The Status of Genetic Biodiversity in British Columbia

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Table of Contents

1. Introduction

Variation in topography, climate and glacial history in British Columbia has facilitated the evolution of species by reducing dispersal between populations adapted to different environments. As a result, many species in British Columbia occur as complexes of geographically distinct sub-species differing in appearance, behavior and genetic make-up Cooke & MacDonald 2001).[i, ii, iii, iv, v, vi] Some of these sub-species have recently been shown to represent true species, endemic to our region,[vii] and it is nearly certain that additional unnamed species exist, particularly in taxonomic groups that have as yet received relatively little attention from science (e.g., bryophytes, invertebrates). Even in well-studied plant and animal taxa it is likely that some species remain undescribed in glacial refuges, on islands or mountain ranges, or in isolated freshwater drainages. Many other sub-species isolated historically in coastal British Columbia, Beringia and the Rocky Mountains diverged from ancestral types as glaciers advanced, and then radiated out from these historic refuges as glaciers retreated to hybridize with ancestral forms previously restricted to the south and east.[viii, ix, x, xi, xii] Depending on their degree of differentiation, their frequency of hybridization, and the fitness of hybrids, these hybrid 'suture' zones may represent regions of very high genetic diversity and rapid evolution.[xiii] However, because human activities modify natural landscapes and species distributions, humans may also influence the rate of evolution and persistence of populations uniquely adapted to the British Columbia landscape.

Assessing the conservation status of genetically distinct lineages is complicated by several practical realities. Hence, although more than 60 species inhabiting B.C. have been subjects of genetic analysis (Table 1.), practical limits on research and the very large number of unstudied species precludes the genetic classification of most below the species level. As a consequence, biologists use simplifying concepts and metrics to establish rules of thumb for conserving genetic diversity and, where it exists, use genetic data along with observations of size, shape, appearance and behaviour (collectively called *phenotype*) to identify distinctive lineages. Because a working knowledge of these concepts and metrics is essential to assessing genetic diversity and identifying evolutionarily significant lineages below the species level, background and examples are provided below.

2. What is Genetic Variation?

Genetic variation can be thought of as a species' tool kit for life, with some genes being more or less useful in current environments (*adaptive genetic variation*) and others having no current influence, despite being potentially influential in the future or past (*neutral genetic variation*). Like a well-equipped toolbox, genetically diverse organisms are thought to be better-adapted to the challenges of life, to pass on those traits to descendents, and to contribute positively to the persistence of populations and species. This may be particularly true for populations at the periphery of a species' range, where individual organisms are more likely to encounter and potentially adapt to novel environmental challenges, such as those associated with climate change.[xiv, xv]

Like tools, genes vary in their frequency of use, interaction with companion genes, and occurrence in populations. In nature, new genes arise via mutation regularly, with beneficial, deleterious or no detectable effect on the individuals carrying them. At the level of populations, mutations persist depending on their effect on individuals and the size and isolation of populations. Conserving genetic diversity at the population-level is an overall goal of biodiversity conservation because genetic variation affects the adaptability and viability of organisms, populations and species.[xvi, xvii]

Table 1. Summary of population genetic studies in BC.

Studies were only included if the natural populations were sampled and based on populations in British Columbia. For some well-studied species, only representative studies related to genetic structure are noted. Each study is summarized in terms of information related to evidence for adaptive divergence (AD), population differentiation (DIFF), population-level genetic variability (VAR), author-suggested ESU status (ESU), localized data which cannot be readily extrapolated (Local) and phylogeographic patterning (Phylogeo). Citations are listed in a separate reference section preceeding Literature Cited.

