

Subspecific selectivity by a mammalian herbivore: Geographic differentiation of interactions between two taxa of *Sciurus aberti* and *Pinus ponderosa*

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Summary

We compared host selection by two subspecies of Abert's squirrel, a highly specialized and selective herbivore. Both subspecies are restricted to stands of ponderosa pine, upon which they are ecologically dependent, but the two subspecies are geographically disjunct and each is closely associated with stands of trees that represent strongly differentiated chemical races. The criteria by which trees were selected as sources of phloem by each subspecies of squirrel included heritable features of xylem oleoresin and phloem. Trees that were potentially available to the subspecies of squirrel in Colorado differed substantially in biochemical features from trees that were available to the subspecies in Arizona; as a result, chemically mediated feeding patterns were distinct between the two squirrel subspecies. Based on multivariate analysis of chemical characteristics, trees utilized by the squirrels for feeding (target trees) differed significantly from control trees (non-target trees) for each subspecies. However, the discriminant functions that separated target trees from non-target trees within a site generated different patterns of predicted classification when applied to trees at the other site. Vertebrate herbivores that are feeding specialists can exert selection pressures in populations of their host plants, and results suggest that geographically differentiated herbivore–host interactions can produce different sets of selection pressures, which may result in different evolutionary outcomes. Such geographic differentiation is a potentially important evolutionary aspect of chemically mediated mammal–plant interactions.

Keywords: biogeography; geographic differentiation; herbivory; mammal–plant interactions; *Pinus*; *Sciurus*

Introduction

The nature of chemically mediated ecological and evolutionary interactions between mammalian herbivores and host plants remains poorly understood (e.g. Spencer, 1988; Harborne, 1993; Thompson, 1994). Many investigators question whether significant evolutionary interactions occur at all, given the dietary breadth and therefore presumed weak or diffuse selection pressures exerted by the majority of mammalian herbivores. However, vertebrate herbivores that are feeding specialists, such as Abert's squirrel, Stephens' woodrat (*Neotoma stephensi*; Vaughan, 1982), the giant panda (*Ailuropoda melanoleuca*; Schaller *et al.*, 1985) and spruce grouse (*Dendragapus canadensis*; Mueller, 1993), may act as strong selective agents in populations of their host plants (Snyder, 1993). Furthermore, geographically differentiated host populations can present differentiated populations of such herbivores with different trophic choices. The majority of studies that have described mammalian herbivore–host plant interactions did not address this geographic component because they were undertaken either at the level of individual populations, or at the whole

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species level (e.g. cladistic analyses; Thompson, 1994). As Thompson points out, this gap in our understanding of the evolutionary consequences of interactions between vertebrate herbivores and their hosts can be addressed only by investigating the geographic structure of interactions, since different sets of ecological conditions can be expected to produce different sets of evolutionary outcomes.

We report here on differential herbivory upon two distinct varieties of ponderosa pine (*Pinus ponderosa*) by two distinct subspecies of Abert's squirrel (*Sciurus aberti*), a highly specialized and selective herbivore. We undertook this comparative study to determine the factors that might mediate patterns of selectivity between geographically disjunct and morphometrically differentiated subspecies of a mammalian herbivore and its host, which is comprised of chemically and genetically differentiated races. We investigated a broad array of potentially attractive and deterrent host features, some with known genetic components. Geographic differentiation of selective herbivory that is mediated by such traits can potentially lead to different evolutionary outcomes in different populations. The features of xylem oleoresin included flow rate and monoterpene composition, both of which are under strong genetic control in the genus *Pinus* (Hanover, 1966; Gansel and Squillace, 1976; White and Nilsson, 1984), which includes ponderosa pine (Smith, 1964, 1967, 1977). Phloem characteristics included elemental accumulation, for which genetic control is also known for various plants including conifers (Glass and Perley, 1972; Epstein, 1973; McLean and El-Kassaby, 1986).

