Evolutionary History and Population Genetics of Fraser Fir and Intermediate Fir, Imperiled Appalachian Endemics

Fraser fir at Mt. Rogers, Va.

Intermediate fir at Canaan Valley, W.V.

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Ecology and Management of High-Elevation Appalachian Forests

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Firs (*Abies*): Description

Fraser fir foliage, Roan Mountain, Tenn./N.C.

- *Abies* second largest genus in Pine Family (Pinaceae)
  - ~45 species worldwide, ~10 in North America and Mexico
- Pyramidal conifers
- Upright deciduous cones
- Flat, blunt-tipped needles

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Central/Southern Appalachian firs

- Two taxa
  - Fraser fir (*Abies fraseri*)
  - Intermediate/Canaan fir (*Abies balsamea* var. *phanerolepis*)
- Small, fragmented populations
- Under threat by exotic pest and climate change
- Both related to balsam fir
- Both associated with red spruce

Fraser fir at Mt. Rogers, Va.

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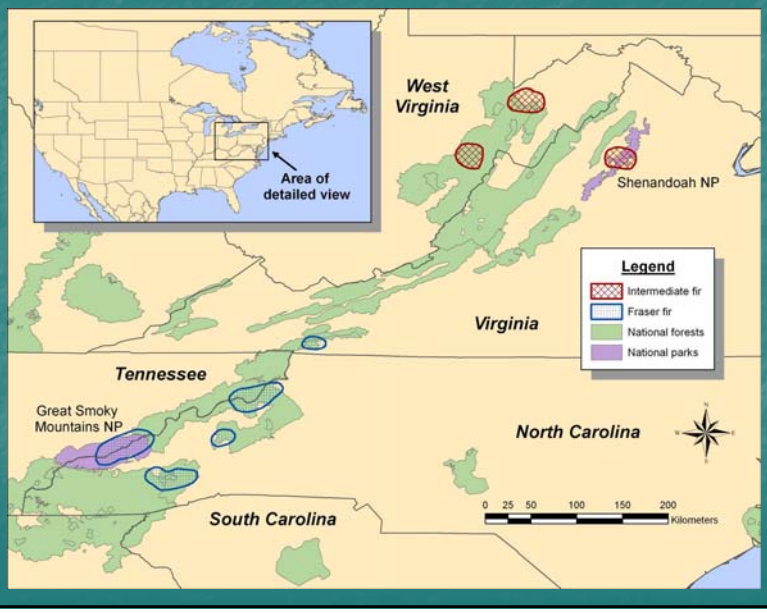
Central/Southern Appalachian firs



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Fraser fir

- Six main populations in North Carolina, Tennessee and Virginia
- Boreal species
- Moist and cool conditions
  - Mostly found above ~1,300 m (5,500 ft)
  - Dominant tree species above ~1,800 m (5,900 ft)

Fraser fir-red spruce in Great Smoky Mountains National Park

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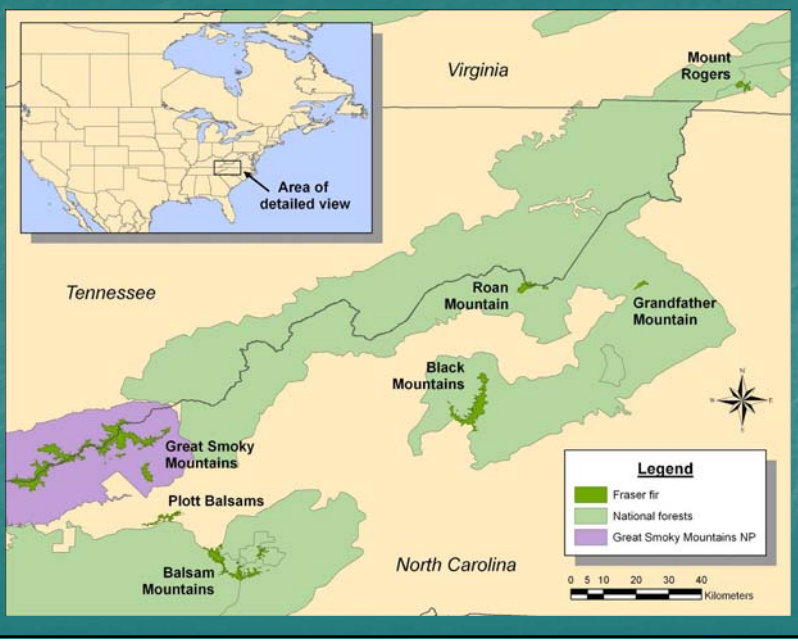
Fraser fir