Species	AD	Diff	Var	ESU	Local	Phylogeo.	Cit.
Amphibians							
Tailed frogs (*Ascaphus truei*)		●			●		61, 78
Spotted frogs (*Rana pretiosa*)		●				North clade	28
Coastal giant salamanders (*Dicamptodon tenebrosus*)					●		18
Pacific giant salamanders (*D.aterrimus, D. copei*)						Ancient vicariance	14, 69
Plethodontid salamander (*Plethodon vandykei, P. idahoensis)*						Ancient vicariance	14
Birds							
Marbled murrelets (*Brachyramphus marmoratus*)		●					26
Ancient Murrelets (*Synthliboramphus antiquus*)		●					55
Spotted Owl (*S. occidentalis caurina*)						Introgression	30
Peregrine falcons (*Falco peregrines*)		●	●				10
Sharp-tailed grouse (*Tympanuchus phasianellus*)						Coastal cluster	67
Blue grouse (*Dendragapus obscurus*) ssp.		●		●		Coastal cluster	3
Steller's jay (*Cyanocitta stelleri* spp.)		●				Refugial	11
Timberland sparrow (*Spizella taverneri*)				●			40
Sagebrush Brewer’s sparrow, (*S. breweri breweri*)		●	●				19
Song sparrow (*MeIospiza melodia*)						Refugial	87, 57
Yellow warbler (Dendroica petechia).		●				West & Coastal clade	52
Common Yellowthroat (*Geothlypis trichas*)		●				Western cluster	45
Chestnut-backed chickadee (*Poecile rufescens*)		●	●				12
Freshwater Fishes							
Threespine stickleback (*Gasterosteus aculeatus*)						Refugial	54
Northern clingfish (*Gobiesox maeandrichs*)		●					35
Salish sucker (*Catostomus* sp)		●		●			50
Dolly Varden (*Salvelinus malma*)		●				Hybridization	71, 58
Bull trout (*S. confluentus*)		●	●			Hybridization	72
Rainbow trout/steelhead (*Oncorhynchus mykiss*)	●	●	●	●			47, 33,39
Westslope cutthroat trout (*O. clarki lewisi*)		●	●				73
Kokanee (*O. nerka*)	●	●					74
White sturgeon (*Acipenser transmontanus)*		●		●			9, 65
Intertidal and Anadromous Fishes and Molluscs							
Northern abalone (*Haliotis kamtschatkana*)		●	●				81
Tidepool sculpin (*Oligocottus maculosus*)		●					2
Eulachon (*Thaleichthys pacificus*)		●					48, 4
Holarctic skipper (*Hesperia comma*)		●					25
Lingcod (*Ophiodon elongatus*)					●		82
Sockeye salmon (*Oncorhynchus nerka)*	●	●	●		●		77, 83
Chinook salmon (*O. tshawytscha*)		●					75, 29

Table 1. **Summary of population genetic studies in BC.**

Studies were only included if the natural populations were sampled and based on populations in British Columbia. For some well-studied species, only representative studies related to genetic structure are noted. Each study is summarized in terms of information related to evidence for adaptive divergence (AD), population differentiation (DIFF), population-level genetic variability (VAR), author-suggested ESU status (ESU), localized data which cannot be readily extrapolated (Local) and phylogeographic patterning (Phylogeo). Citations are listed in a separate reference section preceeding Literature Cited.