To ascertain the effects of geographic differentiation upon these interactions, we tested: (1) the extent to which chemical and physiological variability in the southwestern race of *Pinus ponderosa scopulorum* was associated with observed patterns of feeding on inner bark by *Sciurus aberti aberti*; and (2) whether specific factors associated with selective herbivory by *S. a. aberti* were the same as those known to mediate feeding patterns by the geographically disjunct subspecies *S. a. ferreus* in the Rocky Mountain race of *P. p. scopulorum*.

Few mammals are as dependent upon a single plant species as is Abert's squirrel upon ponderosa pine. The level of its ecological reliance on this single tree species arguably surpasses that of such classic dependencies as the giant panda's upon approximately 25 species of bamboo (Schaller *et al.*, 1985) and of the koala upon approximately 30 species of eucalyptus (Lee and Martin, 1988), since populations of both of these specialists routinely feed on several host species within given geographic areas. Abert's squirrel is typically restricted to stands of ponderosa pine, upon which it is ecologically dependent (Keith, 1965). Seasonally, Abert's squirrel subsists primarily or solely upon inner bark from specific individual ponderosa pine trees, which can be heavily defoliated by the squirrels' feeding activities (Keith, 1965; Farentinos, 1972a,b; Patton, 1975; Hall, 1981; States *et al.*, 1988; Snyder, 1992, 1993). Abert's squirrel may impose directional selection pressures within populations of host trees because it feeds preferentially on trees with specific genetically controlled traits and because target trees suffer significant fitness impacts (Snyder, 1992, 1993, in press). Conversely, the potential for selective pressures imposed by the trees upon populations of the squirrel can only be inferred at this time from the squirrel's geographic restriction to, and ecological dependence upon, ponderosa pine forests.

Ponderosa pine is the most widely distributed conifer in North America, ranging from British Columbia south to Durango, Mexico, and from California east to Nebraska. Across this range, it is differentiated into several distinct morphological, genetic and chemical taxa, and also shows substantial genetic and biochemical variability within populations (Smith, 1977; Conkle and Critchfield, 1988). Abert's squirrel inhabits stands of ponderosa pine in the Rocky Mountains from extreme southern Wyoming to southern New Mexico and Arizona in the United States, and along the Sierra Madre Occidental from northwestern Chihuahua to western Durango in Mexico. Within this range, the squirrel is differentiated into six geographically disjunct, morphometrically distinct

subspecies (Hoffmeister and Diersing, 1978). The subspecies we studied (*S. aberti ferreus* and *S. aberti aberti*) belong to groups representing the highest dissimilarity among all locality clusters used in the morphometric analysis of Hoffmeister and Diersing (1978), which included all six subspecies. The two subspecies of squirrel inhabit stands of ponderosa pine that are strongly differentiated and are often referred to as 'races' (Smith, 1977; Conkle and Critchfield, 1988). Although the squirrel–pine trophic interactions and their consequences reported here have been studied intensively for several years both in Colorado (Snyder, 1992, 1993) and in Arizona (Snyder and Linhart, 1994), this study is the first to investigate the potential for different evolutionary outcomes in geographically differentiated squirrel–pine interactions.

Methods

At the Bald Mountain Scenic Area in Colorado, 30 target trees and 30 corresponding non-target trees were identified, tagged and mapped in 1985. The site and criteria for designating trees have been described previously (Snyder, 1992). At the Pearson Research Natural Area in Arizona (described in Avery *et al.*, 1976), 40 target trees and 40 corresponding non-target trees were identified in 1990. Target trees were designated based upon unambiguous evidence of current twig-clipping by Abert's squirrels and reports of previous twig-clipping in these trees from a published record spanning 60 years of use of individual trees at this site (Avery *et al.*, 1976). Non-target trees were designated on the basis of similarity in size and close physical proximity to matched target trees, and no record of attack during this 60-year period.

At both sites, qualitative and quantitative xylem characteristics were measured. Oleoresin exudation pressure and monoterpene composition are known to affect patterns of attack in ponderosa pine by a variety of herbivores (e.g. Smith, 1977), including Abert's squirrel (Snyder, 1992). Oleoresin flow rates were used as a relative measure of exudation pressures. Flow rates were determined by methods modified slightly from Smith (1977) as detailed in Snyder (1992). Xylem oleoresin collected from individual trees was subsequently analysed by gas–liquid chromatography for percent composition of eight monoterpenes (α -pinene, β -phellandrene, β -pinene, 3-carene, limonene, myrcene, γ -terpinene and terpinolene). The handling and analysis of oleoresin samples were performed according to methods modified slightly from Smith (1977) as detailed in Snyder (1992).

