

Chapter 15

Comparative phylogeography of north-western North America: a synthesis

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Introduction

Phylogeography is concerned with the principles and processes that determine the geographic distributions of genealogical lineages, within and among closely related species (Avice *et al.* 1987; Avice 2000). Although this field of study is very new (only a little more than a decade has passed since the term ‘phylogeography’ was first coined; see Avice *et al.* 1987), the scientific literature in this research area is now voluminous.

To date, most phylogeographic investigations of natural populations have focused on multicellular animals (Hewitt 1993; Patton *et al.* 1994; daSilva & Patton 1998; Eizirik *et al.* 1998; Avice 2000; Hewitt 2000; Schaal & Olsen 2000; Sullivan *et al.* 2000). This bias is due in large part to the ready availability of population-level genetic markers afforded by the animal mitochondrial genome. The more slowly evolving chloroplast genome, in contrast, often does not provide sufficient variation to reconstruct phylogeny at the populational level (Soltis *et al.* 1997; Schaal *et al.* 1998; Schaal & Olsen 2000). Phylogeographic data have accumulated so rapidly for animal taxa that it has been possible to compare phylogeographic structure among codistributed species. In fact, one of the most profound recent contributions of molecular phylogeography is the construction of *regional phylogeographic* perspectives that permit comparisons of phylogeographic structure among codistributed species, and subsequent integration of genealogical data with independent biogeographic and systematic data.

Probably the best-known regional phylogeographic analysis for North America involves animals from the southeastern USA (reviewed in Avice 2000). Avice and colleagues demonstrated that similar phylogeographic patterns are present in a diverse array of animals, including freshwater and marine fish, turtles, birds and invertebrates. A high degree of phylogeographic concordance was observed across taxa, with a pronounced distinction in mitochondrial (mt) DNA haplotypes between populations from the Atlantic coast and those from the Gulf coast. This concordance implicates shared historical factors in shaping the genetic architecture of

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these diverse taxa. Despite this wealth of data for animals, only one such study has been completed for a plant species from this region (*Liriodendron tulipifera*; Sewell *et al.* 1996). Nevertheless, as recently noted by Avise (2000), one of the earliest regional phylogeographic comparisons of codistributed organisms actually involved plants from the Pacific Northwest of North America (reviewed in Soltis *et al.* 1997). Similarly, a substantial body of phylogeographic data has now accumulated on European trees (see Chapter 14), and the combination of these data with analyses of multiple animal species has allowed a multi-kingdom approach to European phylogeography (see Chapter 13, and references therein; see Willis & Whittaker (2000) on the importance of refugia).

Here we attempt to begin to reconstruct a comprehensive regional phylogeography for north-western North America that encompasses examples from both the plant and animal literature. Our general goals are to: (i) demonstrate the complexity and caveats of such an undertaking for an area that is both geologically and ecologically highly complex; (ii) explore the roles of vicariance, dispersal and refugia in structuring genetic diversity in the region; and (iii) highlight the need for additional data from this region and stimulate similar efforts for other geographic areas.

The geographic scope of this chapter encompasses the western coast of North America from southern Alaska to northern California, east to the Rocky Mountains of British Columbia, western Montana and central Idaho (Figure 15.1). This region contains the world's greatest extent of mesic, temperate coniferous forests, whose unique biota is our principal focus. The area can be divided longitudinally into three parts; the western coastal mountains (the Cascades and Coast Ranges), the northern Rocky Mountains of the eastern interior, and the low-lying intervening Columbia River Basin or Plateau. Moist westerly winds bring a maritime climate (wet, mild winters and cool, relatively dry summers) to the coastal mountains, and this climatic influence penetrates eastward to the northern Rocky Mountains. The rain-shadow of the Cascade Range, however, produces a broad extent of steppe and shrub-steppe ecosystems that largely isolate the mesic forests of the coastal mountains from those of the interior. The ecological isolation of the two mountain ranges is partially circumvented in the north by the Okanogan Highlands and in the south by the Central Oregon Highlands (Figure 15.1).

Mesic, temperate coniferous forests are characterized by the late successional dominance of western hemlock, *Tsuga heterophylla*, and often western redcedar, *Thuja plicata*; they have been referred to as the *Tsuga heterophylla* Province or Zone (Franklin & Dyrness 1973; Daubenmire 1978), or simply 'cedar-hemlock' ecosystems (Daubenmire & Daubenmire 1968). Subalpine and boreal forests replace mesic temperate forests at higher elevations and latitudes, respectively, and are generally dominated by mountain hemlock, *Tsuga mertensiana*, spruce, *Picea* spp. and fir, *Abies* spp. West of the summits of the Cascade Range, mesic forests extend from sea level to the subalpine, but on the east slope of the Cascades and in the Rocky Mountains cedar-hemlock forests are sandwiched between xerophytic forest ecosystems at low elevations and a well-developed subalpine zone. Xerophytic

