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Disjunct Eastern Hemlock Populations of The Central Hardwood Forests: Ancient Relicts or Recent Long Distance Dispersal Events?

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Abstract

Eastern hemlock (*Tsuga canadensis*) is an evergreen conifer with a contiguous distribution extending from the southern Appalachian Mountains north to Nova Scotia and west across the Great Lakes region. Eastern hemlock is threatened with extirpation from much of this range by an introduced pest, the hemlock woolly adelgid (Orwig et al. 2002). In addition to the contiguous distribution, many small, isolated populations are located within the central hardwood forest region of Kentucky, Indiana, and Ohio (Braun 1928, Potzger and Friesner 1937, Van Stockum 1979). These disjunct populations form clearly delineated, often monospecific stands associated with unique natural features such as north facing cliffs and box canyons (Hart and Shankman 2005). Disjunct populations have long been of interest to biologists and two primary hypotheses for their origin have been proposed: 1) They are the product of rare long distance dispersal events (Gamache et al. 2003, Nathan 2006), or, 2) Remnants of what was once a portion of the contiguous distribution (Daubenmire 1931, Richardson et al. 2002). If long distance dispersal was responsible for the formation of these populations, we predict the resulting genetic bottlenecks to result in low within-population diversity, a correlation by distance to source populations and large between-population differences. Conversely, if these populations represent post-glacial relicts, we predict within-population diversity to be dependent on population size, no correlation by distance to source populations, and low between-population differences.

To evaluate these hypotheses we amplified microsatellite loci from DNA samples of 480 trees located in 17 disjunct populations (including one in MCNP), and 7 reference populations in the contiguous distribution (Figure 1). Standard descriptive for molecular data were calculated, including allelic richness, identification of alleles unique to single populations, and observed and expected heterozygosity (H_o and H_e). Linear regression was used to assess correlations between genetic diversity and population size and distance to source populations. Nei's unbiased genetic distance (Nei 1978) was used to examine for between-population genetic differences.

Of the 21 published microsatellite primer pairs for eastern hemlock (Josserand et al. 2008, Shamblin et al. 2008) we found 15 that consistently amplified products in the expected size range, of which 14 were polymorphic. We chose seven of these to conduct our full survey. The number of alleles of each of these seven loci ranged from 4 to 23 with an average of 10.3. Mean allelic richness across all seven loci for each population ranged from 7.0 to 1.7, with a mean of 5.9 for reference populations and 3.1 for disjunct populations. Disjunct populations also displayed a lower level of observed heterozygosity than expected ($H_o = 0.27$, $H_e = 0.42$) compared to reference populations ($H_o = 0.60$, $H_e = 0.64$). Twelve alleles unique to single populations were identified, with eight located in disjunct populations and four in reference populations.

In disjunct populations, mean allelic richness of populations did increase significantly with population size (Figure

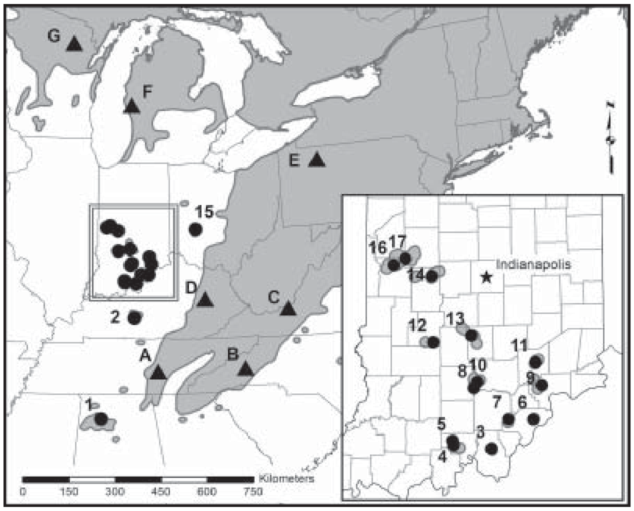

Figure 1: Location of sample populations. Distribution of eastern hemlock (Little 1971) is shaded in grey. Disjunct populations are shown with circles and are numbered 1-18. Reference populations are shown with triangles and are lettered A-G. Names of sample sites are as follows: 1 = Bankhead National Forest, 2 = Mammoth Cave National Park, 3 = Indian Creek, 4 = Hemlock Cliffs, 5 = Yellow Birch Ravine Nature Preserve, 6 = 14 Mile Creek, 7 = Whiskey Run, 8 = Guthrie Creek, 9 = Big Creek, 10 = Hemlock Bluff Nature Preserve, 11 = Muscatatuck River, 12 = Greens Bluff Nature Preserve, 13 = Trevlac Bluff, 14 = Big Walnut Creek, 15 = Clifton Gorge Nature Preserve, 16 = Turkey Run State Park, 17 = Shades State Park, A = Fall Creek Falls State Park, B = Pisgah National Forest, C = Mountain Lake Biological Station, D = Red River Gorge, E = Allegheny National Forest, F = Manistee National Forest, G = Cathedral of the Pines State Natural Area.