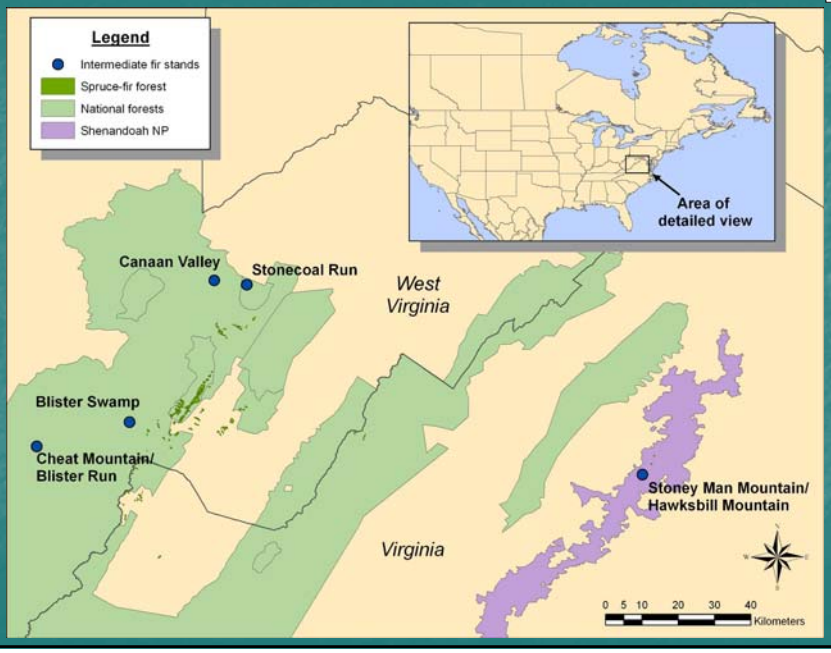
Intermediate/Canaan fir

- Very limited distribution
- West Virginia (including Canaan Valley)
  - High-elevation boggy sites (like northern balsam fir)
  - ~4 populations
- Virginia: Shenandoah N.P.
  - High-elevation ridge top sites
  - 2 small stands

Canaan Valley State Park, West Virginia

Shenandoah National Park, Virginia

Intermediate fir



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Balsam woolly adelgid

- Since 1950s, extensive Fraser fir mortality from exotic balsam woolly adelgid (BWA)
  - ~90 percent mortality in Great Smoky Mountains, Black Mountains
  - Younger trees largely escape infestation
  - New generation now reaching at which infestation might re-occur

Fraser fir snags at Clingman's Dome, Great Smoky Mountains

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Balsam woolly adelgid

- More recently, BWA has resulted in mortality in intermediate fir stands
  - Does balsam fir/intermediate fir have some resistance to BWA?

Intermediate fir mortality, Canaan Valley State Park, W.V.

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Climate change

- Will changing climate push Fraser fir off the mountain tops?
  - Fraser fir-red spruce forest could be eliminated with 3° C increase in mean temperature
- Are small, fragmented intermediate fir populations at particular risk?

Roan Mountain population from Grassy Ridge Bald, N.C./Tenn.

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Evolutionary relationships

- Genetic studies: taxa closely related
  - Fraser fir, intermediate fir and balsam fir have been classified as varieties of the same species
- Clinal variation complicates delineation
  - North to south (balsam, intermediate and Fraser fir): cone bract length, leaf oils, wood properties

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Balsam fir (*Abies balsamea*)

Abies balsamea cones
(University of New Brunswick)

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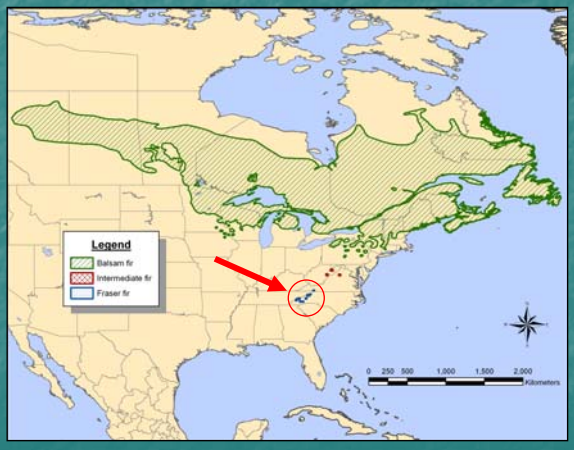
Fraser fir (*Abies fraseri*)