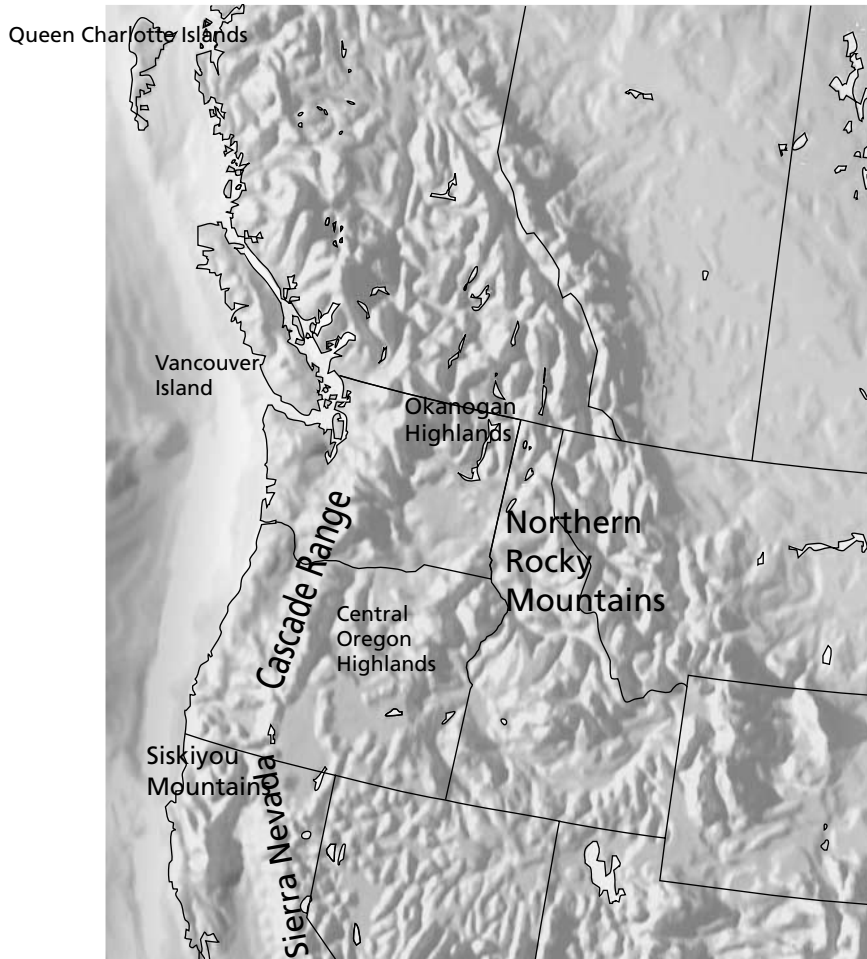


Figure 15.1 The Pacific Northwest of North America, showing relevant geological features.

forests include those dominated by Douglas-fir, *Pseudotsuga menziesii*, ponderosa pine, *Pinus ponderosa*, and in some places juniper *Juniperus* spp. In the Rocky Mountains, the Clearwater River drainage in Idaho is the southern extent of cedar–hemlock ecosystems. This drainage, thought to be a refugium during the Pleistocene or earlier (Daubenmire 1952; Detling 1968), plays a pivotal role in some of the phylogeographic hypotheses proposed below. The southern limit of cedar–hemlock forests in coastal mountains lies in a zone from southwestern Oregon to coastal northern California, i.e. the ecosystem boundary is largely congruent with the southern limit of the Cascade Range. South of the Cascades, the Sierra Nevada Range differs in geology, and a warmer, more Mediterranean climate fosters a substantial change in biota.

Current distributional patterns

A region as complex as north-western North America is, of course, home to species with a wide array of distributional patterns. Although patterns involving species occurring in alpine, boreal, Columbia Plateau, Great Basin and other habitats exist, these will not be discussed here; we will focus on the three major patterns outlined below.

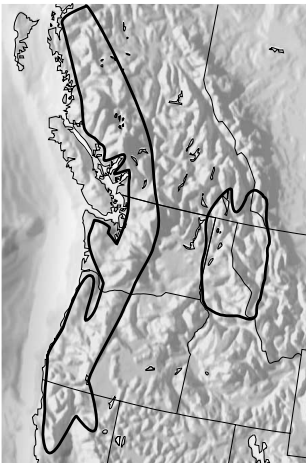
Mesic forest disjunct pattern

One of the most compelling distributional patterns associated with the mesic, temperate forests of the region is the disjunction of conspecific populations between Pacific coastal and interior Rocky Mountain habitats (Figure 15.2). Ecosystem dominants, western hemlock and western redcedar are the most obvious disjuncts, but populations of at least 60 other plants and numerous animal and fungal species (Johnson 1987) are currently separated by 300 km of arid habitats of the Columbia Basin.

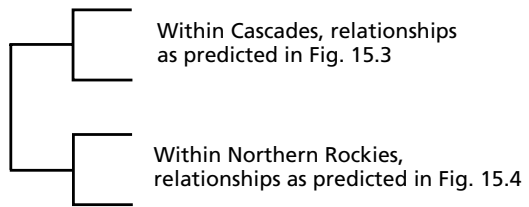
Cascade/Sierran pattern

Many coastal species reach their current northern or southern limits at the Cascade/Sierran transition (see Figure 15.1), resulting in the ready distinction

Generalized Mesic Forest Disjunct Distribution



Ancient Vicariance Hypothesis



Inland Dispersal Hypotheses

1: Northern Route 2: Southern Route

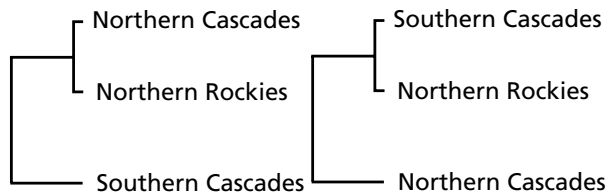
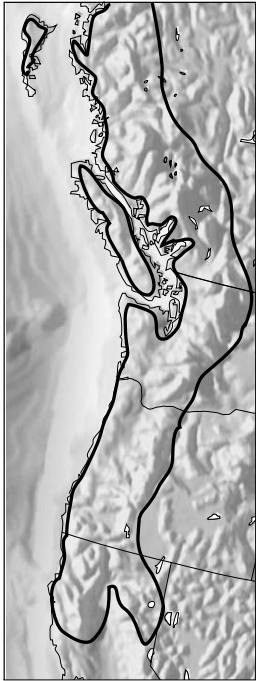


Figure 15.2 Mesic forest disjunct distribution and phylogeographic hypotheses. Over 100 species demonstrate this disjunct distribution, with populations in the Cascade/Sierran region and isolated populations in the northern Rock Mountains. Three hypotheses, involving either vicariance or dispersal, have been proposed for the genesis of the interior populations, and the phylogeographic predictions of each are shown.

Generalized Cascade/
Sierran Distribution



Clinal Environment Hypothesis

Isolation by distance

Single Pacific Coast Refugium Hypothesis

Star phylogeny with very recent coalescence times

Multiple Refugia Hypotheses

1: North-South Recolonization 2: Multiple Coastal Refugia

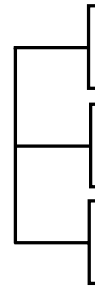
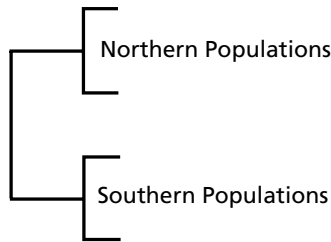


Figure 15.3 Cascade/Sierran distribution and phylogeographic hypotheses. Several hypotheses have been erected regarding the role of past events in structuring genetic variation in coastal species. All but one of these involve at least one Pleistocene refugium.

between Cascadian and Sierran ecosystems. Many other species, however, span the boundary, suggesting an ecological and historical connection between the now-contiguous major ecosystems (Figure 15.3).