Species	AD	Diff	Var	ESU	Local	Phylogeo.	Cit.
Coho salmon (*O. kisutch*)		●		●			63
Arctic grayling (*Thymallus arcticus*)		●	●				68
Mammals							
Water vole (*Microtus richardsoni*)						Recent dispersal	14
North American deer mouse (*Peromyscus maniculatus*)					●		59
Northwestern deer mouse (*P. keenii)*					●		16
Northwestern badger (*Taxidea taxus jeffersonii*)	●	●					42
Fisher (*Martes pennanti*)		●					21
American marten (*Martes americana*)		●					64
Wolverine (*Gulo gulo*)							15
Mountain sheep (*Ovis dalli*)		●	●				84, 44
Boreal caribou (*Rangifer tarandus*)		●	●			Dispersal barrier	49
Gray wolf (*Canis lupus*)							88
Brown bear (*Ursus arctos*)		●		●		Dispersal barrier	56,79
Kermode bear (*Ursus americanus* pop. *kermodei*)		●	●				46
Butterflies and Skippers							
Moth (*Grevia politella*)							13
Dingy Fritillary (*Boloria improba*)		●	●				8
Dragonflies and Damselflies							
Enallagma damselflies (*Enallagma hageni, E. ebrium*)		●	●			Recent dispersal	76
Coleopterans							
Nebria charlotte, N.haida			●	●			17
Ferns and Fern Allies							
Sword fern (*Polystichum munitum*)						South clade	66
Conifers							
Pacific yew (*Taxus brevifolia*)		●	●				23
Western larch (*Larix occidentalis*)		●	●				38
Douglas fir (*Pseudotsuga menziesii*)		●	●		●		24
Yellow cedar (*Chamaecyparis nootkatensis*)		●	●				60
Sitka spruce (*Picea sitchensis*)	●	●				Hybrid zone	6, 53
Whitebark pine (*Pinus albicaulis*)		●	●				41
Western white pine (*P. monticola*)						North clade	70
Lodgepole pine (*P. contorta*)		●					80
Monocots							
Avalanche lily (*Erythronium montanum*)		●	●				1
Eelgrass (*Zostera marina*)					●		31
Dicots							
Pacific madrone (*Arbutus menziesii*)		●	●				5
Garry oak (*Quercus garryana*)		●	●				62
Golden paintbrush (*Castilleja levisecta*)			●				27
Red alder (*Alnus rubra*)		●	●			North clade	66, 85
Impatiens sp.						Introgression	86
Piggy Back Plant (*ToImiea menziesii*)						North/South clade	66
Fringe cup (*Tellima grandiflora*)						North clade *mix	66
Threeleaf foamflower (*Tiarella trifoliata*)						North clade	66
Stink currant (*Ribes bracteosum*)						North clade	66
Dusky willow (*Salix melanopsis*)						Recent dispersal	51

2.1. Genetic Variation, Divergence and Population Size

Larger populations typically retain more genetic diversity[xviii], but at all levels of organization diversity also depends on history, the distribution of population and life history traits of species. The actual number of individuals in a population, referred to as the *census population size,* tends to overestimate genetic diversity because many factors act to reduce the variety of genes inherited by successive generations. Thus, geneticists use the term *effective population size* (N_e): a quantity that estimates the number of individuals contributing genes to future generations, and the rate at which populations lose genetic variation in time. Factors such as population sex ratio, mating system, population bottlenecks and growth rate, inbreeding and population fragmentation can all influence the N_e and in doing so, affect the ability of populations to retain genetic variation .[xix] There are multiple methods for estimating N_e; some based on the demographic traits known to influence N_e, others based on molecular markers.[xx, xxi, xxii]

Genetic patterns in isolated populations are governed by the forces of mutation, drift and selection. In this case, N_e influences how genetic variation is retained in populations and, potentially, how effectively they respond to natural selection and environmental change. Ideally, selection removes deleterious genes and favours beneficial ones, leading to changes in gene frequency that facilitate adaptation. This process can act rapidly in small, isolated populations, such as those on real or habitat islands, and it has undoubtedly contributed to the divergence of isolated populations in coastal archipelagos, mountain ranges, drainages and specialized habitats (*e.g*., karst, bogs) in British Columbia. For these reasons, conserving historically isolated populations is likely to further the goal of genetic conservation at that species level.

In contrast, small population size is also known to facilitate reductions in genetic diversity and population viability, particularly in once widely-distributed species that have become isolated due to habitat loss and fragmentation, or suffered severe reductions in population size due to exploitation. Several B.C. species have experienced severe population fragmentation and decline, including woodland caribou, Vancouver Island marmot, many species associated with Garry oak ecosystems, and those inhabiting historically fishless freshwater lakes and dammed rivers. Severe reductions in genetic diversity become more likely in such species because random effects are more likely to also eliminate beneficial genes from small populations, such as in the case that a single male sires all of the females in a remnant caribou herd.

