, so the amount of cold needed to kill HWA will vary throughout a winter and between winters (Elkinton et al., 2017; MacQuarrie et al., 2024). It should also be borne in mind that HWA populations can recover rapidly from heavy mortality from winter cold events.

Field studies generally corroborate the relationship between cold winter temperatures and HWA mortality and suggest that the continued spread and eventual range of HWA are controlled by the timing and severity of winter temperatures (Cheah, 2017; McClure & Cheah, 2002; Paradis et al., 2008). More recent modelling by Ellison et al. (2018) and Cornelsen et al. (2024) suggests that HWA is likely to spread throughout almost the whole range of Eastern Hemlock, including the Maritime Provinces of Canada by the middle or the end of the century, depending upon warming scenarios.

There are, however, a variety of methods that can be employed to combat the HWA threat, including chemical, biological and silvicultural approaches, with the highest chance of success integrating as many approaches as possible (Mayfield et al., 2020).

Population densities of HWA can be controlled on ornamental hemlocks, in groves of trees and increasingly at larger scales by a variety of chemical insecticides (Mayfield et al., 2020). Foliar applications of horticultural oil or insecticidal soap are effective against HWA on accessible trees, but the procedure must be repeated often and is challenging to apply on large trees and in forests (McCarty & Addesso, 2019; McClure, 1987). Systemic treatments with neonicotinoid insecticides such as imidacloprid are absorbed by the plant and translocated by the xylem to the twigs where HWA feed and are considered most effective at controlling HWA (Mayfield et al., 2020), although they may affect populations of non-target invertebrates (Hakeem, 2008). During spring or autumn, the chemicals can be injected directly into the tree stem, applied to the soil beneath Eastern Hemlock trees or sprayed directly onto the stem surface (Limbu et al., 2018; Quinterno et al., 2023). There is evidence that some treatments have given protection from HWA for up to 7 years (Benton et al., 2016). For treating trees in sensitive aquatic habitats, direct stem injection should be used to minimise the risk to nontarget species.

Soil imidacloprid applications, including soil drenches, soil injections or time-release tablets (Mayfield et al., 2020) are considered more effective than stem injections (Cowles et al., 2006). Older trees and trees heavily infested with HWA can be treated with a trunk spray of another systemic neonicotinoid, dinotefuran, to quickly kill off HWA but because this chemical does not remain effective for more than a few months (Joseph et al., 2011), trees need to be treated with systemic chemicals for continued protection against HWA (Mayfield et al., 2020) or dinotefuran can be mixed with imidacloprid for a longer lasting impact (Limbu et al., 2018).

Biological control also offers possibilities. In eastern United States, where hemlocks have shown little resistance to HWA and where there are no effective native predators, control of this pest in forested situations across broad landscapes is difficult and relies on a variety of insect predators from Asia and northwest USA (Mayfield III, Bittner, et al., 2023). These biological control agents have been the major focus of a coordinated effort of federal and state agencies, university scientists and private industries since 2001 to develop research, management approaches and technology transfer to help stop the spread of HWA (Onken & Reardon, 2011). Numerous types of predators have been introduced in eastern North America with varying levels of success including Coleoptera (Coccinellidae and Derodontidae) and Diptera (Chamamyiidae) (Mayfield III, Bittner, et al., 2023).

Several beetles have been introduced to combat HWA, including *Sasajiscymnus tsugae* Sasaji & McClure and several *Scymnus* species (Coleoptera, Coccinellidae). *Sasajiscymnus tsugae* from Japan was first released in 1995 in Connecticut (Cheah & McClure, 1996; McClure & Cheah, 1999) and over 3.4 million individuals have been subsequently released in eastern USA (Mayfield III, Bittner, et al., 2023). While this predator was effective in feeding on HWA in Japan, there is no field evidence to show that it has established successfully or provided any control of HWA in North American forests, and it is no longer a focus of management (Mayfield III, Bittner, et al., 2023). Since the late 1990s *Scymnus sinuanodulus* Yu & Yao and *S. ningshanensis* Yu & Yao beetles from China have been reared and released in eastern forests but they have not established independent populations and are no longer being reared. *Scymnus camptodromus* Yu & Liu, also from China, is still being considered for future rearing and potential release (Mayfield III, Bittner, et al., 2023).