Northern Rocky Mountain pattern

The mesic, temperate (cedar–hemlock) forests of the Rocky Mountains occur only at middle elevations and only in the northern portion of the range (Figures 15.1 and 15.4). Within this area, however, species with strong affinities to coastal forests are not uniformly distributed. Much of the diversity in inland mesic-adapted species occurs south of the limits of the last Cordilleran glacial advance, with diversity highest in the Clearwater River drainage. In contrast, a few coastal-disjunct species occur only in similar forests north of glaciation. A few plant species (including mountain hemlock) from the subalpine zone of the Cascade/Sierras occur in the subalpine zone of the northern Rocky Mountains. Thus, the biogeographic discontinuity in the Rocky Mountains spans two distinct elevational ecosystems. Species of low-

elevation xerophytic forests of the Rocky Mountains, on the other hand, exhibit more complex distributional patterns, including abundant widespread species and more localized low-elevation endemics.

Historical overview

The modern distributional patterns outlined above are best understood in light of the geological history of the region, coupled with evidence of past biotic distributions inferred from palaeobotanical data. The Rocky Mountains are the oldest mountains in western North America, having attained significant relief during the Eocene (45–36 mya). The oldest record of co-occurring coniferous forest elements (including *Thuja* and *Tsuga*) comes from the middle Eocene Republic flora from the west slope of the Rockies in north-eastern Washington (Graham 1999). From that time on, many fossil localities indicate the existence of montane coniferous forests throughout the Rocky Mountains (Graham 1993, 1999). In contrast, major uplift of the Cascade/Sierra chain did not occur until the Pliocene (5–2 mya), and fossil sites with coniferous forests do not predate this time. The rise of the Cascade/Sierras produced a rain shadow that led to the development of essentially modern steppe vegetation on the Columbia Plateau by the end of the epoch (Graham 1999). Thus, by the end of the Tertiary: (i) coniferous forests probably dominated substantial portions of the Cascade/Sierra and Rocky Mountains; (ii) the two ranges were probably largely ecologically isolated; and (iii) mesic temperate (cedar–hemlock) forests were apparently present in the Rocky Mountains, and are predicted to have been supported by the maritime climate in the coastal mountains.

Pleistocene glaciation had enormous impact on the geographic distribution of organisms of the region. During this epoch, 100 000-year cycles created by variation in the earth's orbit (Milanovitch cycles) repeatedly buried at least half of the region under cordilleran and alpine ice for 90 000 years each cycle (Delcourt & Delcourt 1993). For example, during the last glacial maximum ($\approx 20\,000$ BP), treelines were lowered as much as 1000 m, but forest zones were not necessarily shifted down into low-elevation basins (Barnosky *et al.* 1987). In the Columbia Basin and adjacent lowlands, cold, dry steppe (sagebrush/grass) and, later, pine woodland/steppe occupied most areas until late Holocene (Mack *et al.* 1978a,b). On the coast, relatively wet conditions prevailed during full glacial times, with western hemlock generally present in forests or parklands, often with subalpine (e.g. mountain hemlock or spruce) and tundra elements in the vicinity (Heusser 1985). Thus, a large refugium for mesic temperate forest elements existed along the coast south of glaciation, and additional refugia probably existed in other unglaciated coastal areas (e.g. the western Olympic Peninsula, Vancouver Island and the Queen Charlotte Islands). Pollen records document the northward spread of western redcedar along the Pacific coast during early and middle Holocene, suggesting postglacial dispersal from a southern refugium (Barnosky *et al.* 1987). However, no mesic forest refugium from the Sierras or southern Cascades has yet been identified from fossil data.

The arrival of mesic forests to glaciated portions of the northern Rocky

Mountains appears to have been recent. Based on several sites studied by Mack *et al.* (e.g. 1978a,b), western hemlock did not become established in these areas until 2500–1500 years ago. However, no Quaternary pollen sites have been studied from mesic forest habitats south of glaciation in the northern Rocky Mountains. Thus, the full-glacial fate and Holocene history of cedar–hemlock forests of the inland region ‘. . . remain a puzzle’ (Mehring 1985).

Hypotheses

The geological and climatic history outlined above suggests a number of hypotheses about the patterns of genetic architecture that might be expected in species exhibiting each of the three major distributional patterns. For each distributional pattern, we propose alternative hypotheses that take into account currently observable aspects of the physical environment (e.g. populations separated by unsuitable habitat) and conditions (e.g. glacial refugia, dispersal avenues) that others have hypothesized to have affected the genetic architecture of multiple species. The historical information in molecular data provides a means of testing and refining biogeographic hypotheses, which until recently have been based on a fragmentary fossil record.

Mesic forest disjunct distributions

‘Ancient vicariance’

Our first hypothesis for disjunct distributions requires the continuous occurrence of mesic forests in the Cascades and the northern Rocky Mountains in the past (perhaps dating back to the Eocene), with subsequent attenuation of east–west gene flow by the Cascadian rain shadow of the late Pliocene. Considerable genetic divergence at both cytoplasmic and nuclear loci would be predicted to exist between coastal and inland populations (see Figure 15.2). Recolonization of deglaciated lands would involve differentiated coastal and inland genotypes, which in some cases might come into contact in central British Columbia. Taxa that are not confined to strictly mesic temperate habitats might exhibit even higher levels of east–west differentiation, or even be represented by Cascadian/Rocky Mountain sister species. Members of these lineages might represent early Tertiary colonists of various primordial Cascadian and Rocky Mountain habitats. Within both the coastal and the inland populations, genetic variation would be structured following hypotheses restricted to each of these regions (Figures 15.3 and 15.4).