Overall, N_e is the single most important parameter affecting genetic diversity and distinctiveness in populations, and is therefore a key parameter to aid decisions related to gene conservation. Meta-analyses of natural populations suggest that N_e averages about 11% of the census population size.[xxiii] Thus, in a population totalling 300 individuals, we should expect genetic variation to decline at a rate expected if only 33 individuals were present. Management recommendations for Ne range from 500 to 5,000,[xxiv,xxv] implying that maintaining census populations of 5,000 to 50,000 individuals will be required for long-term viability.[xxvi]

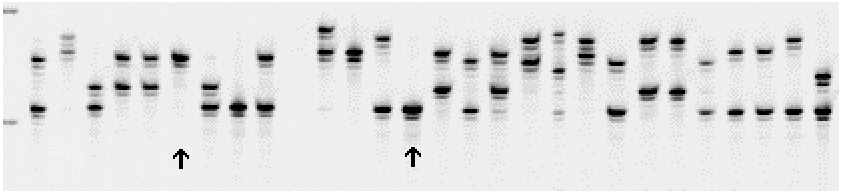
For the majority of populations, which do exchange genes via dispersal and pollination, the maintenance of dispersal corridors is often prescribed to conserve diversity, particularly for fragmented populations of formerly wide-ranging species. By maintaining genetically effective dispersal, managers may achieve recommended targets for N_e at the landscape scale. In doing so, however, care should be taken not to facilitate dispersal among populations known to differ genetically differentiated populations, because there is a potential that individuals adapted to different ecological conditions will produce hybrids that reduce population viability overall.

Examples of genetic incompatibility between populations and, more so, mismatches between individual genotype and local environmental conditions are becoming well-known. In B.C., a long history of research on conifers has shown dramatic effects of genotype on performance in provenance trials, wherein seeds from widely different regions are planted together in a 'common garden.' Results from these trials form the basis of rules governing seed transfer within the province, and are also informing policy for gene and ecosystem conservation under climate change. In contrast, because natural dispersal often occurs over very long distances, even among populations isolated in space (*i.e.*, via pollination, seed dispersal and juvenile dispersal), over-emphasizing the separate management of ecologically exchangeable groups has the potential to waste scarce conservation resources and impede the success of recovery programs.

2.2. How is Genetic Variation Measured?

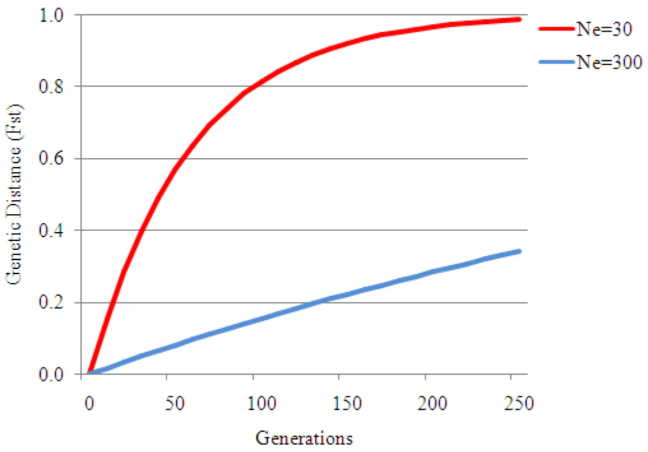
Genetic variation is assessed using a variety of DNA markers representing versions of a particular gene (*alleles*), collectively resembling a bar-code (Figure 1). The fraction of identical alleles in different individuals is used to infer their *relatedness*. The fraction of individuals in two populations with identical alleles is also used to infer rates of current and historic dispersal between populations and their level of genetic distinctiveness overall. Similarity in allele frequency is often summarized as F_{ST}, which estimates *genetic distance* between populations and ranges from values near zero for populations that mix regularly, to values up to 1 for populations with no shared ancestry. However, interpreting genetic distance also depends on population size () because gene frequencies change more slowly in larger populations.[xxvii] Thus, in two island populations of N_e 30 and 300, and receiving the same number of mainland immigrants annually, we expect the smaller population to diverge markedly within 20 generations (e.g. $F_{ST} \geq 0.2$), whereas the larger population would require 140 generations to reach a similar degree of distinctiveness. Thus, even small values of F_{ST} may indicate long periods of isolation between large populations, such as those residing on island versus mainland sites or in different river drainages or lakes.

