

Fire Drives Transcontinental Variation in Tree Birch Defense against Browsing by Snowshoe Hares

John P. Bryant,^{1,*} Thomas P. Clausen,² Robert K. Swihart,³ Simon M. Landhäusser,⁴ Michael T. Stevens,⁵ Christopher D. B. Hawkins,⁶ Suzanne Carrière,⁷ Andrei P. Kirilenko,⁸ Alasdair M. Veitch,⁹ Richard A. Popko,⁹ David T. Cleland,¹⁰ Joseph H. Williams,¹¹ Walter J. Jakubas,¹² Michael R. Carlson,¹³ Karin Lehmkuhl Bodony,¹⁴ Merben Cebrian,¹⁵ Thomas F. Paragi,¹⁶ Peter M. Picone,¹⁷ Jeffrey E. Moore,¹⁸ Edmond C. Packee,¹⁹ and Thomas Malone¹⁹

1. Box 306, Cora, Wyoming 82825; 2. Department of Chemistry and Biochemistry, University of Alaska, Fairbanks, Alaska 99775; 3. Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907; 4. Department of Renewable Resources, Centre for Enhanced Forest Management, 751 General Services Building, University of Alberta, Edmonton, Alberta T6G 2E3, Canada; 5. California State University, Stanislaus, Turlock, California 95382; 6. Forestry Program, University of Northern British Columbia, 3333 University Way, Prince George, British Columbia V2N 4Z9, Canada; 7. Department of Environment and Natural Resources, Government of the Northwest Territories, Scotia Centre—5th Floor, Yellowknife, Northwest Territories X1A 3S8, Canada; 8. Department of Earth Sciences Science and Policy, School of Aerospace Sciences, University of North Dakota, Grand Forks, North Dakota 58202; 9. Department of Environment and Natural Resources, Government of the Northwest Territories, P.O. Box 130, Norman Wells, Northwest Territories X0E 0V0, Canada; 10. U.S. Forest Service, Eastern Regional Office and Southern Research Station, Rhinelander, Wisconsin 54501; 11. Department of Ecology and Evolution, University of Tennessee, Knoxville, Tennessee 37996; 12. Maine Department of Inland Fisheries and Wildlife, Bangor, Maine 04401; 13. British Columbia Ministry of Forests and Range, Forest Genetics and Tree Breeding, Kalamalka Forestry Centre, 3401 Reservoir Road, Vernon, British Columbia V1B 2C7, Canada; 14. U.S. Fish and Wildlife Service, Koyukuk/Nowitna National Wildlife Refuge, P.O. Box 287, Galena, Alaska 99741; 15. U.S. Department of the Interior, Bureau of Land Management, Glennallen Field Office, Box 147, Glennallen, Alaska 99588; 16. Alaska Department of Fish and Game, Division of Wildlife Conservation/Region 3, Fairbanks, Alaska 99701; 17. Connecticut Department of Environmental Protection, Sessions Woods Wildlife Management Area, P.O. Box 1550, Burlington, Connecticut 06013; 18. Duke University Marine Laboratory, Beaufort, North Carolina 28516; 19. School of Natural Resources and Agricultural Sciences, Forest Sciences Department, University of Alaska, Fairbanks, Alaska 99775

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ABSTRACT: Fire has been the dominant disturbance in boreal America since the Pleistocene, resulting in a spatial mosaic in which the most fire occurs in the continental northwest. Spatial variation in snowshoe hare (*Lepus americanus*) density reflects the fire mosaic. Because fire initiates secondary forest succession, a fire mosaic creates variation in the abundance of early successional plants that snowshoe hares eat in winter, leading to geographic variation in hare density. We hypothesize that fire is the template for a geographic mosaic of natural selection: where fire is greatest and hares are most abundant, hare browsing has most strongly selected juvenile-phase woody plants for defense. We tested the hypothesis at multiple spatial scales using Alaska birch (*Betula neoalaskana*) and white birch (*Betula papyrifera*). We also examined five alternative hypotheses for geographic variation in antibrowsing defense. The fire-hare-defense hypothesis was supported at transcontinental, regional, and local scales; alternative hy-

potheses were rejected. Our results link transcontinental variation in species interactions to an abiotic environmental driver, fire. Intakes of defense toxins by Alaskan hares exceed those by Wisconsin hares, suggesting that the proposed selection mosaic may coincide with a geographic mosaic of coevolution.

Keywords: tree birch, snowshoe hare, forest fire, antibrowsing defense, selection mosaic.

Introduction

Environmental conditions and community context vary across the geographic range of many, if not most, species. Thus, sympatric species may experience spatially varying intensities or types of interaction, potentially creating a geographic mosaic of population dynamics, natural selection, and coevolution (Sanford et al. 2003; Thompson 2005a, 2005b). Geographic variation in species interactions has been documented with increasing frequency in marine (Sotka and Hay 2002; Jormalainen et al. 2008), salt marsh

* Corresponding author; e-mail: ffjpb@wyoming.com.

(Pennings et al. 2001, 2003; Goranson et al. 2004), and terrestrial (Benkman et al. 2003; Castells et al. 2005; Thompson and Fernandez 2006; Craig et al. 2007; Tamura and Hayashi 2008) systems. Unfortunately, such documentation is rarely accompanied by well-defended explanations for the drivers of geographic variation. We describe a transcontinental pattern of variation in birch chemical defense and snowshoe hare density. Using a series of studies at continental, regional, and local scales, we identify the likely driver of the geographic variation we observed. Spatial variation in forest fire appears to function as the predominant determinant of variation in hare-birch interactions.