‘Inland dispersal’

A contrasting hypothesis is founded on the presumed absence of mesic forests in the Rocky Mountains until postglacial times and relatively recent colonization coming eastward from the Cascade/Sierra. Assuming north–south differentiation in Cascade/Sierran populations (see below), one subhypothesis (‘inland dispersal–north’) involves eastward dispersal of northern genotypes across the Okanogan Highlands. This results in an intraspecific phylogeny with a sister relationship between northern Cascadian and Rocky Mountain populations (see Figure 15.2). Alternatively, popu-

Northern Rocky Mountain Distribution

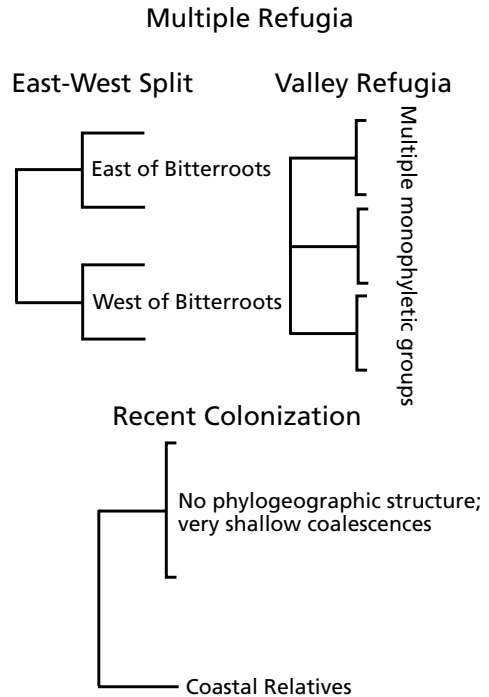
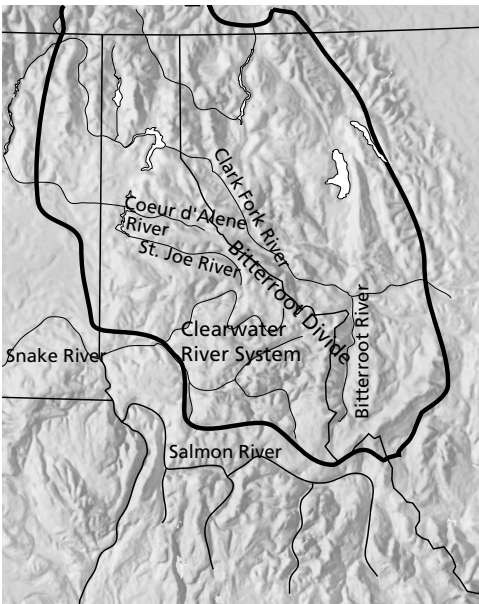


Figure 15.4 Northern Rocky Mountain distribution and phylogeographic hypotheses. The timing of population origin and the isolation associated with geographic features (rivers and mountain ranges) are hypothesized as major factors underlying the structure of genetic variation in inland mesic forest denizens. Phylogeographic predictions are shown for these three hypotheses.

lations from the northern Rockies might be nested within populations from the northern Cascades. Also, because dispersal is hypothesized to be post-Pleistocene, coalescence times should be quite short within the northern Cascades/northern Rockies clade. A second subhypothesis is similar, except eastward dispersal occurs across the central Oregon highlands ('inland dispersal-south'), resulting in a sister relationship between northern Rocky Mountain and southern Cascade/Sierran populations (see Figure 15.2). Because both alternative subhypotheses are based on recent dispersal, predicted genetic patterns include: (i) little or no differentiation between the coast and inland populations, except perhaps in organisms with very short generation times (e.g. insects); and (ii) levels of polymorphism that attenuate with distance from source populations on the coast.

Because dispersal from the coast to the northern Rockies has been hypothesized because of a lack of palaeobotanical records of mesic forest plants in the inland region during the Pleistocene, we restrict our attention to an inland dispersal rather than colonization of the coast ranges from an inland refugium.

Cascade/Sierran distributions

Figure 15.3 illustrates an example of a species with a Cascade/Sierran distribution. Because mountain glaciers covered substantial portions of the region during Pleistocene glacial maxima, all but the first hypothesis below involve refugia in shaping the genetic structure on the landscape.

'Clinal environment hypothesis'

This hypothesis is founded on the fact that the Cascade/Sierran chain is of relatively uniform age, but throughout the Cenozoic a clinal environmental gradient probably existed, from relatively cool and moist in northern latitudes to warm and dry in the south. As is seen today, some species occupy only a portion of this climatic gradient, whereas others have a broad latitudinal distribution. Under this hypothesis, the latter species should exhibit gradual shifts (at most) in the frequencies of neutral nuclear markers, and variation in cytoplasmic genomes, if present, would not show congruent patterns across multiple species.

'Single Pacific Coast refugium'

If a single Pacific Coast refugium existed, and there was apparently at least one (Barnosky *et al.* 1987), relative genetic uniformity would be predicted if the refugium was small. That is, very shallow coalescence times should be seen in all species; neither north–south patterns nor congruent patterns of divergence among species would be predicted.

'Multiple refugia'

Many authors have posited the presence of more than a single coastal refugium (e.g. MacDonald & Cook 1996; Soltis *et al.* 1997). Thus, we can subdivide this hypothesis into: (i) the 'north–south recolonization' subhypothesis in which there are two refugia, one coastal, perhaps in the vicinity of Vancouver Island or the Queen Charlotte Islands, and a second in the mountains south of glaciation, perhaps the Siskiyou; and (ii) the 'multiple coastal' subhypothesis, in which there are more than two refugia scattered along the coast and in other lowlands west of the Cascades. Under the 'north–south' subhypothesis, we would predict a pattern of divergence into northern and southern clades (especially in haploid, uniparentally inherited cytoplasmic genomes), and there should be congruent patterns across multiple species (see Figure 15.3). Within each of these clades coalescence times would likely be short. Under the 'multiple coastal' refugia subhypothesis, we would predict multiple reciprocally monophyletic clades, within which coalescence times would be short. Relationship among these clades might be star-like (i.e. represented by very short internodes that are difficult to resolve), and this pattern should recur across multiple species (Figure 15.3).

Northern Rocky Mountain distributions*'Multiple refugia'*

Our first hypothesis associated with the northern Rocky Mountains is based on small-scale isolation of populations across the heterogeneous mountain environ-

ment. The Bitterroot crest separates mesic forest habitats on the east and west slopes of the range, and major river canyons (Figure 15.4) result in a series of relatively isolated mid-elevation, mesic, riverside forest ecosystems. This isolation probably increased during glaciation, as mesic habitats contracted at the expense of both expanding subalpine forests and tundra above and cold steppe below (Barnosky *et al.* 1987). This hypothesis thus posits a series of refugia, across the dissected mountain topography. The expected intraspecific phylogeny could contain an 'east–west split', or multiple monophyletic groups associated with multiple 'valley refugia' (Figure 15.4), with differing population sizes and histories potentially fostering differing branch lengths. Refugial areas are expected to be supported by multiple congruent phylogenies. An additional prediction of this model is that northern, glaciated portions of the region would have been colonized by genotypes found in adjacent unglaciated habitats, or by Cascadian genotypes that dispersed eastward across the Okanogan Highlands after glaciation.