2, P=0.035), as estimated by the known areas of these populations. Disjunct populations showed neither a decrease in genetic diversity as distance to source populations increased (Figure 3, P=0.55), or positive correlation between genetic distance (F_{st}) and spatial distance (Figure 4, P=0.87). Finally, while patterns of between-population genetic distance were complex, no strong pattern of differences between disjunct populations were observed between disjunct populations.

In summary, our results support the expectations of the glacial relict hypothesis, where the species is expected to have been once more widespread in this region following the last glacial maximum and has since contracted to the small, isolated populations observed today. There is little evidence to support the formation of these populations through long-distance dispersal events from source populations. Our conclusion agrees with previous understandings of how "relict" communities in the central hardwood forest had formed (Braun 1928) and with results found in other conifer systems worldwide (Richardson et al. 2002, Zhang et al. 2005). Our data also suggest the presence of separate glacial refugia on both sides of the southern Appalachian Mountains, with several unique alleles and clades found only in populations west of the Appalachians, such as the population sampled at Mammoth Cave National Park. This pattern of distinct eastern and western refugia largely corresponds with findings by Potter et al. (2012). If true, this pattern should be of particular interest to conservation efforts to preserve the

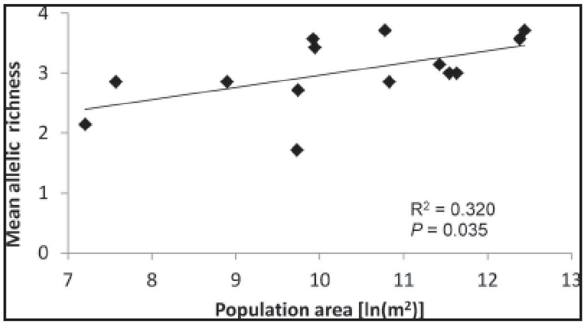

Figure 2: Population size of disjunct populations, as estimated by geographic area of stand, is positively correlated (P=0.035) with mean allelic richness of each population across all seven microsatellite loci. Area of stand was determined using aerial infrared imagery which was only available for the state of Indiana. Therefore, the three disjunct populations not located in Indiana are not included in this analysis.

diversity of genetic resources in eastern hemlock in light of the threat posed by the hemlock woolly adelgid.

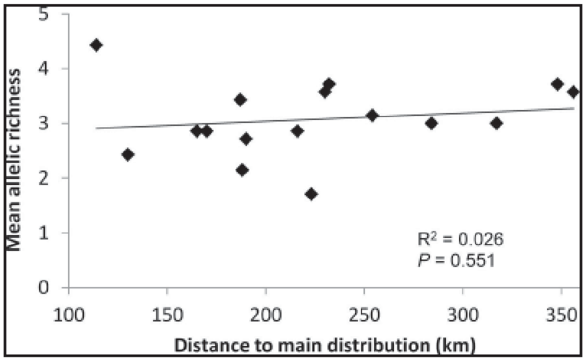

Figure 3: Mean allelic richness is not significantly correlated with distance to the contiguous distribution for the 17 disjunct populations. Distance to contiguous distribution was calculated with the straight line distance to the closest border of Little's 1971 contiguous distribution.

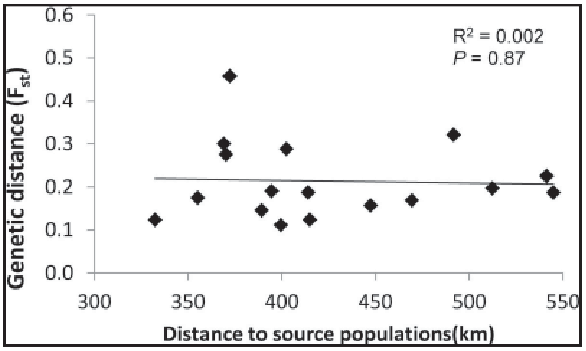

Figure 4: Genetic distance (F_{st}) is not significantly correlated with geographic distance to potential source populations for the 17 disjunct populations. Geographic distance was calculated as the mean distance to the four reference populations to the southwest of the disjunct populations.

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