The boreal forest occupies 10% of Earth's ice-free terrestrial surface and is the second most extensive terrestrial biome, after tropical forests (Saugier et al. 2001). Since the last Ice Age, fire has been the dominant disturbance regimen across the vast North American boreal forest (Stocks et al. 2002), resulting in a fire mosaic at least 6,000 years old (Flannigan et al. 2001). The highest percent annual area burned (PAAB; fig. A1A in the online edition of the *American Naturalist*) and the highest incidence of fire (fig. A1B) occur in the continental northwest, with less fire to the south and east (Fox 1978; Johnson 1992; Stocks et al. 2002; Lloyd et al. 2006). Spatial variation in the density of snowshoe hares exhibits a similar pattern, presumably in response to fire-induced alteration of habitat (Grange 1949, 1965; Fox 1978; Ferron and St.-Laurent 2008). Fire resets boreal forest to early seral stages. Early to midsuccessional boreal forest is prime hare habitat because it contains an abundance of preferred winter food and dense cover used for evading predators (Paragi et al. 1997).

Increased hare densities exert strong selection on woody plants by virtue of browsing pressure. Hare browsing in winters of high density severely reduces subsequent growth, competitive ability, and survival of juvenile-phase (Kozłowski 1971) seedlings and saplings (Aldous and Aldous 1944; Wolff 1980; Radvanyi 1987). The evolutionary response to browsing has been increased defense in juvenile-phase woody plants (Bryant and Kuropat 1980; Bryant 1981; Bryant et al. 1983; Reichardt et al. 1984; Swihart and Bryant 2001). We propose that fire provides the template on which a geographic mosaic of natural selection unfolds. Specifically, we posit a fire-hare-defense (FHD) hypothesis in which transcontinental variation in fire drives spatial variation in hare density (Grange 1949, 1965; Fox 1978; Paragi et al. 1997; Ferron and St.-Laurent 2008) and hence transcontinental variation in the juvenile-phase antibrowsing defense of boreal woody plants. Verification of the FHD hypothesis would be the first evidence that variation in a physical force (fire) is the independent variable in a chemically mediated plant-herbivore interaction of transcontinental scope.

Circumstantial evidence supports the FHD hypothesis. Fire is greater and hares reach greater densities in Alaska than in Maine and New England (Murray 2000; Rexstad and Kielland 2006). Juvenile-phase birch and aspen (*Populus*) from Alaska are more resistant to hare browsing than counterparts from Maine and New England (Bryant et al. 1994). Within eastern North America, snowshoe hare density is higher in Maine than in New England (Murray 2000), and Maine birch and aspen are more resistant to hare browsing than their New England counterparts (Swihart et al. 1994). Additionally, a meta-analysis summarizing the resistance of northern woody plants to mammals found that juvenile-phase browsing resistance increased with latitude in nine of 10 studies involving hares (Swihart and Bryant 2001). When coupled with the positive correlation of snowshoe hare density and latitude in North America (Murray 2000; Ferron and St.-Laurent 2008), the meta-analysis provides more evidence for a transcontinental effect of hares on plant defense.

Resistance to browsing often is determined by specific plant secondary compounds. In tree birches, epidermal resin glands exude defensive compounds onto the surface of current-year twigs of the juvenile phase (Lapinjoki et al. 1991; Raatikainen et al. 1992; Taipale et al. 1994; fig. 1). Alaska birch (*Betula neoalaskana* Sargent) is the most browsing-resistant North American tree birch (Bryant et al. 1994; fig. 1). Its defense resides in the toxic triterpene papyriferic acid (PA; Reichardt 1981; Reichardt et al. 1984). Epidermal resin glands exude dammarane triterpenes including PA. Resin of shrub birch (*Betula nana* subsp. *exilis* [Sukaczew] Hultén and *Betula glandulosa* Michaux) con-

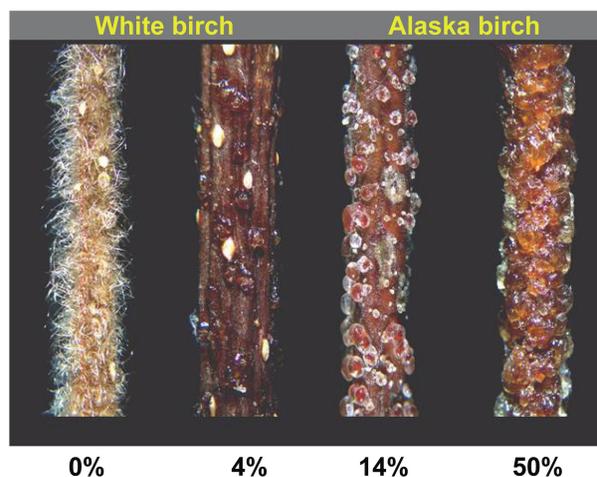


Figure 1: Photographs of the current-year twigs of individual birches (left, white birch; right, Alaska birch) illustrating the observed range of resin glands that produce papyriferic acid (PA). Numbers below each twig refer to percent of the twig's biomass made up of PA.

tains PA and the structurally similar 3-O-malonylbetulafolientriol oxide I (Reichardt et al. 1987; Williams et al. 1992). Birch resin can be a potent antifeedant (Reichardt et al. 1984), reducing protein digestion by nearly half (Sinclair et al. 1988). For tree, tall shrub, and low shrub birches, resin gland density is highest for species in the north-western portion of North America and lower for species with more southern and eastern distributions (fig. A2 in the online edition of the *American Naturalist*). An exception is in the Canadian Arctic Archipelago and northwest Greenland, where indigenous shrub birch does not produce resin glands and snowshoe hares do not occur. Geographic variation in density of resin glands thus provides more circumstantial evidence for a positive association between plant defense and snowshoe hare density.