'Recent colonization'

This alternative hypothesis for genetic patterns within the northern Rocky Mountains is founded on the assumption of a recent, postglacial colonization of the region. Genetic markers would be unlikely to vary between the east and west slopes of the range, among river canyons, or between glaciated and unglaciated habitats (Figure 15.4). Whether the species dispersed into the area via a northern or southern route might be inferred from its lack of differentiation from one Cascadian genotype in an intraspecific phylogeny, but the place of origin and direction of migration would be equivocal unless a unidirectional attenuation in the frequency of markers existed.

Case studies

Mesic forest disjunct taxa

The genetic structures of several plant species with disjunct distributions in the mesic forests of the Cascades/Coast Ranges and northern Rockies have been examined using cytoplasmic (cp) DNA and/or nuclear markers (Table 15.1). Four of these, *Tellima grandiflora*, *Tiarella trifoliata*, *Alnus rubra* and *Polystichum munitum*, have nearly identical distributions from southeastern Alaska to central California, mostly west of the Cascade crest, with disjunct populations in the Rocky Mountains. All four of these species exhibit the north–south pattern of cpDNA differentiation (reviewed in Soltis *et al.* 1997; see below) in the coastal portions of their ranges. *Tellima grandiflora*, *Tiarella trifoliata* and *Polystichum munitum* show a congruent pattern in which the cpDNA of populations from the northern Rockies is identical to the northern coastal genotype. Isozyme data for western white pine, *Pinus monticola*, show a similar pattern of close relationship between northern Rocky and northern Cascade populations and more distant relationships to populations in the southern Cascades and Sierras (Steinhoff *et al.* 1983). These patterns are consistent

Table 15.1 A compilation of plant and animal taxa that exhibit a disjunct distribution in the mesic forests of the Pacific Northwest and for which genetic data have been examined.

	Major group: family	Life history	Genetic data	Reference
Plant species				
<i>Tellima grandiflora</i>	Magnoliophyta: Saxifragaceae	Herbaceous perennial	cpDNA	Soltis <i>et al.</i> (1991)
<i>Tiarella trifoliata</i>	Magnoliophyta: Saxifragaceae	Herbaceous perennial	cpDNA	Soltis <i>et al.</i> (1992)
<i>Alnus rubra</i>	Magnoliophyta: Betulaceae	Tree	cpDNA	Strengé (1994)
<i>Polystichum munitum</i>	Pteridophyta: Dryopteridaceae	Herbaceous perennial	cpDNA	Strengé (1994)
<i>Pseudotsuga menziesii</i>	Coniferophyta: Pinaceae	Tree	Allozymes	Li and Adams (1989)
Animal species				
<i>Dicamptodon ensatus/aterimus/tenebrosii/copei</i> complex	Caudata: Dicamptodontidae	Metamorphic and paedomorphic salamanders	Allozymes	Daugherty <i>et al.</i> (1983) Good (1989)
<i>Ascaphus trueii/montanus</i> complex	Anura: Ascaphidae	Metamorphic frogs	Allozymes MtDNA RAPDs	C. H. Dougherty unpubl. Nielson <i>et al.</i> (2001) Ritland <i>et al.</i> (2000)
<i>Microtus richardsoni</i>	Rodentia; Muridae	Semiaquatic vole	mtDNA sequences (cyt b)	Demboski and Sullivan (unpublished)
<i>Rana pretiosa</i> complex	Anura: Ranidae	Metamorphic frog	Allozymes	Green <i>et al.</i> (1996)
<i>Plethodon vandykeii/idaheensis</i> complex	Anura: Plethodontidae	Metamorphic salamanders	Allozymes	Howard <i>et al.</i> (1993)

cpDNA, chloroplast DNA; mtDNA, mitochondrial DNA; RAPDs, randomly amplified polymorphic DNA.

with the ‘inland dispersal–north’ hypothesis of recent colonization of the northern Rockies, perhaps via the Okanogan Highlands. In contrast, in *Alnus rubra*, the cpDNA of populations from the northern Rockies is identical to the southern coastal genotype, consistent with recent colonization via a southern route (‘inland dispersal–south’), such as the highlands of central Oregon. Contrasting isozyme data were reported for Douglas fir (Li & Adams 1989), a species that extends beyond mesic habitats. In this case, coastal and inland populations are well differentiated, suggesting relatively ancient vicariance.

Studies suggesting both ancient vicariance and inland dispersal also exist in the animal literature. Relatively few animal examples exist for the disjunct mesic forest communities, and most of those are amphibians (Table 15.1). Good (1989) examined allozyme variation in the genus *Dicamptodon* (giant salamanders); Howard *et*

al. (1993) examined allozyme variation in the *Plethodon vandykei*/*P. idahoensis* complex; Nielson *et al.* (2001) examined mtDNA sequence variation (cyt b and ND2 genes) in *Ascaphus* (tailed frogs). In spite of the differences in methodologies, these studies have a common conclusion; the divergence of the inland forms from the coastal forms is the deepest split. Thus, each of these examples suggests an ancient vicariance and persistence of inland populations throughout the Pleistocene (see Figure 15.2). Unfortunately, the fact that the first two examples involve allozyme data prevents us from applying the statistical phylogenetic hypothesis tests described below (e.g. parametric bootstrap tests) as these are primarily devised for DNA sequence data.

A contrasting case study involves water voles, *Microtus richardsoni*, which occur in moist meadows within conifer forests along the coast, and exhibit a disjunct distribution in the Rocky Mountains. Preliminary cyt b sequence data (J. Demboski & J. Sullivan, unpublished) deviate from the common patterns seen in the amphibians. First, only a single species appears to be present. Secondly, inland populations are nested with populations from the northern Cascades, supporting the hypothesis of recent inland dispersal across the Okanogan Highlands ('inland dispersal–north' hypothesis; see pp. 325–6). A statistical test of this data set is described below.

Thus, the current distributions of the flora and fauna of the northern Rocky Mountains are probably the result of numerous vicariance and dispersal events of varying age, and similarities in the composition of *mesic* forests in the Cascades and northern Rockies apparently arose, at least in part, through a complex series of relatively recent migrations into the northern Rockies. These colonization events appear to have come from multiple refugia, across different inland migration routes.