Laricobius predatory beetles (Coleoptera, Derodontidae) specialise in adelgids, and *L. nigrinus* Fender from western North America and *L. osakensis* Shiyake & Montgomery from Japan have been the major species studied and released in eastern North America, including Canada (Mayfield III, Bittner, et al., 2023; Parks Canada, 2025). *Laricobius nigrinus* adults actively feed on developing adelgid sistens nymphs during winter, and over 360,000 have been released into eastern forests since the early 2000s (Mayfield III, Bittner, et al., 2023). Unlike other biocontrol agents released for HWA, *L. nigrinus* has dispersed and become widely established at many southeast USA locations (Foley et al., 2019; Jubb et al., 2021) and in some northern areas (Crandall et al., 2023; Mausel et al., 2011). Predator establishment and abundance are so high in some locations that they are being collected and redistributed to other locations (Mayfield III, Bittner, et al., 2023). Hybridisation between *L. nigrinus* and the eastern *L. rubidus* LeContre has been documented, and the rates have been stable over time (Mayfield III et al., 2015; Wiggins et al., 2016). Establishment and recovery are key elements in a successful biocontrol programme, and while there is evidence that the presence of *L. nigrinus* has led to improved branch growth (Preston et al., 2023), there has not yet been field proof that *Laricobius* predators are improving hemlock tree health. Since 2012, over 76,000 *L. osakensis* have been released into eastern North America and that has led to the establishment of populations, and the collection and

redistribution of adults to additional locations (Mayfield III, Bittner, et al., 2023). It is too early to document the impact of this predator on HWA populations or Eastern Hemlock health (Toland et al., 2018).

A new advance in the battle to control HWA is the use of silver flies *Leucotaraxis argenticollis* (Zetterstedt) and *L. pineperda* (Malloch) (Diptera, Chamaemyiidae), originating from the Pacific Northwest of North America (Mayfield III, Bittner, et al., 2023) which feed on both the overwintering and the summer generations of HWA (Kohler et al., 2008). Genetic investigations have shown that these flies have distinct lineages specific to different adelgid prey on different hosts in western versus eastern North America. (Havill et al., 2018). The use of *Leucotaraxis* spp. combined with other biocontrol agents ensures that both generations of HWA will be fed on, which should further reduce HWA populations, as otherwise HWA can recover rapidly following even large reductions in the spring generation (Crandall et al., 2020).

Another potential type of biocontrol agent being investigated to diminish HWA populations is the use of entomopathogenic fungi (Limbu et al., 2018). These naturally occurring fungi can penetrate the cuticle of HWA, deplete their nutrients and kill them. The fungi then release spores from the dead host to infect and kill additional HWA. Reid et al. (2010) identified 20 fungal genera and 79 entomopathogenic isolates from HWA on hemlocks in eastern North America, and *c*. 5 insect-killing fungal species associated with HWA have been identified (Gouli et al., 2013; Reid et al., 2010). These have exhibited up to 82% HWA mortality on individual branches (Gouli et al., 1997). Applications of fungi are most effective during late summer and autumn when HWA are without their protective wool (Parker et al., 2004). An increase in naturally occurring fungal entomopathogens associated with abnormally high rainfall is believed to have contributed to a regional decline in HWA abundance in northeast USA during 2018–2019 (Chandler et al., 2022).

Recent research has investigated silvicultural treatments to increase sunlight on residual Eastern Hemlock trees in the hope of reducing HWA impacts and increasing hemlock vigour (Mayfield III, Jetton, et al., 2023). This is based on several findings that unshaded hemlocks had lower HWA survival than shaded trees due to increased mortality of summer aestivating sistens (Brantley et al., 2017; Hickin & Preisser, 2015; McAvoy et al., 2017). Several studies have also shown that Eastern Hemlocks growing in created canopy gaps had an increase in growth such as new shoot production, basal area increment, and crown area and a decrease in foliage transparency compared to unreleased control trees (Fajvan & Hille, 2023; Mayfield III, Jetton, et al., 2023; Miniat et al., 2020). Findings suggest that small canopy gaps improve the physiological tolerance of Eastern Hemlock to HWA but maintained adelgid populations, which if combined with biological control may provide a more stable source of prey for predators (Mayfield III, Jetton, et al., 2023).

Successful biocontrol efforts will require an array of predators that attack all life stages of HWA to reduce their populations to nondamaging levels (Onken & Reardon, 2011). Future work integrating silviculture, biocontrol and chemical control efforts is needed to continue to protect Eastern Hemlock from HWA impacts. Some progress has been made in cloning individuals that are potentially HWA-resistant (Kinahan, Grandstaff, et al., 2020). Moreover, since *Tsuga chinensis* has proven to grow vigorously in eastern North America and to be very resistant to HWA, it may be a suitable replacement in managed landscapes (Weston & Harper, 2009).