Figure 1. A microsatellite gel revealing neutral genetic variation in individual song sparrows (*Melospiza melodia*). Each column represents an individual's genotype at a one microsatellite gene (locus). Columns with two strong black bands indicate 'heterozygous' birds with a different allele on each of two chromosomes. 'Homozygotes' have the same allele on each chromosome, appearing as a single band, identified in the figure below with arrows. Bands in the same horizontal plane indicate that some individuals carry the same allele, with each horizontal row corresponding to the number of nucleotides (length) of each allele surveyed at this gene.



Two additional metrics used to assess the status of genetic diversity in populations include: *heterozygosity*, or the fraction of individuals in populations that carry two different alleles of a particular gene; and *allelic richness*, the number of different alleles of a particular gene present in a population. Because heterozygosity and allelic richness are each reduced as populations decline or become isolated, and influence the ability of populations to adapt to change, such declines can be used as an indication that management action to supplement populations or create facilitate dispersal may be required (Figure 2).

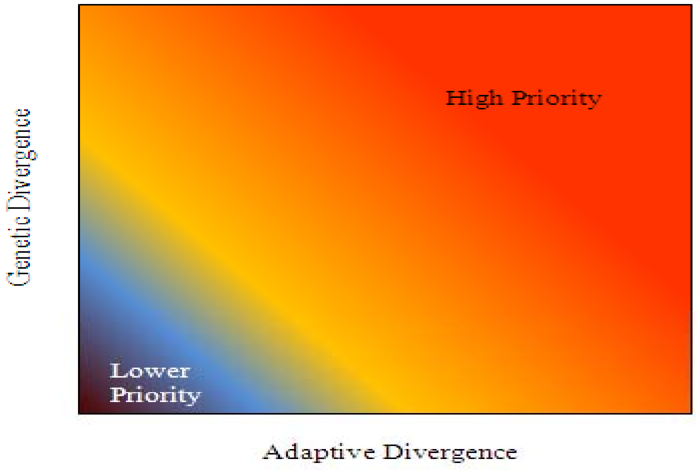
Figure 2. This figure shows the effect of effective population size on the accumulation of genetic divergence over time. In this example, two populations are instantaneously and permanently isolated from a source population. The population with the N_e=30 quickly attains complete divergence (Fst=1.0).



