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EASTERN HEMLOCK DECLINE AND PERSISTENCE OF DISJUNCT POPULATIONS NEAR ITS SOUTHERN BOUNDARY

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ABSTRACT

Eastern hemlock (*Tsuga canadensis*) is a long-lived, shade tolerant tree species that sometimes occurs in pure stands on lower slopes and stream valleys of Appalachian forests in eastern North America. The range of eastern hemlock extends from southern Quebec and Ontario southward to Georgia and along the Cumberland Plateau to Alabama. Eastern hemlock is currently being threatened by the hemlock woolly adelgid (*Adelges tsugae*), a defoliating insect. The decline of eastern hemlock is consistent with the contagion hypothesis of range collapse, and disjunct eastern hemlock populations near the southern boundary of the species may not be extirpated because of their geographic isolation.

INTRODUCTION

Geographic ranges of organisms are dynamic, and range features (e.g. size and shape) are the results of organism characteristics and complex interactions with the surrounding environment both past and present (Brown *et al*., 1996; Channell and Lomolino, 2000a). The abundant-center distribution is a longstanding theory in biogeography. The theory is based on the assumption that a species' range should contain more favorable habitat near the center where populations should be larger and less variable (Sagarin and Gaines, 2002). Habitat quality is assumed to decrease with increasing distance from the core where populations should become more fragmented (Brown, 1984; Channell and Lomolino, 2000b). The demographic hypothesis of range collapse is based on the abundant-center distribution theory and assumes when extinction forces arise, a species' range should implode and the last populations should persist near the core of the historic distribution. The demographic hypothesis also assumes that population size influences extinction, which is not always true. A number of plant and animal species (e.g. American chestnut (*Castanea dentata* (Marsh.) Borkh.) and California condor (*Gymnogyps californianus* Shaw)) now exist only at the periphery of their former ranges because of the spatial dynamics of the particular extinction force rather than population density.

Extinction factors often move across the landscape like a contagion. When such movement occurs, the last location impacted should be the most isolated from the initial location of the extinction force, regardless of the point of origin (Lomolino and Channell, 1995, 1998; Channell and Lomolino, 2000b). Extinction factors that move in such a manner are generally transferred through anthropogenic activities such as the introduction of alien pests (Lomolino and Channell, 1995). Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is currently facing an extinction force in the hemlock woolly adelgid (*Adelges tsugae* Annand; HWA) and may become another species restricted largely to the periphery of its current range. The decline of eastern hemlock attributed to HWA is unique because the spatial dynamics of extirpation can be observed and documented as they occur.

Eastern hemlock decline within the core of the species' range has been widely documented by independent studies (e.g. Orwig *et al*., 2002; Ellison *et al*., 2005; Lovett *et al*., 2006). However, dispersal of the HWA to disjunct eastern hemlock populations has not been discussed. This void in the literature may be the result of the complex nature of range collapse dynamics that are difficult to empirically test. Here, using field observation, eastern hemlock and HWA literature, and current biogeographic theory, I present the hypothesis that eastern hemlock populations removed from the contiguous range of the species may not become infested. I focus on disjunct eastern hemlock populations near the southern range boundary of the species.

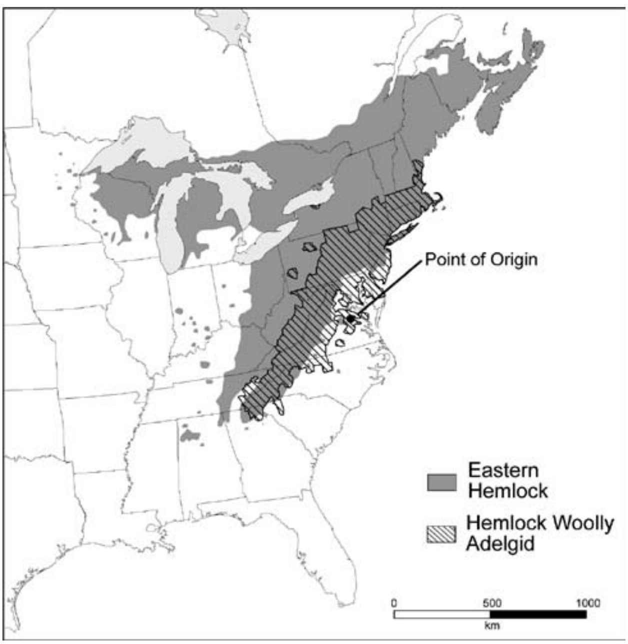

Figure 1. Range of eastern hemlock and the hemlock woolly adelgid in eastern North America (from Little 1971 and U.S.D.A. 2006).