To test the FHD hypothesis, we used the juvenile phase of two widespread tree birches, Alaska birch and white birch (Dugle 1966; fig. A2A). We predict that hare density correlates positively with fire and that juvenile-phase birch defense correlates positively with hare density. We focused on tree birch and snowshoe hares for two reasons. First, it is probable that tree birch and snowshoe hares have co-occurred throughout the 6,000-year formation of the modern boreal forest fire mosaic: tree birch macrofossils dating from 10,000 years BP (Hopkins and McCulloch 1966; Hopkins and Smith 1981) and tree birch pollen dating from 9,500 years BP (Hu and Brubaker 1993) have been found in western Alaska and central interior Alaska; snowshoe hares were in Beringia in full glacial time (20,000 years BP; Dixon 1984), in the Canadian Rocky Mountains 10,000 years BP (Fedje et al. 1995), and in Pennsylvania at 13,000 years BP (locality information for Faunmap locality Frankstown Cave, PA; <http://mapserver.museum.state.il.us/faunmapweb/onesite.php?siteID=890>). Because selective browsing by snowshoe hares over a few decades can alter the defense profile of modern boreal forest vegetation (Bryant and Chapin 1986), we presumed that 6,000 years of selective browsing by hares could affect geographic variation in defense. Second, we know of no other boreal herbivore or set of boreal herbivores that could have initiated transcontinental variation in defense. Insect herbivory is an unlikely cause, because stem-feeding insects such as the bronze birch borer (*Agrilus anxius* Gory) do not attack the small-diameter twigs (MacAloney 1968) that contain PA (Reichardt et al. 1984). In winter, all boreal browsing mammals except tree squirrels (*Tamiasciurus* spp.) and caribou (*Rangifer tarandus*) regularly feed on tree birch (Bryant and Kuropat 1980). However, only cervids (deer) forage over the entire landscape. Moose (*Alces alces*) are the only cervids residing over the entire range of the comparatively highly defended Alaska birch, and they were rare in interior Alaska until early in the twentieth century (Huntington 1993).

In addition to FHD, we tested five competing explanations for geographic variation in defense. (1) Requirements of snowshoe hares for more food when temperature is low (Pease et al. 1979) explains more intense selection for defense in the north (Swihart and Bryant 2001). Support for the temperature hypothesis depends on finding an inverse correlation between defense and temperature. (2) Availability of nutrients to plants affects the evolution of defense by the juvenile phase (Bryant and Kuropat 1980; Bryant et al. 1983). Geographic variation in soil fertility arises over time as differences in bedrock geochemistry influence biogeochemistry (Jenny 1941; Thompson and Turk 1991; McBride 1994; Chapin et al. 2006). We use the relation between bedrock geochemistry and defense to test this soil-related ecotypic variation hypothesis. Support depends on finding an effect of bedrock on defense of birches grown in a common garden from seed of mother trees growing in shallow stony soil of different chemistry but occurring in the same PAAB regime. (3) On a short time-scale, nutrient supply affects antibrowsing defense via altered carbon/nutrient balance (Bryant et al. 1983). Increased N supply reduced PA production by tree birches in one growing season (Bryant et al. 1987; Mattson et al. 2004). We use common garden experiments to test the carbon/nutrient balance hypothesis. Support depends on finding no difference in defense among populations of different geographic origin growing in a common environment. (4) The act of herbivory sometimes induces defense (sensu Karban and Baldwin 1997), indicating that greater defense in areas with more hares might be caused by browsing per se rather than selection for defense. We protected birches grown in common gardens from browsing, thereby permitting a test of the induced defense hypothesis. Support is inferred if no differences in defense are found among protected populations of different geographic origin. (5) Latent, undetected spatial variables might produce geographic variation in birch defense. We presumed that such an effect would be distance dependent, with strongest similarities in defense occurring between the most proximal populations and increased distance between populations diluting the relationship. Specifically, the distance dependence hypothesis predicts a positive correlation for population pairs in terms of differences in defense (Δ defense) and their spatial separation (Δ distance). Support for the hypothesis depends on finding a correlation between Δ defense and Δ distance that is stronger than the positive correlation expected between Δ defense and the between-population difference in PAAB (Δ PAAB). Note that neither fire per se nor fire suppression was considered a plausible alternative explanation for geographic variation in defense: juvenile tree birch is primarily found shortly after fire when fire reoccurrence is rare. Moreover, birch resin is highly flammable; hence, fire

would incinerate seedlings and saplings and cause selection against increased resin production. Finally, fire suppression is minimal in the far north, yet variation in defense still occurs there.