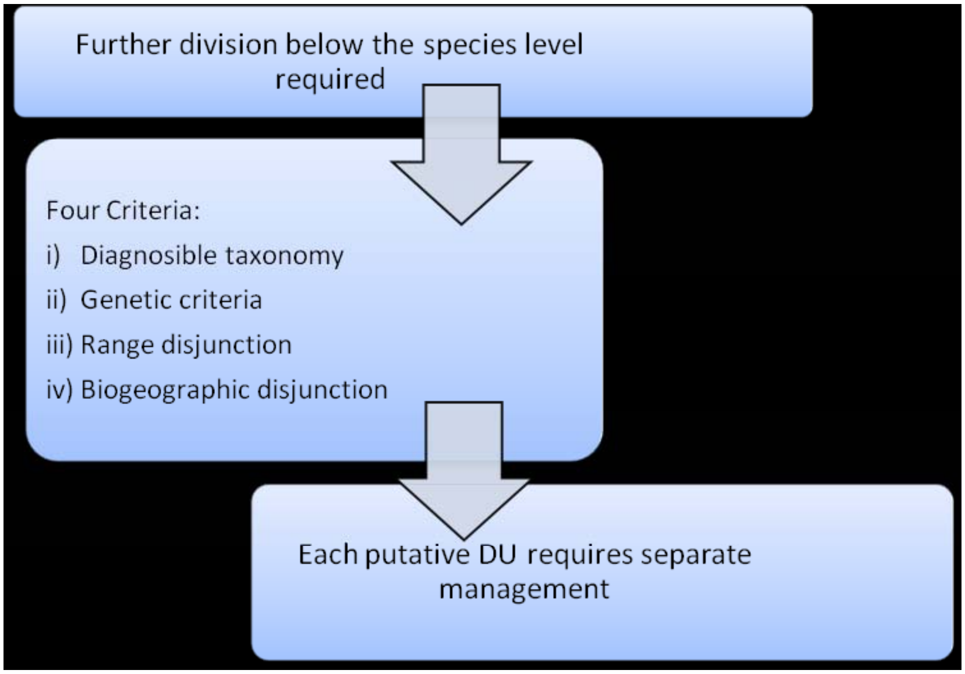
2.3. Adaptive vs Neutral Genetic Variation

Examples above concern the application of neutral genetic variation to assess the status of populations because the underlying theory is simple and widely accepted. Genes representing adaptive traits have also proved difficult to isolate and describe theoretically. There is also considerable variation in the adaptive value of particular traits, some being closely linked to fitness while others may provide marginal advantage. Thus, scientists also employ differences in phenotype, especially size, shape and colouration, to identify differences among populations, sub-species and species where these differences are known to be inherited as opposed to environmental in origin (very common in plants). Because the emphasis on adaptive versus neutral genetic differences for prioritizing conservation actions can be contentious, neutral and adaptive differences are typically considered on a continuum (Figure 3), wherein increased divergence in phenotype or genotype increases conservation priority. These ideas have recently been formalized to assist in identifying and prioritizing *Designatable* or *Evolutionarily significant* units below the species level (Text box 1).

Figure 3. Craig Mortiz suggested that the continuous nature of genetic and adaptive divergence required that these two characteristics be jointly considered in the prioritization of population for conservation. Entities with the highest priority are those showing marked neutral genetic and adaptive divergence, whereas populations which show low levels of divergence in either axis would received lower priority (adapted from Moritz 2002).



Adapted from Moritz 2002



Text Box 1. Identification of Designatable Units.[xxviii] In general, species are reproductively compatible and inclusive units, whereas subspecies typically represent subsets of populations that can be reliably distinguished by morphological or ecologically relevant characteristics. The degree of taxonomic division varies widely across taxa, due largely to differences in research history, with some designations representing cases of over (not reliably distinguished) and under-description (distinguishable but as yet unnamed). This recognition led to the development of the term *evolutionarily significant unit* (ESU).[xxix] The definition of an ESU is being revised as methods and scientific understanding improve but, in general, ESUs show marked genetic divergence from species or subspecies under consideration and thus are presumed to represent an irreplaceable evolutionary lineage within particular species. A contentious aspect of ESU designation concept and classification systems in general, is that divergence is a gradient and evolution is a process, making the application of thresholds problematic. The ESU concept as adopted in Canadian legislation is referred to as a *designatable unit* (*DU*). The DU concept recognizes that populations of particular species often require different management approaches.[xxx] Recognition of DUs below the species level consider evidence of: i) diagnosability, ii) genetic divergence (neutral or adaptive differences in genotype and phenotype), iii) presence of disjunct populations and iv) presence in distinct biogeographic regions. Units satisfying any of these criteria are considered further as a DU, whereas units lacking all four attributes are be rejected as DUs and managed as part of a larger unit. Green (2005) summarizes the guidelines for DU designation in accordance with COSEWIC.[xxxi] In British Columbia, three DUs have been identified within Pacific Salmon species: Interior Fraser Coho, Sakinaw Lake Sockeye and the Cultus Lake Sockeye; each being genetically divergent and adaptively distinct.