At both sites, phloem was extracted from twigs with terminal needle clusters collected in the upper crowns of trees, where feeding by squirrels is concentrated. In Colorado, twigs were clipped with a rope-pull tree pruner mounted on a 9 m extension pole, and brought to the laboratory for immediate processing. In Arizona, twigs were obtained by severing them from larger branches with a 20-gauge shotgun, and stored at 5°C until they were brought to the laboratory for processing. Collections were made during late autumn and winter, the peak phloem-feeding seasons. Phloem was peeled from twigs with a drawknife, air-dried and pulverized to a fine powder in a steel, motorized grinder. All samples were analysed for percent total non-structural carbohydrates (Hodge and Hofreiter, 1962) as a measure of energy content, and for concentrations of Ca, P, K, Mg, Mn and Na (potential attractants) and Al, Cu, Fe and Si (potential deterrents). The rationale for focusing on these particular features of the phloem is discussed by Snyder (1992). Elemental analysis was performed using an inductively coupled plasma spectrometer as described by Snyder (1992).

Univariate and multivariate statistical analyses involving characteristics of target and non-target trees are described in Snyder (1992). Discriminant function analysis was also performed using chemical characteristics of trees from all four groups (i.e. target trees in Arizona, non-target trees in Arizona, target trees in Colorado and non-target trees in Colorado) to determine how differences

between target and non-target trees within sites compared with differences between sites. In addition, we used the discriminant functions that separated target trees from non-target trees within each site to predict group classification of each tree at the other site. These analyses were performed separately for characteristics of phloem and for characteristics of xylem oleoresin.

Results

Of the 40 target trees designated in Arizona in 1990, 37 showed signs of continued use (i.e. inner bark feeding) in 1995. Of the 40 non-target (control) trees designated in 1990, none showed evidence of use in 1995. In Colorado, target trees were not always used in each year of the study (detailed in Snyder, 1992, 1993), but none of the non-target trees designated in 1985 showed evidence of use over the following 12 years.

Characteristics of xylem oleoresin

In Arizona, discriminant function analysis based solely on oleoresin characteristics correctly classified 80.6% of the target trees and 55.9% of the non-target trees as a target or non-target tree respectively (overall correct classification = 67.7%). Differences were not significant ($F = 0.871$, $P = 0.55$). Of the oleoresin characters measured, the level of β -pinene contributed most to the discrimination between target trees and non-target trees. Oleoresin flow rates were not significantly different between target trees ($2.37 \pm 0.34 \text{ ml day}^{-1}$) and matched non-target trees ($2.20 \pm 0.36 \text{ ml day}^{-1}$; $P = 0.74$). Oleoresin from target trees had significantly lower levels of β -pinene ($0.60 \pm 0.34\%$) than oleoresin from matched non-target trees ($5.14 \pm 1.95\%$; $P = 0.03$). Oleoresin from target and non-target trees did not differ significantly in levels of β -phellandrene ($0.03 \pm 0.01\%$ and $0.04 \pm 0.02\%$ respectively; $P = 0.59$). Results from previous chemical analyses of target and non-target trees in Colorado are detailed in Snyder (1992). In those investigations, discriminant function analysis based solely on characteristics of xylem oleoresin correctly classified 89.5% of the cases as either target or non-target trees ($P < 0.0001$). Oleoresin flow rate and levels of β -phellandrene and β -pinene in the oleoresin contributed most to the discrimination between target trees and non-target trees in Colorado.