Abies fraseri cones

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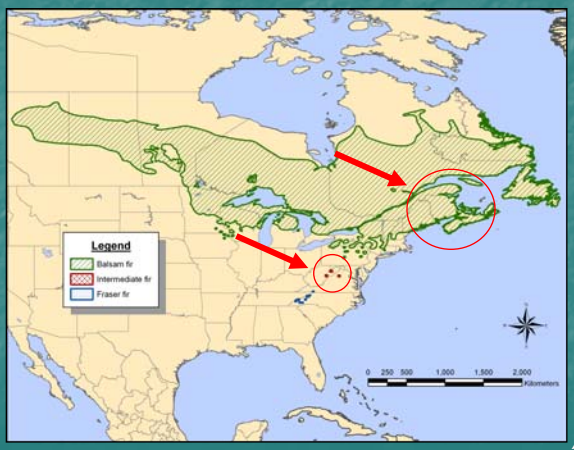
Intermediate/Canaan fir (*Abies balsamea* var. *phanerolepis*)



Abies balsamea var. *phanerolepis* cones, Shenandoah National Park

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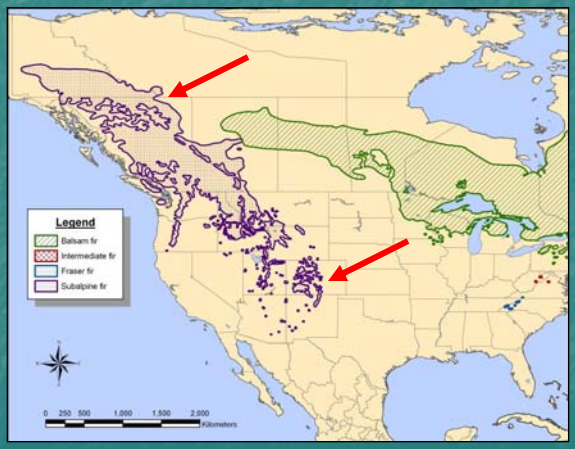
Subalpine fir (*Abies lasiocarpa*)



Abies lasiocarpa cones
(Philip Haddock, California Native Plant Society)

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Research questions

1) How much genetic variation exists in Fraser fir and intermediate fir?
2) How closely related are these firs to each other and to balsam fir?
3) What do the genetic relationships of these taxa tell us about their recent biogeographical history?

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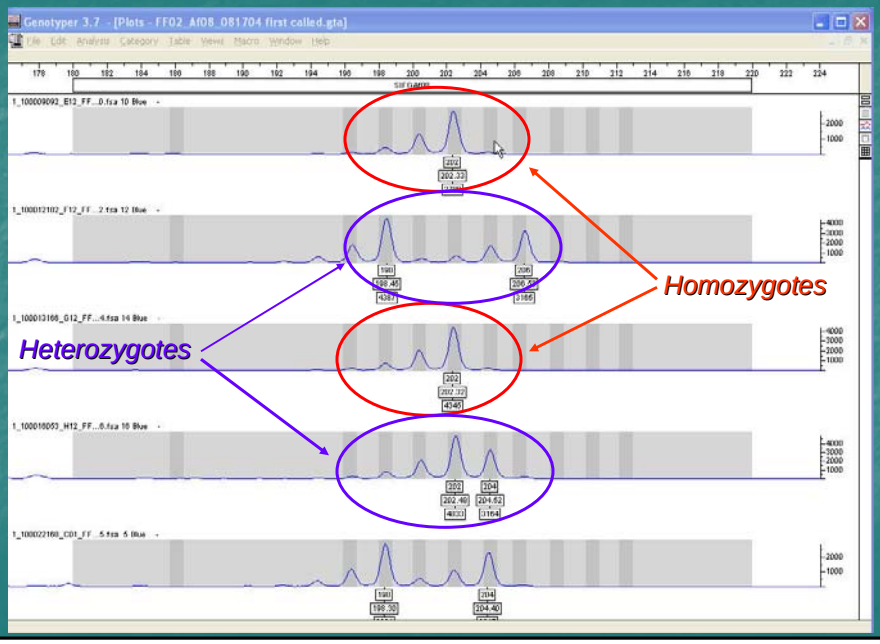
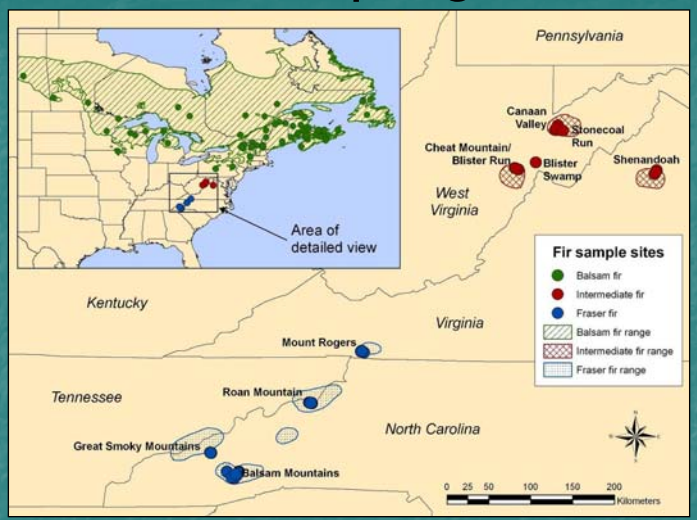
Microsatellite molecular markers