Cascade/Sierran taxa

Molecular studies of both plants and animals centred primarily on the Cascade/Sierran region suggest a recurrent pattern of genetic differentiation. In a diverse array of plants, including the angiosperms *Tolmiea menziesii*, *Tellima grandiflora*, *Tiarella trifoliata*, *Alnus rubra* and *Ribes bracteosum* and the fern *Polystichum munitum*, cpDNA data indicate two clades of populations that are geographically structured (Soltis *et al.* 1989a, 1991, 1992, 1997; Table 15.2). A northern group consists of populations from Alaska to central or southern Oregon; populations from central Oregon southward to northern California form a southern clade (reviewed in Soltis *et al.* 1997).

Similar patterns of north–south genetic differentiation are apparent in several animals from north–western North America (Table 15.2). Analysis of mtDNA markers in the moth *Greya politella* revealed the presence of northern and southern clades comprising populations from Washington, Oregon; and Idaho and California, respectively (Brown *et al.* 1997). Allozyme and cytological data suggest a north–south pattern of differentiation in rainbow trout, *Onchorynchus mykiss* (Thorgaard 1983; Hatch 1990; Reisenbichler *et al.* 1992; Ostberg & Thorgaard 1999). For example, Hatch (1990) reported that 'the area south of the Coos River (central Oregon) was marked by sharp transition in four enzymes . . .'. Allozyme data for the urodele

Table 15.2 A compilation of plants and animals that exhibit a Cascade/Sierran pattern of genetic differentiation in northwestern North America.

	Major group: family	Life history	Genetic data	Reference
Plant species				
<i>Tolmiea menziesii</i>	Magnoliophyta: Saxifragaceae	Herbaceous perennial	cpDNA	Soltis <i>et al.</i> (1989a)
<i>Tellima grandiflora</i>	Magnoliophyta: Saxifragaceae	Herbaceous perennial	cpDNA	Soltis <i>et al.</i> (1991)
<i>Tiarella trifoliata</i>	Magnoliophyta: Saxifragaceae	Herbaceous perennial	cpDNA	Soltis <i>et al.</i> (1992)
<i>Alnus rubra</i>	Magnoliophyta: Betulaceae	Tree	cpDNA	Strenge (1994)
<i>Ribes bracteosum</i>	Magnoliophyta: Grossulariaceae	Shrub	cpDNA	Soule <i>et al.</i> (1995)
<i>Polystichum munitum</i>	Pteridophyta: Dryopteridaceae	Herbaceous perennial	cpDNA	Strenge (1994)
<i>Erythronium montanum</i>	Magnoliophyta: Liliaceae	Herbaceous perennial	Allozymes	Allen <i>et al.</i> (1996)
<i>Pinus jeffreyi</i>	Coniferophyta: Pinaceae	Tree	Allozymes	Furnier and Adams (1986)
<i>Pinus contorta</i> subsp. <i>latifolia</i>	Coniferophyta: Pinaceae	Tree	Allozymes	Wheeler and Guries (1982)
<i>Pinus monticola</i>	Coniferophyta: Pinaceae	Tree	Allozymes	Steinhoff <i>et al.</i> (1983)
Animal species				
<i>Greya politella</i>	Lepidoptera: Prodoxidae	Holometabolous insect	mtDNA	Brown <i>et al.</i> (1997)
<i>Onchorynchus mykiss</i>	Actinopterygii: Salmonidae	Anadromous fish	cytogenetic; mtDNA (control region)	Thorgaard (1983) Ostberg and Thorgaard (1999)
<i>Dicamptodon ensatus/ tenebrosil/copei</i> complex	Caudata: Dicamptodontidae	Metamorphic and paedomorphic salamander	Allozymes	Daugherty <i>et al.</i> (1983) Good (1989)
<i>Plethodon vandykei</i>	Caudata: Plethodontidae	Metamorphic salamander	Allozymes	Howard <i>et al.</i> (1993)
<i>Rhyacotriton cascadae/ olympicus/keezeri/ variegatus</i> complex	Caudata: Rhyacotritonidae	Metamorphic salamander	Allozymes	Good and Wake (1992)
<i>Ascaphus truei</i>	Anura: Ascaphidae	Metamorphic frog	Allozymes mtDNA sequences (cyt b and ND2)	Dougherty (1979) Nielson <i>et al.</i> (2001)
<i>Sorex monticolus/ sonomae</i> coastal complex	Insectivora: Soricidae	Insectivorous shrew	mtDNA sequences (cyt b)	Demboski and Cook (2001)

Abbreviations as in Table 15.1.

amphibians *Dicamptodon* and *Plethodon vandykei* complex show an initial deep split between the Cascades/Sierras and the Rocky Mountains (see above), but within the former region a distinct north–south structuring of genotypes (and taxonomy in *Dicamptodon*) is also observed (Good 1989; Howard *et al.* 1993). Demboski and Cook (2001) examined cyt b variation among coastal endemic shrews in the *Sorex monticolus* complex. *Sorex monticolus* has classically been considered to be widespread in western North America, with *S. bendiri* and *S. pacificus* restricted to small areas in coastal Oregon. All of the samples from the coast (coastal *S. monticolus* samples plus *S. bendiri* and *S. pacificus*) form a coastal clade, and within that clade, haplotypes partition in a north–south pattern (Demboski & Cook 2001).

Allozyme and cpDNA data also reveal that some species have lower levels of genetic variation in the northern portion of their ranges than in the southern portion. In *Tolmiea*, *Tellima* and *Polystichum* the northern clade consists of a single haplotype, whereas multiple cpDNA genotypes occur in the southern clade (Soltis *et al.* 1989a, 1991, 1997). Reduced allozyme variation was detected in northern populations of *Erythronium montanum* and *Pinus monticola* (Steinhoff *et al.* 1983; Allen *et al.* 1996). Such patterns of diversity are observed in multiple European taxa, and are thought to be associated with dispersal from southern refugia (e.g. Hewitt 1999; Chapters 13 and 14 this volume).