EASTERN HEMLOCK AND THE HEMLOCK WOOLLY ADELGID

Eastern hemlock is a long-lived, shade tolerant species that sometimes occurs in almost pure stands on lower slopes and stream valleys of Appalachian forests in eastern North America. Eastern hemlock modifies microclimatic and pedologic characteristics of inhabited sites and is considered a keystone species (Orwig *et al*., 2002; Ellison *et al*., 2005). The range of eastern hemlock extends from southern Quebec and Ontario southward to Georgia and along the Cumberland Plateau to Alabama (Fig. 1). Disjunct populations are present in southern Michigan, western Ohio, southern Indiana, Kentucky, Tennessee, Alabama, Georgia and east of the Appalachian Mountains. Characteristics of many disjunct populations have been documented, including those in southern Indiana (Friesner and Potzger, 1944), Alabama (Segars et al., 1951; Harper, 1952; Hart and Shankman, 2005), Georgia (Bormann and Platt, 1958) and North Carolina (Oosting and Hess, 1956).

Currently, eastern hemlock is threatened by the defoliating HWA. The HWA is a small, aphid-like insect native to Japan that was first documented in eastern North America near Richmond, Virginia in the 1950s (Souto *et al*., 1996). The HWA has spread from the central Appalachian Mountains and now occurs in the northern and southern range of eastern hemlock (Fig. 1). The adelgid feeds on ray parenchyma of newly developed twigs, causing needle loss and eventually tree mortality (Young *et al*., 1995). The HWA has infested and killed eastern hemlock in all size and age classes. It has been hypothesized that eastern hemlock could functionally disappear from eastern forests over the next several decades because the species does not generally re-establish after mortality caused by the HWA and is being replaced throughout its range by mixed hardwoods and sometimes *Rhododendron* species in the south (Ellison *et al*., 2005). The loss of eastern hemlock is predicted to have long-term impacts on ecosystem structure and function (Lovett *et al*., 2006). The adelgids are parthenogenetic and reproduce rapidly (twice annually) (McClure, 1989a). They are mainly transported by wind, but also by birds and mammals, including humans (McClure, 1989b, 1990). The HWA is currently dispersing in a diffuse pattern through the contiguous range of eastern hemlock at *ca*. 30 km $year^{-1}$. The dispersal and impacts of the HWA through the contiguous range of eastern hemlock illustrate the contagion hypothesis defined by Lomolino and Channell (1995) and Channell and Lomolino (2000a, 2000b).

In the northern section of its range, eastern hemlock typically occurs in almost pure stands with sparse understories. In the southern section of its range, eastern hemlock typically occurs in mixed stands in riparian zones and in moist protected coves (Ellison *et al*., 2005; Shankman and Hart, 2007). Although in the southern portion of its range eastern hemlock is not ubiquitous across the landscape but is largely confined to riparian areas, populations are not widely scattered and are linked by valleys created by the well-developed stream networks of the unglaciated Appalachian Highlands.

In specific locations, the advancement of the HWA through the northern range of eastern hemlock has been slowed by cold temperatures. Winter temperatures below -30 °C have led to high mortality of HWA, but populations have quickly recovered and HWA may eventually develop resistance to cold as northward migration continues (Parker *et* *al*., 1998, 1999). In general, HWA dispersal has proceeded unimpeded. The HWA is also advancing through the southern range of eastern hemlock. Near its southern range boundary, eastern hemlock occurs in isolated populations disjunct from the contiguous range. These populations are confined to deeply incised stream valleys and are more widely scattered across the landscape relative to populations within the contiguous boundary. Disjunctions at its southern extent have been shown to be reproductively viable and stable populations that provide the same ecosystem functions as elsewhere in its range (Hart and Shankman, 2005).

SOUTHERN RANGE OF EASTERN HEMLOCK

Once the HWA reaches the southern boundary of the contiguous range of eastern hemlock, diffuse dispersal will cease because the HWA is host specific to *Tsuga*. In many cases, long distances separate disjunct eastern hemlock populations from the contiguous range. For the adelgid to infest outlying populations at eastern hemlock's southern boundary in Tennessee, Alabama, and Georgia, it must colonize new sites via jump dispersal over long distances. For example, disjunct populations at the southernmost boundary of eastern hemlock in Alabama are separated from the contiguous range by *ca*. 300 km. Also, gaps exist in the presence of disjunct populations near its southern boundary as eastern hemlock is largely absent from north-central Alabama for reasons that have yet to be explained. The spatial pattern of eastern hemlock occurrence near its southern boundary will not foster jump dispersal or "island hopping" of the HWA from one population to another until the southernmost extent is reached. The unfavorable habitat (i.e. lack of eastern hemlock) between the contiguous range and the disjuncts at the boundary may require the HWA to follow the sweepstakes mode of dispersal (i.e. long distance dispersal with low probability of success) to reach the full southern range of its host.