- Tandem repeats of simple motif DNA sequences (e.g., GT or AAT) amplified by polymerase chain reaction (PCR)
  - Highly polymorphic, co-dominant, consistent, relatively easy to use
- Loci developed from Fraser fir at the USDA Forest Service Southern Institute of Forest Genetics in Saucier, Mississippi
  - 10 microsatellite loci in this study

Microsatellite analysis



Sampling



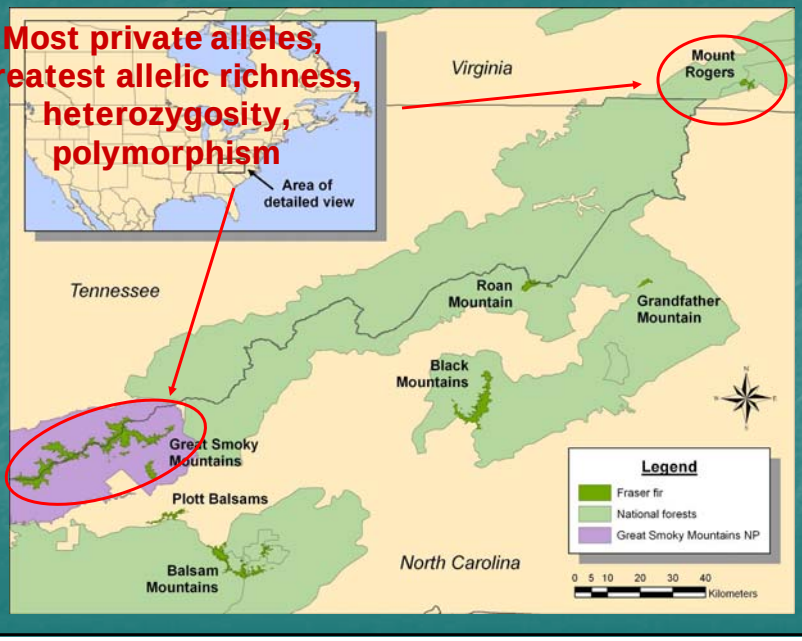
- 80 Fraser fir
- 74 balsam fir
- 61 intermediate fir
- 10 subalpine fir

Genetic diversity

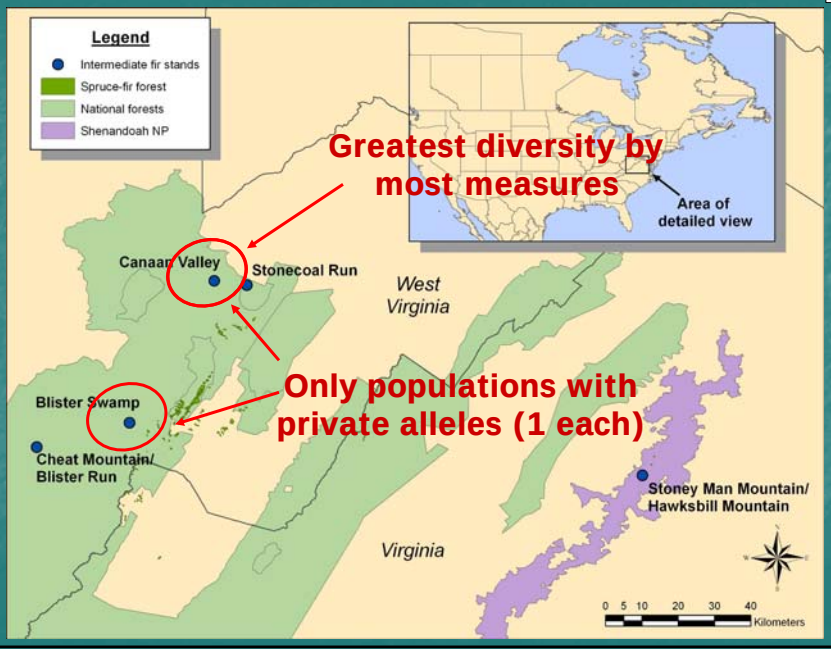
	Mean alleles	Allelic richness	Private alleles	Observed heterozygosity	Inbreeding Coeff.
Fraser	6.2	2.7	6	0.308	0.235
Intermediate	6.4	3.2	2	0.303	0.358
Balsam	8.6	3.7	15	0.343	0.391