Characteristics of phloem

In Arizona, discriminant function analysis based solely on chemical characteristics of phloem correctly classified 79.5% of target trees and 71.8% of non-target trees as either a target or non-target tree respectively (overall correct classification = 75.6%; $F = 2.78$, $P = 0.005$). Phloem from target trees had marginally greater concentrations of sodium ($44.31 \pm 3.82 \mu\text{g g}^{-1}$) than phloem from matched non-target trees ($35.82 \pm 2.39 \mu\text{g g}^{-1}$; $P = 0.07$); levels of non-structural carbohydrates were not significantly different between phloem from target trees and matched non-target trees. By comparison, in previous work in Colorado, discriminant function analysis based solely on characteristics of phloem correctly classified 97.6% of trees as either target or non-target trees ($P < 0.001$; Snyder, 1992). Concentrations of sodium and non-structural carbohydrate in the phloem contributed most to the discrimination between target trees and non-target trees in Colorado.

Discriminant function analyses involving both sites

To facilitate the comparison of feeding patterns by the two subspecies of squirrel in stands of the two races of tree, we performed an additional discriminant function analysis using chemical characteristics of trees from the four groups (i.e. target and non-target trees in Arizona, target and

non-target trees in Colorado; Fig. 1). The first discriminant function clearly demonstrates chemical differentiation between the two races of tree (i.e. trees in Colorado *vs* trees in Arizona). The second discriminant function separates trees on the basis of class (i.e. target *vs* non-target). As we found using the within-site discriminant function analyses (described in the previous paragraphs), there was greater discrimination between target trees and non-target trees in Colorado than in Arizona, both in phloem chemistry and xylem oleoresin characteristics.

In addition, we used the discriminant functions that separated target trees from non-target trees within each site to predict group classification of each tree at the other site (Table 1). The dis-

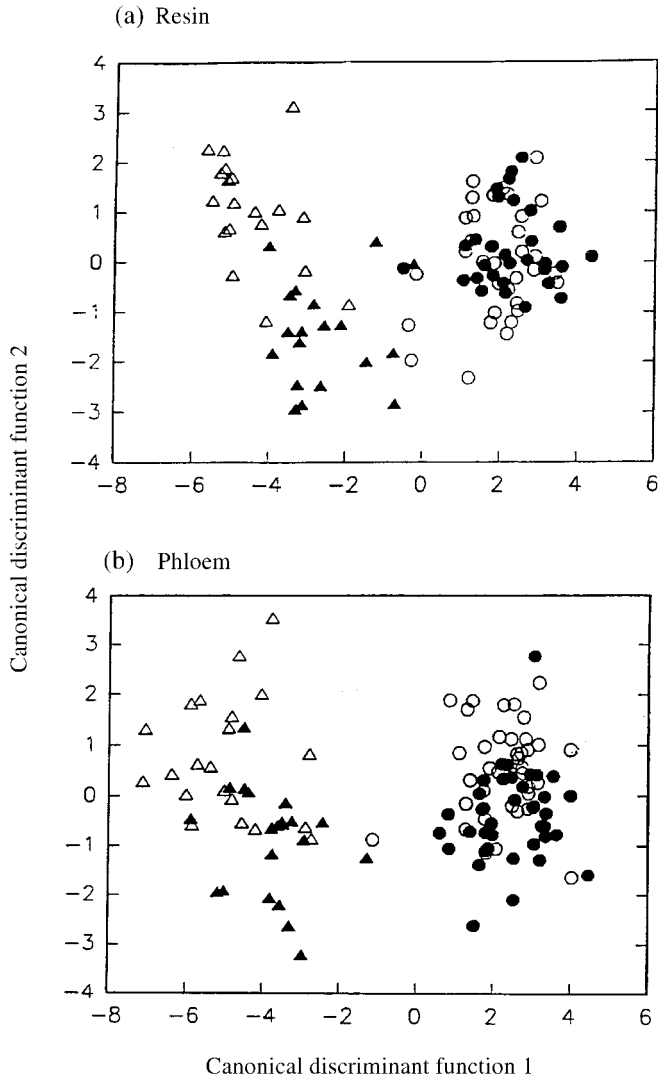


Figure 1. Plots of discriminant function scores from discriminant analysis of four groups of trees (Arizona target trees, solid circles; Arizona non-target trees, open circles; Colorado target trees, solid triangles; Colorado non-target trees, open triangles).