Of the hypotheses proposed above for the Cascade/Sierran region (see above), much of the data are in very close agreement with in scenario proposed as part of the ‘multiple refugia—north–south recolonization’ hypothesis (Table 15.2, Figure 15.3). However, the considerable support for a northern and southern refugium does not preclude the possibility that other of our proposed hypotheses explain the pattern of genetic variation in other species. For example, in *Heuchera micrantha*, another member of Saxifragaceae displaying the Cascade/Sierran distributional pattern, no pattern of north–south genetic differentiation was detected with either cpDNA restriction sites (Soltis *et al.* 1989b) or allozymes (Ness *et al.* 1989), as predicted by the ‘clinal environment hypothesis’. Significantly, considerable genetic variation was present among populations of *H. micrantha*, but the phylogeny obtained was essentially a starburst.

Although there is agreement in both the plant and animal literature that refugia have played a major role in the recolonization of areas of the Pacific North-West, there is less agreement as to the possible locations of these refugia. In several of the plant species analysed for cpDNA variation, a few populations having southern genotypes appear to have survived in northern glacial refugia on the Olympic Peninsula of Washington and Prince of Wales Island, Alaska (reviewed in Soltis *et al.* 1997). Studies on three-spine sticklebacks, *Gasterosteus aculeatus* (O’Reilly *et al.* 1993), song sparrows, *Melospiza melodia* (Zink & Dittmann 1993), and black bears, *Ursus americanus* (Byun *et al.* 1997) have suggested that the Queen Charlotte Islands represent an important refugium for animal taxa. However, other interpretations of refugia for these animal species are equally plausible (Orti *et al.* 1994; Demboski *et al.* 1998). Furthermore, there are no genetic data for plants that clearly support the Queen Charlotte Islands as a refugium. Other mtDNA studies have identified the

Columbia River as a possible refugium for populations of white sturgeon, *Acipenser transmontanus* (Brown *et al.* 1992), and bull trout, *Salvelinus confluentus* (Taylor *et al.* 1999).

Northern Rocky Mountain taxa

There are only a limited number of genetic studies of plant species distributed in the northern Rocky Mountains (Table 15.3), and these present a complex picture of phylogeographic history. Sequence data from the cpDNA of *Cardamine constancei*, an endemic species of mesic forests of the northern Rocky Mountains, provide strong support for the 'multiple refugia' hypothesis (see Figure 15.4). Three major haplotype lineages are geographically structured, suggesting long isolation of populations in separate refugia (Brunsfeld & Sullivan, unpublished). Isozyme data from Douglas-fir revealed substantial differentiation between northern and southern Rocky Mountain populations (Li & Adams 1989), leading the authors to suggest that Douglas fir existed in a refugium in the northern Rockies during the Pleistocene. These data, however, do not reveal any differentiation among populations that might suggest multiple refugia. This might be attributable to high gene flow known to occur in conifers, or the species may not have been confined to isolated mesic forest refugia because of its extremely wide ecological amplitude. Similarly, isozyme data from 19 populations of western larch (*Larix occidentalis*) from the northern Rockies (Fins & Seeb 1986) show little interpopulational differentiation, providing possible support for the 'recent colonization' hypothesis (see Figure 15.4).

Examples of genetic studies of animal species restricted to the northern Rockies are also limited. However, Good and Sullivan (unpublished) have examined cyt b

Table 15.3 Plant and animal taxa from mesic forests of the northern Rocky Mountains for which genetic data are available.

	Major group: family	Life history	Genetic data	Reference
Plant species				
<i>Cardamine constancei</i>	Magnoliophyta: Brassicaceae	Herbaceous perennial	cpDNA	Brunsfeld and Sullivan (in prep)
<i>Larix occidentalis</i>	Coniferophyta: Pinaceae	Tree	Allozymes	Fins and Seeb (1986)
<i>Pinus monticola</i>	Coniferophyta: Pinaceae	Tree	Allozymes	Steinhoff <i>et al.</i> (1983)
Animal species				
<i>Spermophilus columbianus</i>	Rodentia: Sciuridae	Granivorous rodent	mtDNA restriction sites	MacNeil and Strobeck (1987)
<i>Tamias ruficaudus</i>	Rodentia: Sciuridae	Granivorous rodent	mtDNA sequences (cyt b)	Good and Sullivan In prep
<i>Ascaphus montanus</i>	Anura: Ascaphidae	Metamorphic frog	mtDNA sequences (cyt b)	Nielson <i>et al.</i> (2001)

variation in a sample of Columbian ground squirrels collected from across the southern end of their range (Oregon, Idaho and Montana); differentiation ranges up to 4.5% uncorrected divergence among the easternmost and westernmost samples. This is consistent with an east–west pattern of differentiation (see Figure 15.4), although additional sampling is certainly required. Good and Sullivan (unpublished) also examined *cyt b* variation in 175 red-tailed chipmunks *Tamias ruficaudus*, collected from across the range of this species, and found two well-differentiated eastern and western haplotype clades in this species as well, separated by 4.5% uncorrected sequence divergence (similar to the differentiation seen in Columbian ground squirrels). This example also supports an east–west split, and haplotype diversity appears to be highest among the samples from the Clearwater drainage. Nielson *et al.* (2001) examined *cyt b* and ND2 variation within the Rocky Mountain tailed frog, *Ascaphus montanus*, and found a deep divergence in populations from the Salmon River Mountains, suggesting a north–south split in this species within the northern Rocky Mountains. Thus, the limited data currently available suggest the existence of multiple refugia impacting the genetic structure of multiple taxa in the northern Rockies. This is not congruent with data (reviewed above) that suggest a recent colonization of the region from the coast. Reconciling these conflicting data will require additional studies employing more comparable genetic data and focusing on taxa that are more ecologically similar (i.e. confined to mesic forests).

Advances in methods of comparison

Because many phylogeographic studies are focused at or near species limits, analyses of phylogeographic data often involve both population genetics analyses and phylogenetic analyses. The suite of population genetics tools available is reviewed by Hewitt and Ibrahim (Chapter 13); here we focus on advances in phylogenetic analyses that elevate comparative phylogeography from a science in which patterns of similarity are described to a more powerful hypothesis-testing perspective. Page (e.g. 1994) has developed methods that allow a more rigorous assessment of the degree to which different potentially coevolved lineages (such as codistributed taxa) experienced shared history. Such methods as TreeMapping (Page 1994) provide inferences of the number of codivergence events (either codispersal or covicariance) and also allow for randomization tests to estimate the significance of shared history (e.g. Bermingham & Martin 1998; Sullivan *et al.* 2000).