Fraser fir

Most private alleles, greatest allelic richness, heterozygosity, polymorphism



Intermediate fir



Pairwise genetic relationships

	Balsam	Intermediate	Fraser	Subalpine
Balsam	–	0.026	0.058	0.126
Intermediate	0.029	–	0.034	0.130
Fraser	0.094	0.039	–	0.147
Subalpine	0.188	0.254	0.334	–

Upper diagonal: chord (D_C) genetic distances.
Lower diagonal: pairwise F_{st} values (all are significantly different from 0).

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Delineating species

- Eastern firs may best be classified as one species with three varieties
  - Not much differentiation (5.7%, F_{ST} =0.057)
- Subalpine fir, however, is strongly differentiated

A. balsamea var. *balsamea*

A. balsamea var. *phanerolepis*

A. balsamea var. *fraseri*

A. lasiocarpa

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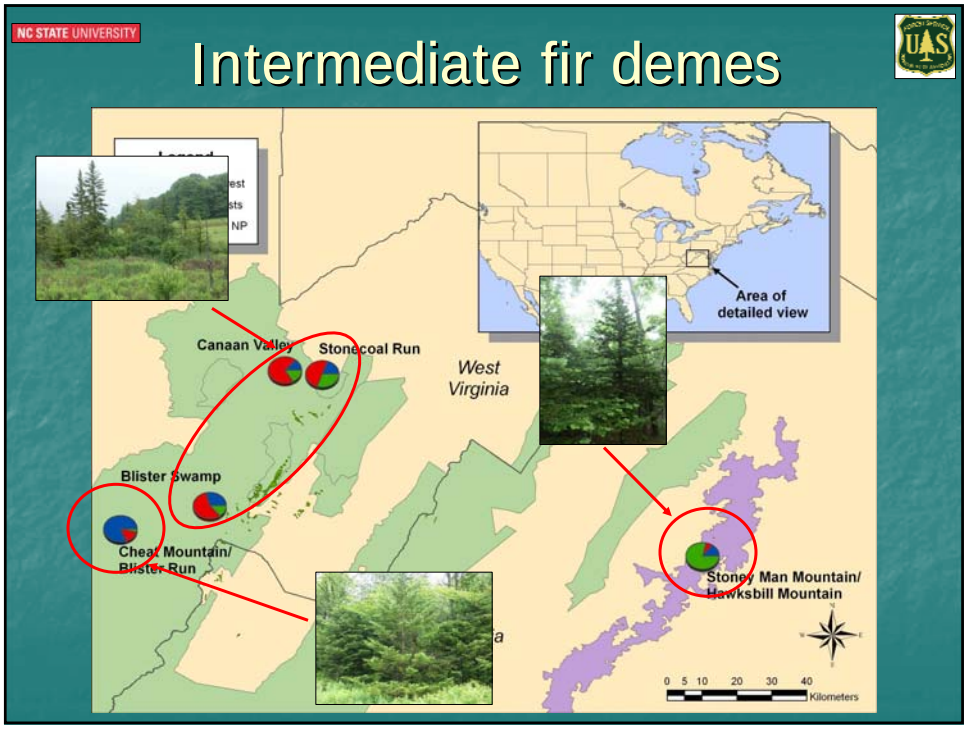
Hidden genetic structure