Table 1. Summary of cross-site discriminant function analyses^a

	Predicted classification	
	Non-target tree	Target tree
<i>Colorado trees classified by Arizona discriminant functions</i>		
Phloem	90.5	9.5
Xylem oleoresin	100.0	0.0
<i>Arizona trees classified by Colorado discriminant functions</i>		
Phloem	1.3	98.7
Xylem oleoresin	1.6	98.4

^aDiscriminant functions generated at each site were used to predict group membership (target tree or non-target tree) for trees at the other site ($38 \leq N \leq 78$). Actual number of target trees and non-target trees was equivalent within each site. Percentage predicted classification is reported using discriminant functions for phloem and for xylem oleoresin.

criminant function that separated target trees from non-target trees based on oleoresin characteristics of trees in Colorado classified all but one tree at the Arizona site as a target tree. The same was true for the discriminant function that separated target from non-target trees based on phloem characteristics.

The discriminant function that separated target trees from non-target trees based on oleoresin characteristics of trees in Arizona classified all trees at the Colorado site as non-target trees. The discriminant function that separated target trees from non-target trees based on phloem characteristics of trees in Colorado classified all but four trees at the Colorado site as non-target trees.

Discussion

Trophic interactions between individual subspecies of Abert's squirrel and individual races of ponderosa pine are strongly associated with specific, geographically differentiated features of host biochemistry. Such geographic differentiation of feeding patterns can potentially lead to different sets of evolutionary consequences for different host populations, since Abert's squirrels may be important agents of natural selection within stands of ponderosa pine (Snyder, 1993).

The southwestern race of *P. ponderosa scopulorum* differs markedly in chemical features from the Rocky Mountain race, and within each group target trees are chemically differentiated from non-target trees (Fig. 1; Table 2). The squirrels' feeding patterns apparently result in part from somewhat similar selection criteria in the two groups. However, because chemical features of trees that are potentially available as sources of inner bark differ between the two chemical races, the consequences of the squirrels' feeding activities are also different and can result in multi-directional selection pressures of different intensities in Arizona compared with Colorado. In both Arizona and Colorado, Abert's squirrel is dependent upon the inner bark of ponderosa pine as a primary source of nutrition, yet the biochemical features of trees that are potentially available as sources of food differ substantially between the two regions (see Table 2). Patterns of dietary selection by the animals might therefore be expected to vary somewhat between the two regions. Extensive genetic differentiation between these tree taxa, including their biochemical profiles, exists primarily because of different spatio-temporal suites of selective pressures that are present in geographically and climatically distinct regions (Smith, 1977; Conkle and Critchfield, 1988). For example, there have

Table 2. Summary of univariate comparisons which illustrate geographic differentiation of selective herbivory by Abert's squirrel upon ponderosa pine

	Colorado			Arizona		
	Target	Non-target	<i>P</i>	Target	Non-target	<i>P</i>
<i>Xylem oleoresin</i>						
Flow rate (ml day ⁻¹)	2.20 ± 0.45	5.30 ± 0.72	< 0.001	2.37 ± 0.34	2.20 ± 0.36	0.746
β-pinene (%)	16.86 ± 1.72	22.62 ± 2.15	0.044	0.60 ± 0.34	5.14 ± 1.95	0.032
β-phellandrene (%)	0.51 ± 0.07	0.81 ± 0.09	0.014	0.03 ± 0.01	0.04 ± 0.02	0.591
<i>Phloem</i>						
Sodium (μg g ⁻¹)	18.00 ± 2.50	9.86 ± 1.50	0.008	44.31 ± 3.82	35.82 ± 2.39	0.075
TNC (%) ^a	6.44 ± 0.44	4.74 ± 0.49	0.013	14.60 ± 0.34	14.55 ± 0.21	0.972
Calcium (μg g ⁻¹)	9385.81 ± 729.25	9823.19 ± 719.73	0.672	5479.72 ± 279.85	7265.31 ± 361.83	< 0.001

^aTotal non-structural carbohydrates.