The HWA is a sessile insect which spends most of its life attached to its host plant. However, there are a few days between egg hatch and the initiation of feeding when nymphs actively move about their host. The nymphs are light in weight and can be carried by wind over great distances (McClure, 1989a). Because the nymphs are pagile (i.e. passively distributed), their dispersal is dependent upon wind speed and direction at the time of their activity, which is generally in the spring. Many disjunct populations of eastern hemlock occur to the south and west of the species' contiguous range. The dominant winds in the southeastern United States are westerlies and would not favor the transport of HWA to the disjunct populations to the south or west. Rare, severe wind events such as those associated with tornadoes or extreme low pressure systems have the potential to transport HWA over great distances. In the southeastern United States, tornadoes are common with the majority occurring in March and April. However, these storms generally follow directional paths to the northeast (Suckling and Ashley, 2006). Thus, most tornadoes in the region move from the periphery towards the contiguous range of eastern hemlock, and would likely not facilitate the long-distance dispersal of HWA to outlying populations.

Not only are disjunct eastern hemlock populations separated from the contiguous range by long distances, but they are also quite small. Some of these populations consist of less than 30 total individuals with as few as five trees that occupy positions in the forest canopy (Hart and Shankman, 2005). Only a small fraction of the regional landscape supports eastern hemlock. Thus, these disjunct populations represent small islands or target areas for HWA colonization. The probability of adelgids being transported by wind to these small eastern hemlock populations must be quite low even if HWA density is high near the southernmost contiguous extent of eastern hemlock. However, relatively large populations of eastern hemlock occur in the William B. Bankhead National Forest (BNF) of north Alabama. These larger populations at BNF represent larger islands of suitable HWA habitat and thus, have a higher probability of being infested. If the HWA reaches these populations, the BNF may serve as a source for jump dispersal to other outlying eastern hemlock populations in Tennessee, Alabama, and Georgia.

Birds are also dispersal agents of the HWA. Adelgids have been documented on birds up to 2 km from the nearest known eastern hemlock individual (McClure, 1990). Adeglids have been documented on a variety of migratory bird species with varied foraging, nesting, and roosting behavior. It is hypothesized that HWA eggs and crawling nymphs can remain attached to birds during migration, including spring migration, which is a time when nymphs are most active (McClure, 1989b, 1990). Thus, birds may be the most effective agents for the long distance dispersal of adelgids. This may be especially true for specific avian species that favor eastern hemlock stands (e.g. black-throated green warbler (*Dendroica virens* Gmelin) and winter wren (*Troglodytes troglodytes* L.); Yamasaki *et al*., 1999). Also, larger populations of eastern hemlock, such as those at the BNF, represent larger target areas for migrating birds (Lomolino, 1990). However, birds have only been documented to transport HWA *ca*. 2 km from eastern hemlock stands (McClure, 1990). This distance is not sufficient to allow for the colonization of disjunct populations near the southern boundary of eastern hemlock.

PERSISTENCE OF DISJUNCT POPULATIONS

If disjunct eastern hemlock populations are not infested by the HWA, and biocontrol and other measures are not successful through the contiguous range, eastern hemlock may become restricted to the periphery of its current distribution and may be included with the number of other species whose ranges have collapsed in an explosive manner and are absent from the core of their historic range (*see* Channell and Lomolino, 2000b). If disjunct populations persist, they will become even more important centers of biodiversity for a variety of species, including terrestrial and aquatic species often associated with eastern hemlock stands (Yamasaki *et al*., 1999; Snyder *et al*., 2002). Even though these disjunct populations are often relatively small, persistent populations are not necessarily those with the highest densities, but those most isolated from the point of contact with an extinction force (Lomolino and Channell, 1995, 1998; Lomolino and Smith, 2001; Channell and Lomolino, 2000a, 2000b). Peripheral populations of eastern hemlock are viable and may provide opportunities to maintain the species. Thus, they should not be overlooked in control and conservation efforts even though many populations are relatively small.

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