- Bayesian clustering program InStruct searched for hidden population structure
  - Combines information from several loci into a single probability model
  - Useful with continuous species distribution
- Used results to determine “demes” in balsam fir, intermediate fir, Fraser fir
  - Delineated three demes in balsam and intermediate, two in Fraser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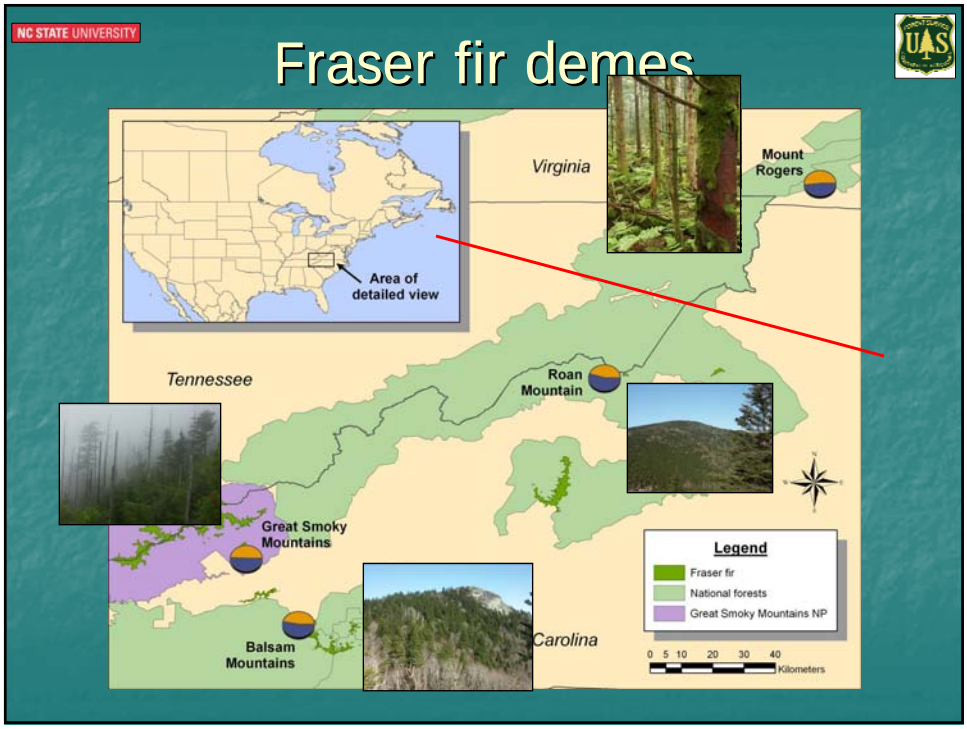
Intermediate fir demes
Canaan Valley
Stonecoal Run
West Virginia
Blister Swamp
Cheat Mountain/ Blister Run
Area of detailed view
Stoney Man Mountain/ Hawksbill Mountain
0 5 10 20 30 40
Kilometers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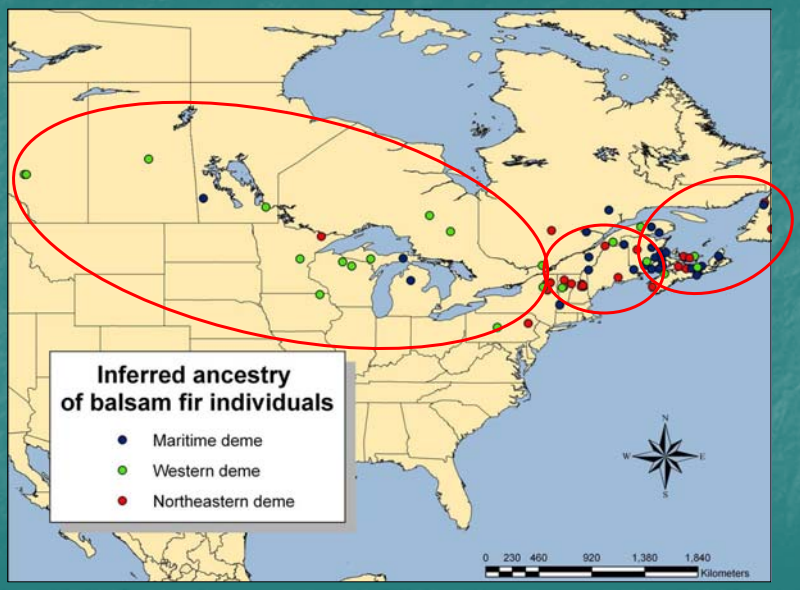
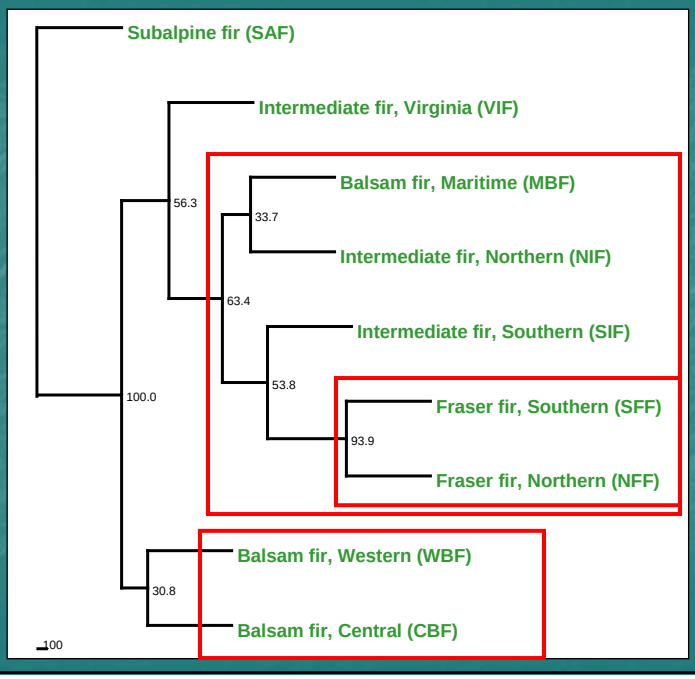
Fraser fir demes
Virginia
Mount Rogers
Area of detailed view
Tennessee
Roan Mountain
Great Smoky Mountains
Balsam Mountains
Carolina
Legend
Fraser fir
National forests
Great Smoky Mountains NP
0 5 10 20 30 40
Kilometers