been two major bark beetle (*Dendroctonus ponderosae* Scolytidae) epidemics and repeated dwarf mistletoe (*Arceuthobium vaginatum* Viscaceae) infestations at our Colorado site during the past 100 years or so (attacks by both species have led to large-scale mortality in this stand; Linhart *et al.*, 1994). In contrast, beetle and dwarf mistletoe activity has been much lower during the same time period at our Arizona site (Avery *et al.*, 1976). The squirrels, also variable, are faced with different suites of trophic choices in different regions (detailed below). These variable sets of ecological conditions have apparently produced squirrel–tree interactions with different characteristics and consequences.

In *S. a. ferreus* living in stands of the Rocky Mountain race of ponderosa pine in Colorado, selective herbivory was associated with: (1) significantly lower levels of β -pinene and β -phellandrene in the xylem oleoresin; (2) a significantly lower oleoresin flow rate; (3) significantly higher concentrations of sodium and non-structural carbohydrates in the phloem; and (4) significantly lower levels of iron in the phloem (Snyder, 1992). Target trees in these populations showed significant reductions of up to 90% in several fitness components, including female cone production, male strobilus production, incremental growth and seed quality (Snyder, 1993).

In *S. a. aberti* living in stands of the southwestern race of ponderosa pine in Arizona, selective herbivory was associated with: (1) significantly lower concentrations of β -pinene in the xylem oleoresin; and (2) marginally higher concentrations of sodium in the phloem. However, oleoresin flow rate and concentrations of non-structural carbohydrates and iron in the phloem were similar in target trees compared with matched non-target trees. In addition, levels of calcium were significantly lower in target trees than in non-target trees. Target trees in this population also produced significantly fewer female cones than non-target trees.

Therefore, for both subspecies, selective herbivory was associated with relatively low levels of β -pinene in the oleoresin and relatively high levels of sodium in the phloem. However, there were several inconsistencies in biochemical correlates of feeding patterns between the two subspecies that warrant examination. In all cases, these inconsistencies (detailed in the following paragraphs) reflect differences in chemical features of potential host trees between the two regions (i.e. geographic differentiation of chemical features of those trees). These features include xylem oleoresin flow rate, levels of β -phellandrene in the oleoresin, and levels of sodium, non-structural carbohydrates and calcium in the phloem (Table 2).

Oleoresin flow rate was significantly lower in target trees than in non-target trees in Colorado. Differences between target and non-target trees were not significant in Arizona, where flow rate was, overall, lower and less variable than in Colorado, and may therefore have been insufficient to deter squirrels from twig-clipping. The mean flow rate of non-target trees in Arizona (2.2 ± 0.36 ml day⁻¹) was essentially equivalent to the target tree flow rate in Colorado (2.2 ± 0.45 ml day⁻¹). In contrast, the flow rate of non-target trees in Colorado averaged 5.3 ± 0.72 ml day⁻¹.

Levels of β -phellandrene were demonstrated with behavioural bioassays to mediate feeding choices by squirrels in Colorado, with target trees having significantly lower levels of this monoterpene (Snyder, 1992). There were no differences in β -phellandrene levels between target and non-target trees in Arizona, where the percentage composition of β -phellandrene is very small, ranging from about 0.02 to 0.06%. These levels are an order of magnitude lower than levels of β -phellandrene in Colorado, and may be too low to mediate feeding patterns in these populations. By comparison, the percentage composition of β -phellandrene in Colorado averaged $0.51 \pm 0.07\%$ for target trees and $0.81 \pm 0.09\%$ for non-target trees.

Levels of sodium were significantly higher in phloem from target trees than in phloem from non-target trees in Colorado ($P = 0.008$); however, in Arizona, levels were only marginally higher in phloem from target trees than in phloem from non-target trees ($P = 0.075$). Sodium was the most

significantly different component of all characteristics of phloem measured in target and non-target trees in Colorado. It was found in twice the concentration in target trees ($18.00 \pm 2.50 \mu\text{g g}^{-1}$) than in matched non-target trees ($9.86 \pm 1.50 \mu\text{g g}^{-1}$). Conversely, sodium was found in much higher concentrations in Arizona than in Colorado, which may explain why sodium selection may be somewhat less intense in Arizona.