In addition to quantifying variation in fire, hare density, and chemical defense, we examined geographic variation in intake of plant defense toxins by captive hares. This secondary objective was motivated by the observation that Alaskan hares can ingest more PA-rich biomass than New England hares (Bryant et al. 1994). Specifically, we compared toxin intake by Alaskan hares and Wisconsin hares, expecting Alaskan hares to be more tolerant of toxins possibly because of more intense reciprocal selection in this high-fire region.

Methods

Study Area and Research Design

We studied the North American boreal forest and its ecotones with the tundra to the north and the temperate forest/prairie to the south, with the exception of northern Quebec, Labrador, and Newfoundland. The geographic range was 23° of latitude and 93° of longitude, and the spatial dimensions were 4,200 km north-south and 6,000 km west-east. The combined ranges of the two birches encompass the study area (Dugle 1966; see fig. A2A), as does the range of snowshoe hare (Murie 1954). The research design was spatially hierarchical (continental, regional, and local): the null hypothesis was no FHD linkage at any spatial scale.

When comparing congeners, entire ranges (fig. A2A) were considered. The conspecific comparisons made at the continental scale used 30 Alaska birch populations and 27 white birch populations. The Alaska birch comparison spanned the species' entire range. The white birch comparison used populations occurring from Manitoba to New England. The regional comparison of Alaska birch occurred in the Mackenzie Basin and used seven populations growing on a 1,200-km transect extending southeasterly from Canada's Mackenzie River Delta (68°N, 134°W) to the Great Slave Lake (61°N, 118°W). The comparison was unique because PAAB, hare density, and birch defense were measured in the same localities, allowing detailed examination of the complete FHD linkage. The regional comparison of white birch occurred in the Great Lakes region and used nine populations growing on an 800-km transect extending from central Wisconsin (44°N, 91°W) to northwest Ontario (51°N, 94°W). At a local scale, defense was compared for saplings from high-PAAB (1%) and low-PAAB (<0.3%) forests containing Alaska birch (Lac La Biche, Alberta; $n = 20$) and white birch (Rhinelander, WI; $n = 16$).

Fire, Hare Density, and Birch Defense

Fire. When comparing congeners, we used points of ignition (fig. A1B) of the 9,462 large (≥ 200 ha) lightning-caused forest fires occurring in Canada from 1959 to 1997 (Canadian Large Fire Database; Stocks et al. 2002) and in Alaska from 1956 to 2002 (Alaska Fire Service database; <http://afsmaps.blm.gov/imf/imf.jsp?site=firehistory>). In conspecific comparisons, we used PAAB. PAAB (percent annual area burned per year) is defined by the expression hectares burned per year in a sampling rectangle/hectares in the rectangle. The area burned per year is associated with a fire's point of ignition; hence, there is potential for error when a point of ignition is near the edge of the area sampled for fire. To minimize this source of error, we used a large sample area (approximately 110 km north-south \times 210 km east-west). The coordinates for the rectangles were computed with the following approximation: $\Delta\lambda(l) = \Delta\lambda(l_0) \times \cos(l_0)/\cos(l)$, where $\Delta\lambda(l_0)$ is the difference between longitudes that bound the sample area containing the birch population centered at the latitude l , $l_0 = 49^\circ\text{N}$ (details in the appendix in the online edition of the *American Naturalist*). Because data were for different time periods (Alaska, 46 years; Canada, 40 years), data were normalized to hectares burned per year before computing PAAB.

Hare Density. When comparing birch congeners at the continental scale, the range of estimates of hare density within the range of the Alaska birch (Keith and Windberg 1978; Krebs et al. 1986; Rexstad and Kielland 2006; Northwest Territory hare survey, <http://www.nwtwildlife.com/sms06/>) was compared with the range of estimates from within the range of the white birch (Green and Evans 1940; Murray 2000). For cyclic populations, hare densities were the average of the 2–4 years of highest density per hare oscillation (one to two oscillations). Peak of hare cycle estimates were used because hare browsing primarily affects vegetation when hare density is high (e.g., Wolff 1980; Radvanyi 1987). The estimates used mark-recapture methods, with the exception of the Northwest Territory hare survey, which used the Krebs et al. (2001) hare fecal pellet density estimate. The Mackenzie Basin regional comparison used the Krebs et al. (2001) hare fecal pellet density estimate. The estimates were done in the PAAB rectangles providing the birch samples. We have no estimate of hare density for the Great Lakes regional comparison. At the local scale, comparisons relied on anecdotal estimates from sources familiar with hare density in Wisconsin (Grange 1949) and Lac La Biche, Alberta (subsistence hunters/trappers).

Birch. We used percent PA (%PA) and gland density

(glands cm^{-1}), as have others (Tahvanainen et al. 1991), as measures of plant defense. Resin glands produce PA (Taipale et al. 1994). Percent PA was used to measure defense in congeneric comparisons and in conspecific comparisons with Alaska birch saplings. Current-year twigs (3 mm diameter, $n = 10$) were collected from 10 winter-dormant saplings (1.5–2 m tall) selected haphazardly from each population. Details of PA assays are provided in the appendix. Resin gland density (glands cm^{-1}) was the defense measure used for white birch saplings in conspecific comparisons. Gland density was also used for Alaska birch seedlings when testing soil-related ecotypic variation, carbon/nutrient balance, and induced defense alternatives. Two persons counted glands on the visible portion of 1 cm of current-year twig (white birch saplings) or main stem (Alaska birch seedlings). Count means were used in statistical analyses. Gland density was used because juvenile-phase North American white birch and all birch seedlings produce little PA (table 1; Julkunen-Tiitto et al. 1996); accurate PA assay is difficult and time consuming when %PA is low (T. P. Clausen, personal observation), and 300 white birch saplings and 891 Alaska birch seedlings were sampled. The two measures have been used interchangeably with success (Tahvanainen et al. 1991) because they are causally related. Resin glands produce PA (Taipale et al. 1994) and are, therefore, tightly correlated, as indicated by a linear regression of white birch gland density on corresponding %PA ($n = 158$; gland density = $1,200\%PA + 8$; $r^2 = 0.78$; $P < .001$).