Balsam fir deme delineation





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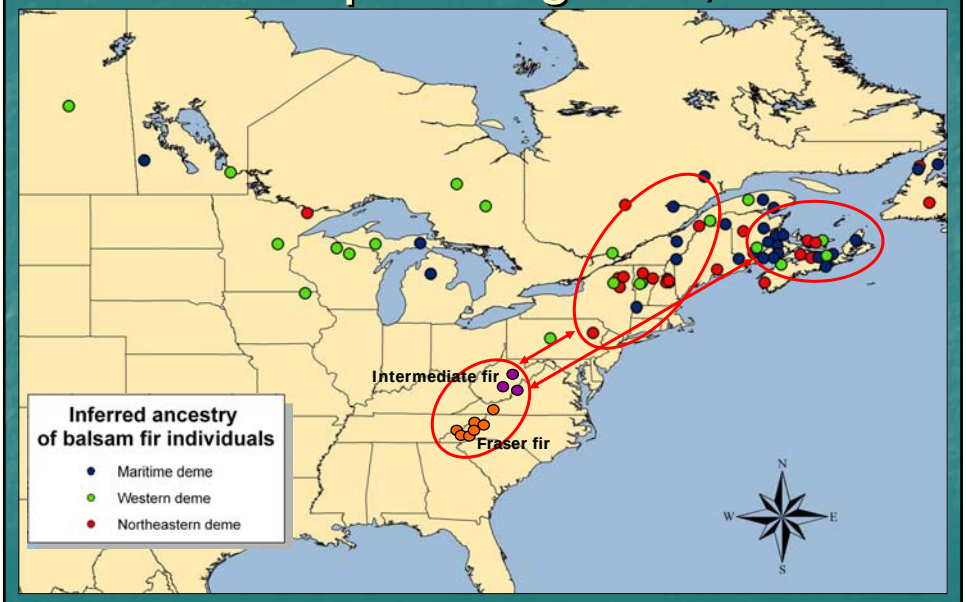
Relationship among taxa, demes



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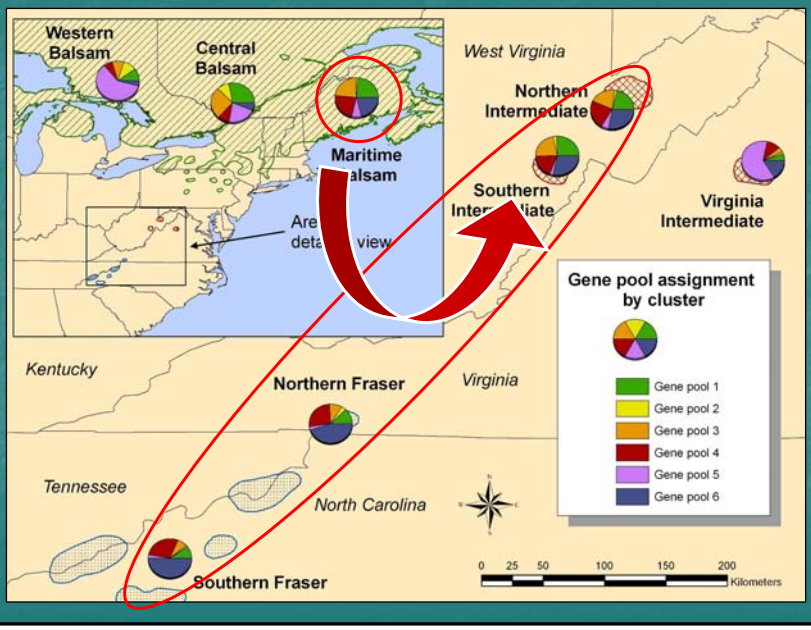
Genetic admixture