Levels of non-structural carbohydrates were significantly higher in phloem of target trees than in phloem of non-target trees in Colorado, yet levels were not significantly different in target and non-target trees in Arizona. After sodium, the level of non-structural carbohydrate was the most important variable separating target from non-target trees in Colorado. In Arizona, levels of non-structural carbohydrate did not differ significantly between target and non-target trees; however, it was found at much higher levels in Arizona, which may make it unnecessary for squirrels in that population to be selective with regard to carbohydrate content.

Concentrations of calcium did not differ significantly between phloem from target trees and phloem from non-target trees in Colorado, yet calcium occurred in significantly lower concentrations in target trees than in non-target trees in Arizona. The nutritional requirements of herbivores may be related more to the relative proportion of dietary calcium *vis-à-vis* other nutrients than to absolute calcium concentrations themselves (Underwood, 1966; Robbins, 1983; Masslich *et al.*, 1988), but it is unclear whether feeding patterns in Arizona and Colorado may be affected by these proportions.

These univariate comparisons between Arizona and Colorado illustrate the complexities of geographic differentiation of squirrel–pine interactions in the two regions. The strong association of squirrel feeding patterns with heritable biochemical variability in potential host trees provides compelling evidence for chemically mediated selective herbivory that can result in different arrays of selection pressures within chemically differentiated taxa of host trees. The extent to which these interactions are differentiated between taxa is underscored by results from our use of discriminant functions that separate target trees from non-target trees within one site to predict group classification of trees within the other site. For example, the discriminant function that used chemical characteristics of either phloem or xylem oleoresin to distinguish between target trees and non-target trees in Arizona predicted that all or most of the target trees at the Colorado site would be classified as non-target trees (and therefore not suitable as sources of phloem). Conversely, discriminant functions that used chemical characteristics of either phloem or xylem oleoresin to distinguish between classes of trees in Colorado predicted that all or most of the non-target trees at the Arizona site would be classified as target trees (Table 1).

We recognize that the feeding patterns of the squirrels may be affected, in part, by characteristics that we did not measure, including the presence and concentration of other chemical compounds such as specific sesquiterpenes or phenolics, the thickness of phloem or other morphological characteristics of trees. In addition, it is possible that features that were associated with feeding patterns may be correlates of other unmeasured causal mechanisms. However, we emphasize that our analyses included a broad and ecologically/physiologically relevant array of both attractive and deterrent characteristics of trees, and that behavioural bioassays with free-ranging squirrels in Colorado demonstrated the direct chemical mediation of selectivity by features that were examined in both populations (Snyder, 1992).

The Abert's squirrel–ponderosa pine system provides the opportunity to explore various aspects of interactions between a mammalian herbivore and its host, including the potential for co-evolution, since Abert's squirrel is extreme for a mammalian herbivore in the degree to which its feeding is specialized upon a single host species, and because selective herbivory within this host species is mediated, at least in part, by genetically determined traits that vary among individual trees. There is good evidence that the squirrel is at least behaviourally adapted to biochemical/

genetic variability in the pine, and that the squirrel can exert natural selection upon the pine (Snyder, 1992, 1993). Preliminary comparisons of gut morphology between *S. aberti* and a parapatric congener that is a feeding generalist (*S. niger rufiventer*) show marked differences, which may be related to Abert's squirrel's extreme trophic specialization (S. Murphy, M. Snyder and Y. Linhart, unpublished data). However, we lack direct evidence that the pine exerts selective pressures upon the squirrel, although this might be expected, given the squirrel's restriction to, and ecological dependence on, the pine.

The results presented here provide evidence of geographic differentiation of squirrel–pine interactions, and imply that such differentiation can lead to different evolutionary outcomes. We are undertaking similar studies of other subspecies of the squirrel to further define the nature of this geographic differentiation, because this is a potentially important evolutionary aspect of ecological interactions between specialized vertebrate herbivores and their host populations.

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