Linking Fire and Birch Defense

Congener Comparison. Points of ignition were compared with the coordinates of 1,353 Alaska birch collections and 725 white birch collections (fig. A1B) provided by the authors and the institutions and individuals named in the acknowledgments. Spatial statistics (Cliff and Ord 1981) were computed using cells of $15,300 \text{ km}^2$ with a span of 1° latitude and an adjustable longitudinal span (correlograms were computed in R, and spatial t -tests were done in S-PLUS 2000). The fire data were tested for autocorrelation using a lag distance of 250 km and Moran's I . For both species of birches, significant positive autocorrelations in wildfire frequency existed up to distances of 1,000

km ($P < .001$ in all instances on the basis of permutation tests with 1,000 simulations). Significant positive autocorrelations also occurred for area burned up to distances of 1,000 km ($P < .001$ for lags ≤ 750 km, $P = .002$ for 750–1000 km). Spatial t -tests using both binary spatial weights and weights of $1/\text{lag}$ distance compared wildfire frequency (mean ± 1 SEM) in cells containing Alaska birch and cells containing white birch. Hare density was measured as described above. Defense was measured using %PA for saplings of Alaska birch ($n = 310$) and white birch ($n = 158$).

Conspecific Comparisons. Mean defense of populations was used in statistical analyses (SYSTAT; Wilkinson 1984) because the population was our experimental unit of interest. Data in the continental and regional comparisons were transformed to meet the linearity assumption (Zar 1974; transformed $\text{PAAB} = (\text{PAAB})/[\text{PAAB} + (K/\text{PAAB})]$, where $K = 4.57 \times 10^{-6}$) before regression of defense on transformed PAAB. At the local scale, comparisons of defense were conducted using t -tests of %PA after arcsine transformation (Lac La Biche) and resin gland density after square root transformation (Rhinelander).

Testing Alternative Explanations

Low Winter Temperature. We tested the winter temperature hypothesis by computing partial correlations between levels of defense for populations of Alaska birch ($n = 20$) and white birch ($n = 12$) and midwinter mean temperature (December–February; Alaska: National Center for Atmospheric Research Earth Observing Laboratory, <http://data.eol.ucar.edu/>; bioclimate profile for Canada: <http://www.cics.uvic.ca/scenarios/bcp/select.cgi>) in the rectangles providing birch samples, while controlling for PAAB. Partial correlations were also computed between defense and transformed PAAB after controlling for temperature.

Soil-Related Ecotypic Variation. The Alaska birch common garden experiment (described below) was used to test for soil-related ecotypic variation. The density of resin glands on stems of seedlings grown from seed obtained from two mother tree populations (mother trees on shallow

Table 1: Hare per capita daily intake (mg hare $^{-1}$ day $^{-1}$) of browse defense toxins

Browse	Toxin	Alaska	Wisconsin	P
Birch	Papyriferic acid	529 ± 83	39 ± 23	.001
Balsam poplar	Salicaldehyde + 6-HCH	$.2 \pm .02$	$.02 \pm .001$.001
Labrador tea	Germacrone	$.5 \pm .2$	$.10 \pm .03$.035

Note: Data are means ± 1 SEM; difference between means tested by one-tailed t -test. 6-HCH = 6-hydroxycyclohex-2-en-1-one.

stony acidic granite soil, mother trees on shallow stony basic limestone soil) from the same PAAB regime were compared.

Carbon/Nutrient Balance and Induced Defense. Seedlings of Alaska birch were grown (protocol in appendix) for one summer at the University of Wisconsin, Madison, from seed collected on a 900-km transect running from the Great Slave Lake (63°N, 118°W) to the Lesser Slave Lake (55°N, 116°W). Each sampled population was separated from others by at least 100 km. At leaf abscission, glands were counted a fixed distance (4–5 cm) above the root crown, eliminating the ontogenetic variation occurring in the seedling phase of birch (Bryant and Julkunen-Tiitto 1995). The white birch test used birches grown by the British Columbia Ministry of Forestry in a provenance garden. Vertebrate herbivores were excluded from plantings. Linear regression of defense on transformed PAAB was used for both experiments.

Unspecified, Distance-Dependent Variation in Defense. We examined partial correlations in pairwise differences in defense (Alaska birch Δ %PA; white birch Δ glands cm^{-1}), distance (Δ distance), and PAAB (Δ PAAB) for Alaska ($n = 528$ pairs) and white ($n = 465$ pairs) birch populations using partial Mantel tests (Goslee and Urban 2007). Significance was assessed using 10,000 permutations.