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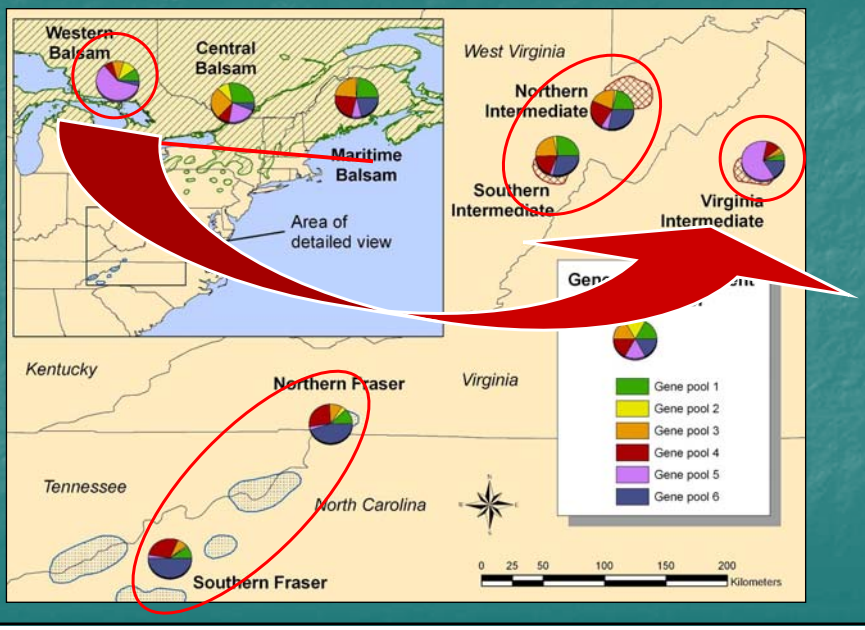
Genetic admixture



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Evolutionary, distributional history

- May have been three main fir glacial refugia during the late Pleistocene, each associated with a balsam fir deme
- Unexpectedly, Fraser fir and intermediate fir more closely related to maritime balsam fir deme than northeastern deme

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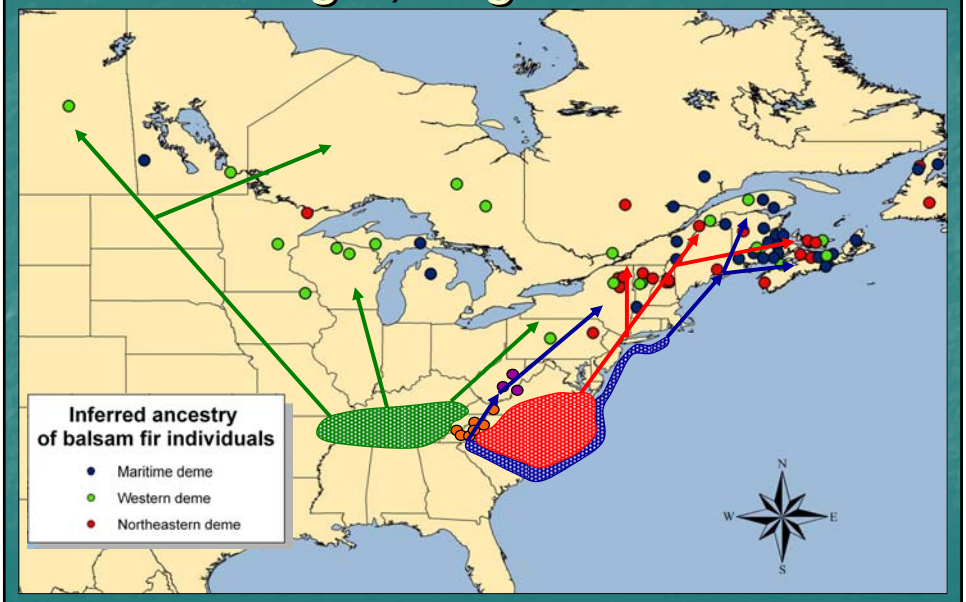
Fir refugia, migration routes



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What's the origin of southern firs?

- Two possibilities (Jacobs *et al.* [1984])
  - "Clinal fragment" hypothesis
    - Fraser, balsam fir indistinct during Pleistocene
    - Clinal variation developed during migration
    - Fraser fir further differentiated by selection, drift
  - "Montane ecotype" hypothesis
    - Bract exsertion an adaptive extreme associated with high elevation/moisture during Pleistocene
    - Fraser fir lost non-exsertedness with isolation
    - Intermediate fir diluted version of adaptive extreme

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Conclusions

- Fraser fir, balsam fir, and intermediate fir probably best considered a single species
- Low levels of genetic diversity in Fraser and intermediate fir
- Fraser fir and intermediate fir are closely related, and both closely related to Maritime balsam fir
- Probable “montane ecotype” origin of Fraser and intermediate fir

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Questions or comments?

Abies balsamea var. *phanerolepis* stand, Canaan Valley State Park, W.V.