TreeMapping certainly represents an improvement over visual comparisons of topologies; however, the approach ignores phylogenetic uncertainty. Phylogeographies are reconciled with each other as if each were estimated with certainty. If relationships among areas are only weakly supported, spurious conclusions might result. A novel method is a Bayesian approach similar to that developed by Huelsenbeck *et al.* (2000) for the assessment of cospeciation between hosts and parasites. Although this approach is very promising, it will require the development of a biogeographic model similar to the model of cospeciation developed by Huelsenbeck *et*

al. (2000). A second approach is use of the parametric bootstrap (e.g. Huelsenbeck *et al.* 1996). One may test for congruence by forcing the data for each species to fit the phylogeographic patterns inferred from the other species of interest, or alternatively, one may test *a priori* hypotheses such as those outlined above.

Hypothesis testing via the parametric bootstrap was performed using data for water voles, *Microtus richardsoni* (Demboski & Sullivan, unpublished). Water voles occur in moist meadows, usually within 3–5 m of streams, and exhibit the disjunct distribution described above. Maximum-likelihood (ML) analysis of the preliminary data (750 bp *cyt b* for 28 voles) supports the hypothesis of inland dispersal across the Okanogan Highlands during glacial retreat (Figure 15.5). In the ML tree, haplotypes found in the northern Rockies are nested within haplotypes found in the northern Cascades, and haplotypes found in the southern Cascades are sister to these. If the data are constrained to fit the ancient vicariance hypothesis that appears to have generated the disjunct distribution of the three amphibians discussed above (reciprocal monophyly of haplotypes found in the Cascades and northern Rockies; see Figure 15.2), the best-likelihood score is 19.270 lnL units worse than the best unconstrained tree. If the disjunct distribution of *Microtus richardsoni* were the result of an ancient vicariance event (see Figure 15.2), we would expect to see data of the nature we observed less than 1% of the time (see Figure 15.2; $P < 0.01$). Thus, by adopting a rigorous statistical framework, we can go beyond visual inspection of

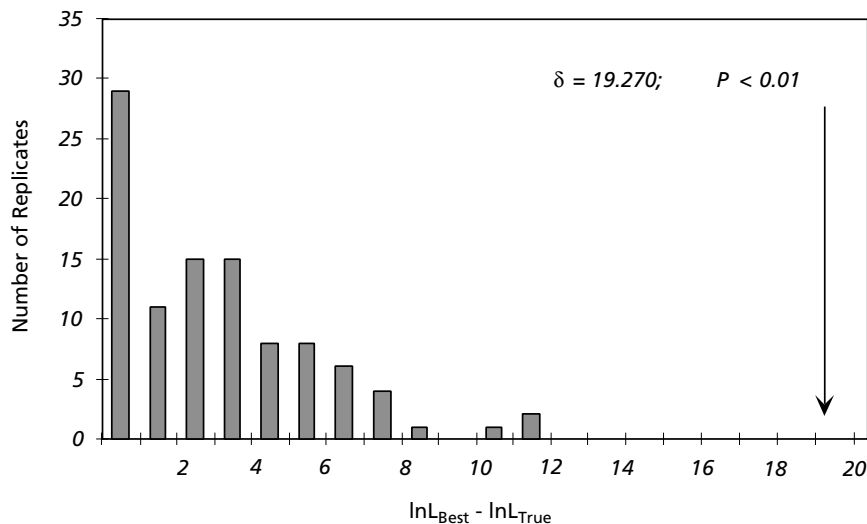


Figure 15.5 Parametric bootstrap test of the ancient vicariance hypothesis in water voles, *Microtus richardsoni*. Phylogenetic analyses of *cyt b* data for water voles supports the ‘inland dispersal—north’ hypothesis. Forcing the data to fit the ancient vicariance hypothesis results in a deterioration of the likelihood score by 19.270 lnL units. The null distribution was generated by simulation, and the ancient vicariance hypothesis can be rejected ($P < 0.01$).

patterns and reject the ancient vicariance hypothesis as an explanation of the genesis of the disjunct distribution for water voles.

Conclusion

Phylogeographic studies of plant and animal species from northwestern North America illustrate a complex history for the biota of this region. Current species distributions appear to result largely from the combined effects of orogeny and glaciation. The geological and climatological complexity of this region has created complex patterns of genetic diversity within species. We have laid a foundation for understanding this variation by elaborating alternative hypotheses that are testable using empirical data. The fragmentary data currently available suggest that vicariance, dispersal and the existence of refugia have worked in concert to produce the species distributions and genetic divergence patterns of the region. Inferences to date have been hampered by a lack of consistency in both the types of data gathered and the analytical approaches used. A clear understanding of regional phylogeography requires coordinated analyses, and future studies should seek to use DNA sequence data that are amenable to analyses at multiple hierarchical levels. More robust, statistical analytical methods need to be employed to elevate phylogeography to a level of rigour common in other fields of science.

Summary

Understanding the causative forces underlying the genetic architecture of any species may be difficult, but it is more challenging for species from geographic areas that have experienced complex and dynamic geological and climatological histories, such as northwestern North America. However, as the number of plant and animal species studied phylogeographically in this region increases, patterns are beginning to emerge, providing consistent support for the roles of glacial refugia, vicariance and overland migration routes in shaping the genetic structures of codistributed species. For example, species with coastal distributions typically exhibit a sharp genetic discontinuity between northern populations and southern populations, probably reflecting isolation in multiple glacial refugia and recolonization to form a continuous distribution. The disjunct distributions of many species between the mesic forests of the Cascades/Coast Ranges and the northern Rocky Mountains could have arisen through a number of processes, such as vicariance caused by the rise of the Cascades and the development of the intervening rain shadow of the Columbia Basin, or more recent colonization of the northern Rockies via northern or southern overland routes from Cascade/Sierran communities. Genetic patterns within the northern Rockies reflect the probable variation in colonization times, with some species showing strong divergence patterns suggestive of multiple refugia, and others exhibiting the genetic homogeneity expected in a recent colonist. Studies of additional species are needed to test the alternative hypotheses further. Comparative phylogeographers have a new arsenal of powerful statistical methods

with which to make inferences on a regional scale. Statistical phylogenetic methods, such as parametric bootstrap analyses and tree mapping, provide means of expanding the field beyond the simple description of pattern, to one based on the statistical testing of hypotheses of shared history.

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