Geographic Variation in Hare Intake of Defense Toxins

Per capita daily toxin intake ($\text{mg hare}^{-1} \text{ day}^{-1}$) was compared for 10 snowshoe hares from Alaska and six from central Wisconsin. The trials used PA-rich birch resin, balsam poplar resin (*Populus balsamifera* L.; toxins are salicylaldehyde and 6-hydroxycyclohex-2-en-1-one [6-HCH]; Reichardt et al. 1990b) and Labrador tea resin (*Ledum groenlandicum* Oeder; toxin is germacrone; Reichardt et al. 1990a). Hares were acclimated over 10 days to toxins by supplementing their rabbit chow diet with resin-rich browse. For 48 h, they were then fed chow adulterated with resin applied at the twigs' resin concentration, and per capita daily toxin intake was computed from resin intake. Untransformed data were analyzed by *t*-tests. Hares were maintained at 0°C in approved animal facilities (University of Alaska, Fairbanks; University of Wisconsin, Madison) and released unharmed where captured.

Results

Tests of FHD Hypothesis

Congener Comparison. Collectively, the congener results support the FHD hypothesis. We found mean (± 1 SEM)

fire frequency to be more closely associated with Alaska birch (26.8 ± 1.7) than with white birch (12.2 ± 1.3 ; fig. A1B; $t = 11.9$, $P < .001$ for binary weights and $t = 12.1$, $P < .001$ for inverse weights). Mean wildfire frequency also was greater in cells containing Alaska birch than in cells with fire but no birches (17.7 ± 1.3 ; $t = 6.3$, $P < .001$ and $t = 7.1$, $P < .001$), whereas no difference was evident for wildfire frequency in cells without birches and those with white birch ($t = 0.3$, $P = .75$ and $t = 0.4$, $P = .70$). Hare density within the Alaska birch's range (2–13 hares ha^{-1}) exceeded hare density reported for the white birch's range (0.1–2 hares ha^{-1}). Visual inspection of differences in gland densities on twigs of individual birches (fig. 1) clearly suggests that Alaska birch is more defended than white birch, an observation confirmed by chemical assays. Alaska birch %PA (mean = 23%, SEM = 3%, range = 6%–50%) exceeded average %PA of white birch (mean = 1.3%, SEM = 0.01%, range = 0%–5%) by more than an order of magnitude ($P < .001$).

Conspecific Comparisons. Conspecific comparisons supported the FHD hypothesis at all spatial scales. At a continental scale, positive correlations existed between levels of chemical defense and PAAB for Alaska birch (fig. 2A) and white birch (fig. 2B). In the Mackenzie Basin region, positive correlations existed between hare density and PAAB (fig. 3A), as well as between %PA of Alaska birch and hare density (fig. 3B). In the Great Lakes region, a positive correlation existed between resin gland density of white birch and PAAB (fig. 3C). PAAB also increased from central Wisconsin to northwest Ontario, and hare density increased from Wisconsin (Murray 2000) to northern Minnesota near the Ontario border (Green and Evans 1940), suggesting a positive correlation between hare density and PAAB, as first noted by Grange (1949, 1965). At the local scale, hare density was highest in the forests with high PAAB at Lac La Biche (S. M. Landhäuser, personal communication) and in Wisconsin (Grange 1949). Mean defense (± 1 SEM) was two- to threefold greater ($P < .001$) in the forests with high PAAB at Lac La Biche (%PA for high = $13\% \pm 0.2\%$; low = $6\% \pm 0.2\%$) and Rhineland (gland density for high = 27 ± 4 glands cm^{-1} ; low = 0.9 ± 0.04 glands cm^{-1}).

Tests of Alternative Explanations

None of the five alternative explanations for geographic variation in chemical defense of birches received support.

Low Temperature. Partial correlations of defense and winter temperature were not significant after controlling for PAAB (Alaska birch: $r = 0.27$, $df = 17$, $P = .19$; white birch: $r = -0.02$, $df = 9$, $P > .50$). In contrast, partial

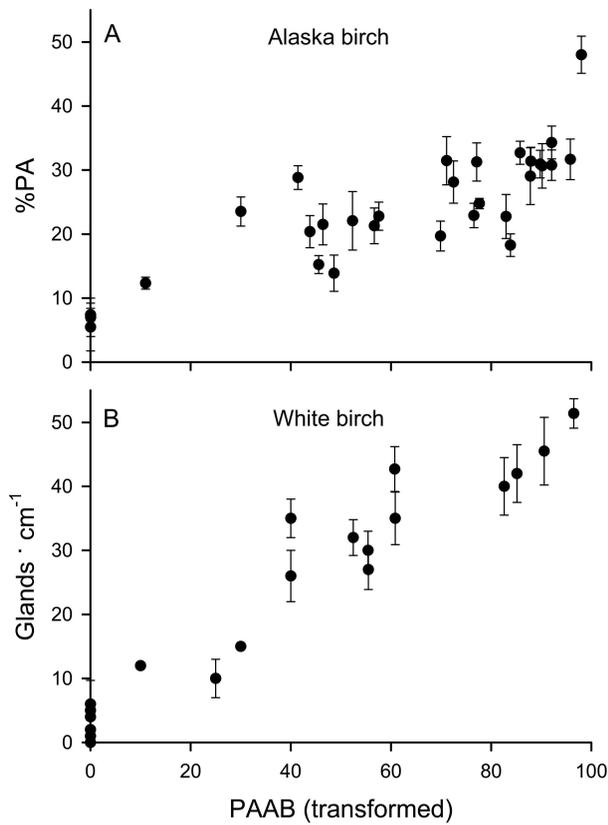


Figure 2: Continental associations between levels of chemical defense for tree birch and the percent of area annually burned (PAAB; after transformation to achieve linearity) in boreal forests of North America. Data are population means \pm 1 SEM. A, Relationship for Alaska birch ($y = 0.26x + 0.08$, $df = 28$, $r^2 = 0.69$, $P < .001$). B, Relationship for white birch ($y = 51x + 2$, $df = 25$, $r^2 = 0.95$, $P < .001$).