11.3 | Climate change

Dunckel et al. (2017) modelled the future climate in Maine and concluded that the mean maximum and minimum temperature (30 year means up to 1990) of 10.8 and −0.3°C, respectively, would change by 2050 to a maximum of 12.6–12.9°C and a minimum of 1.1–1.5°C. Precipitation, with a historic annual mean of 1155 mm, would rise to 1172–1260 mm by 2050. They concluded that by 2050 the northern distribution of Eastern Hemlock will move north by 170 km but will be more thinly spread across the landscape with fewer pure stands. Despite the projected increase in annual precipitation, there will probably be more periods of drought; as noted in Section 8.4, Eastern Hemlock seeds and seedlings are particularly sensitive to drought, likely leading to reduced establishment. The winter survival of Hemlock Woolly Adelgid (HWA; Sections 4.1 and 9.1.1) is likely to increase due to warmer temperatures (Dukes et al., 2009) and is projected to spread north beyond the state of Maine by 2050.

Prasad and Potter (2017) concluded that the overall distribution of Eastern Hemlock in North America will decrease and will be largely restricted to cool and moist habitats. However, the responses of Eastern Hemlock to climate change, to pollution in the form of acid deposition and to HWA are likely to be more complex when considered together; so the future viability and distribution of Eastern Hemlock is uncertain (Rayback et al., 2020; Wilder & Boyd, 2016).

Forest composition is likely to alter, with hardwood species replacing Eastern Hemlock (Catovsky & Bazzaz, 2000; Cook & Williams, 2011; Davis, 2008; Kizlinski et al., 2002; Orwig & Foster, 1998), and this will result in increased water loss from the site (Section 6.5) and reduced carbon fixation. Hadley and Schedlbauer (2002) estimated that annual carbon storage was 3.0 $Mg\,ha^{-1}$ in Massachusetts in a stand where Eastern Hemlock made up 83% of above-ground biomass. This is higher than for younger coniferous and deciduous forests in the northeast, and so a decline in Eastern Hemlock density will likely lead to significantly less carbon storage.

12 | GLOBAL HETEROGENEITY

Genetic diversity of secondary stands in Massachusetts was found to be not significantly different from that of primary stands. Mean allelic richness across all populations was 6.051, while expected heterozygosity H_s was 0.784 and observed heterozygosity H_O was 0.806 (Lumibao et al., 2016). The overall population genetic differentiation was low, as expected in a wind-pollinated tree with wind-dispersed seeds. Genetic diversity of secondary populations appears

to recover rapidly with no founder effect (Lumibao et al., 2016), which has implications for the establishment and naturalisation of Eastern Hemlock around the world.

Although Eastern Hemlock shows comparatively low levels of genetic diversity across its natural range (Section 11), there is some variation. In the southern part of its range, Potter et al. (2008) found a low level of allozyme variation, as measured by the per cent of polymorphic loci (41.1–52.6), a low mean number of alleles per locus (1.32–1.74) and an expected heterozygosity of 0.044–0.083. The inbreeding coefficient F_{IS} was 0.363–0.457, indicating the likely presence of inbreeding within the Eastern Hemlock populations tested (Potter et al., 2008). Shamblin et al. (2008) identified a mean of 5.9 alleles per locus (range 2–14) and observed heterogeneity of 0.45 (range 0.14–0.73) in North Carolina.

Moreover, nuclear microsatellite molecular markers from 58 Eastern Hemlock populations showed four genetic zones within its native range. The north-central zone had larger trees (average diameter 26.9 cm) and comparatively high seedling numbers (1.25/100 m^2) but overall high mortality (7.8%). The northeast zone had smaller trees (8.6 cm), more seedlings (2.51/100 m^2) and lower mortality (4.7%). The warmer southeast and southwest zones had the smallest trees (<7.5 cm) and similar mortality to the northern zones, but the lower altitude southwest zone had the highest number of seedlings (3.94/100 m^2) and was also the most genetically diverse, presumed to be due to it being nearest the likely glacial refugia (Prasad & Potter, 2017). However, even in the southeast, Eastern Hemlock had considerably lower genetic diversity than other conifers (Potter et al., 2008). Heterozygosity of Eastern Hemlock was measured at 0.072 compared to the average of 0.176 across 103 allozyme studies in other species of Pinaceae, while 57.9% of Eastern Hemlock loci were polymorphic, compared to 73% in the other Pinaceae (Hamrick & Godt, 1996). Eastern Hemlock also had lower expected heterozygosity values than *Tsuga mertensiana* (0.087) and *T. heterophylla* (0.142) in British Columbia (Ally et al., 2000; Wellman et al., 2003).

Based on this, it seems that the genetic diversity of all the populations of Eastern Hemlock introduced outside of its native range is limited and will be responding to climatic conditions in a similar way as in its native range.

AUTHOR CONTRIBUTIONS

Peter A. Thomas conceived the idea for this account; Peter A. Thomas and David A. Orwig contributed written material, and both contributed critically to the drafts and gave final approval for publication.

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This study does not include data.

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