correlations of defense and PAAB were positive and significant after controlling for temperature (Alaska birch = 0.76, $P < .001$; white birch = 0.98, $P < .001$), consistent with predictions of the FHD hypothesis.

Soil-Related Ecotypic Variation. Defense of Alaska birch seedlings grown from seed from mother trees on granite soil did not differ from defense of seedlings grown from seed from mother trees on limestone soil (mean glands $\text{cm}^{-1} \pm 1$ SEM: granite, 23 ± 1 ; limestone, 21 ± 1 ; $t = 1.4$, $df = 136$, $P > .50$).

Carbon/Nutrient Balance and Induced Defense. Populations of different origin grown in browsing-protected common gardens revealed differences in levels of defense and also yielded positive correlations between defense and PAAB (Alaska birch: $r^2 = 0.79$, $df = 7$, $P = .001$; white birch: $r^2 = 0.86$, $df = 5$, $P = .003$). The former result is

inconsistent with the carbon/nutrient balance and induced defense hypotheses, whereas the latter result supports the FHD hypothesis.

Unspecified, Distance-Dependent Variation in Defense. For both Alaska and white birch, correlations between Δ de-

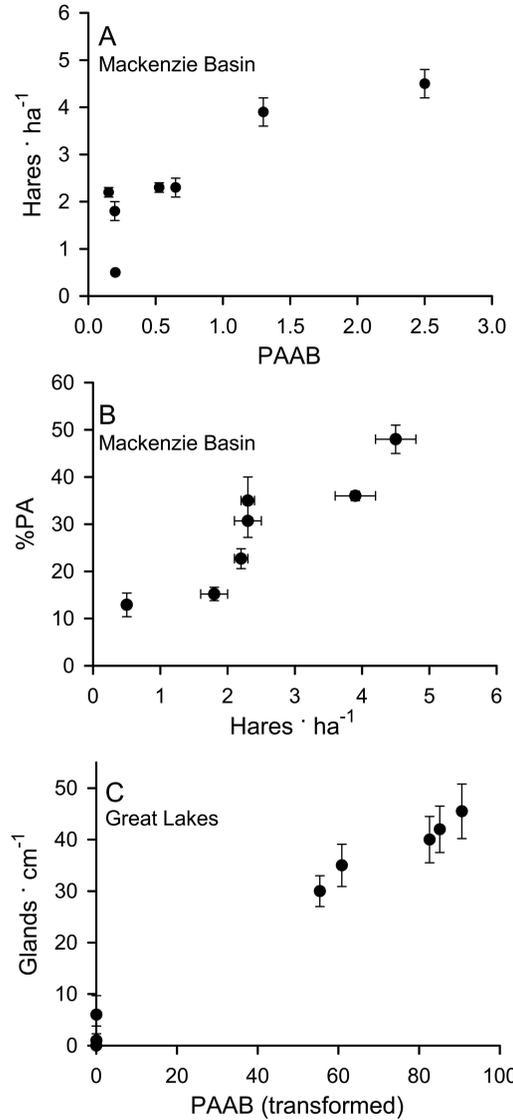


Figure 3: Regional conspecific comparisons related to the fire-hare-defense hypothesis. Data are population means \pm 1 SEM. A, Relationship between hare density and percent of area annually burned (PAAB) in the Mackenzie Basin ($y = 137x + 1$, $df = 5$, $r^2 = 0.77$, $P = .009$). B, Correlation between defense of Alaska birch (%PA) and hare density in the Mackenzie Basin ($y = 0.08x + 0.07$, $df = 5$, $r^2 = 0.81$, $P = .005$). C, Correlation between fire (PAAB transformed) and defense of white birch (resin glands cm^{-1}) in the Great Lakes region ($y = 48x + 2$; $r^2 = 0.98$; $P < .001$).

fense and Δ distance were weaker than correlations between Δ defense and Δ PAAB. Partial Mantel tests for Alaska birch revealed a nonsignificant correlation between Δ distance and Δ defense, after controlling for Δ PAAB ($r = -0.08$, $P > .50$). Results of the same test for white birch yielded a weak but significant partial correlation ($r = 0.22$, $P = .007$). Thus, it is unlikely that a latent, distance-dependent variable is driving geographic variation in defense. Notably, partial Mantel tests of the correlation between Δ defense and Δ PAAB, after controlling for Δ distance, were much stronger and highly significant for Alaska birch ($r = 0.64$, $P < .001$) and white birch ($r = 0.66$, $P < .001$), providing more support for the FHD hypothesis.

Geographic Variation in Hare Intake of Defense Toxins.

Consumption of toxins by Alaskan hares was five (Labrador tea) to 100 times (balsam poplar) greater than for Wisconsin hares (table 1), indicating substantial differences in tolerances to plant toxins for these geographically isolated populations of hares.

Discussion

We tested the FHD hypothesis that transcontinental variation in fire, via the positive effect of fire on hare density (Grange 1949, 1965; Fox 1978; Pease et al. 1979; Paragi et al. 1997), has resulted in corresponding transcontinental variation in antibrowsing defense of juvenile-phase tree birch. When comparing birch congeners, fire frequency and PAAB were greatest within the range of Alaska birch. Likewise, estimates of hare density indicated that hares are most abundant within the range of Alaska birch. Thus, at the level of birch congeners, there is good evidence for the proposed causal linkages between hare density and fire and between birch defense and hare density. Comparisons of conspecific birches supported the FHD hypothesis at continental, regional, and local scales. The Mackenzie Basin comparison is particularly interesting because (1) hares there are so abundant that the Sahtu Dené were called the "hare people" by European explorers (Hiroko 1980) and (2) we were able to document the complete set of positive correlations predicted by the FHD hypothesis.

We found no evidence supporting alternative explanations of geographic variation in birch defense. Winter temperature did not seem to drive defense, since no significant correlation existed between defense and temperature after controlling for PAAB. In contrast, the significant partial correlation between defense and PAAB after controlling for temperature provided more evidence for FHD. Soil-related ecotypic variation cannot explain geographic variation in defense of Alaska birch. Holding mother tree

PAAB regime constant, defense of seedlings grown from seed from mother trees on granite soil versus limestone soil was the same. The carbon/nutrient balance explanation was rejected, because levels of defense differed for birch populations from different geographic localities grown in common gardens. Induced defense also is not a viable explanation of the differences in defense among plants grown in common gardens in the absence of vertebrate herbivory. Moreover, simulated hare browsing actually reduces the defense of Alaska birch saplings, suggesting a lack of induced chemical defense in response to browsing (Chapin et al. 1985). Importantly, variation in levels of defense for garden-grown birches was correlated with PAAB in the areas from which the birches were collected, thus providing very strong support for FHD. Finally, a latent driver of spatial variation in defense, such as the distance among Pleistocene birch refugia occurring in Eurasia (Palmé et al. 2003), is unlikely to explain the patterns we observed. Partial correlations of pairwise differences between distance and defense were weak (and, in one case, negative) compared with partial correlations between PAAB and defense.

We have assumed the preeminence of the hare as the ecological link between fire and antibrowsing defense. The hare's presumed importance does not, however, eliminate a role for other members of the boreal browsing mammal guild. All guild members are fire dependent and forage almost exclusively on early postfire vegetation (Bryant and Kuropat 1980; Bryant et al. 1983). Thus, while the long tenure of hares in the north (e.g., Dixon 1984) makes it the prime candidate for initiation of the fire-defense linkage, it almost certainly is true that other members of the browsing mammal guild now help maintain the linkage.

Although we did not set out to test Thompson's (2005a, 2005b) hypothesis for a geographic mosaic of selection, our results clearly support it at a transcontinental scale. Additionally, our hare-feeding experiments provided circumstantial evidence for the existence of a continental-scale geographic mosaic of coevolution congruent with the proposed transcontinental selection mosaic. Our study is insufficient to determine whether a hare-birch coevolutionary mosaic exists (Gomulkiewicz et al. 2007). However, we believe that further empirical tests of birch-hare selection and coevolutionary mosaics are warranted, especially given the unprecedented spatial scale at which these terrestrial mosaics could operate relative to other previously documented consumer-resource mosaics (e.g., Thompson 2005b; Thompson and Fernandez 2006; Toju and Sota 2006; Siepielski and Benkman 2007; Toju 2008).

To summarize, we found that across spatial scales ranging from continental to local, crown-destroying fire, by affecting vegetation, may have resulted in more intense selection of birch for antibrowsing defense. Local patch-

iness in fire history resulted in more heavily defended birches where fire was more frequent. In the case of Lac La Biche, Alberta, fire patchiness was created by a lake. The more defended birches occurred in the higher PAAB mainland forest, where snowshoe hares are more abundant. The less defended birches occurred on infrequently burned islands in the lake, where hares are rare. At Rhineland, Wisconsin, the forests used were selected on the basis of soil type and forest structure to exploit local spatial heterogeneity in fire (Cleland et al. 2004). Again, forests with a history of more frequent crown-destroying fires contained the most defended birches. Grange (1949) has documented that in the Lake States region, fire-prone forests harbor more hares.

At the continental scale, our results suggest that fire's effect is determined largely by geographic features such as mountain ranges and associated rain shadows. For example, the Alaska birch continental comparison extended from relatively moist western Alaska (Guthrie 2001) to the more arid regions to the east. As aridity increased, PAAB increased, hare density increased, and Alaska birch defense increased. Thus, at the large spatial scale, our data are congruent with Smith's (1970) finding that fire, by affecting lodgepole pine (*Pinus contorta*) cone morphology and the frequency of cone crops, affects selection for cone defense by pine squirrels (*Tamiasciurus* spp.). The implication of our results and those of Smith (1970) is clear. Research on selection mosaics and associated geographic mosaics of coevolution should attempt to determine whether physical forces underlie the mosaics.

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