3. Genetic Diversity in British Columbia

Because genetic changes occur more rapidly when populations are isolated in different environments, most studies of genetic variation in British Columbia have focused on areas of historic isolation and novel environments, including areas at the periphery of species ranges, on islands and in glacial refuges. With the caveat that most recognized taxonomic divisions in British Columbia were made decades ago, and thus may not reliably reflect underlying evolutionary differences, several areas of potential special interest are considered below.

3.1. Geographically Marginal Populations

There is growing evidence that geographically marginal or *peripheral* populations in British Columbia display different genetic make-ups than populations at the core of the species range. Peripheral populations of Sitka spruce (*Picea sichensis*), for example, are known repositories for rare alleles and locally adapted types.[xxxii] The large size and biophysical variability of B.C. also results in many other species existing as peripheral or marginal populations within the province, potentially representing evolutionarily significant lineages. For example, several bird species at the edge of their range in B.C. have their core within the United States or elsewhere in Canada, whereas some arctic species reach their southern extreme in B.C. It is increasingly being recognized that northern and southern range extremities, or leading and rear-edges, have different population structures that may necessitate different conservation strategies in order to maintain the potential for adaptation and enable long-term persistence.

Out of the taxa with available distributional data, more than 1,300 species have peripheral populations in B.C. Some examples of peripheral species in B.C. with geographically marginal populations do show marked genetic variation and are also of conservation concern. These include several species confined to the South Okanagan-Similkameen (*e.g.*, sage thrasher (*Oreoscoptes montanus)*, morman metalmark (*Apodemia mormo*); Behr's hairstreak (*Satyrium behrii Columbia*) and Gulf Islands (*e.g.*, sand-verbena moth (*Copablepharon fuscum*); propertius duskywing (*Erynnis propertius*); Edith's checkerspot (*Euphydryas editha taylori*). Peripheral species or marginal populations in northern B.C. include the eastern pine elfin, *Callophrys niphon*, a butterfly confined in B.C. to the northeast, and the phoebus Apollo (*Parnassius phoebus*) a butterfly that occurs in Siberia, Alaska and the western Yukon, entering B.C. in the NW corner.[xxxiii]

3.2. Island Populations

In many taxa, island populations are recognized as subspecies where phenotypic differences and geographic isolation suggest a history of isolation. An impressive example of the insular effect on genetically based traits is the 'Kermode Bear'. Kermodism is a trait wherein individuals carrying two copies of a recessive allele have a cream-coloured coat. Genetic analyses indicate that most coastal black bears, regardless of color, have descended from populations once restricted to glacial refuges that now mix with continental lineages. Analyses of skeletal morphology also support the identification of most central to north coastal populations as belonging to the Kermode sub-species (*Ursus americanus kermode*). However, the 'Kermode' color morph familiar to most non-biologists remains most common on islands. The high frequency of kermodism on coastal islands (perhaps 10% of individuals in some populations) is consistent with the idea that water barriers to dispersal, small population size and perhaps natural selection related to mate preference and the unique structure of island communities, have acted to increase the frequency of the Kermode allele via *random genetic drift*.[xxxiv]

Much evidence also suggests that the Hecate Strait has been a formidable barrier to dispersal, contributing to the distinctiveness of several bird and mammal species in the Queen Charlottes and adding to the historic importance of the region as a glacial refuge. The Queen Charlotte Islands and Vancouver Island are home to a wide array of subspecies. The Queen Charlottes were the historical home to Dawson's caribou, a small forest caribou subspecies – the last individual of which was shot in 1908. Other mammal subspecies include the largest subspecies of black bear found in North America, and a once relatively common subspecies of ermine now thought to be extinct or at very low numbers. A large number of bird subspecies also occur on these islands, including subspecies of northern goshawk, Stellar's jay, hairy woodpecker, pine grosbeak, and northern saw-whet owl.

Vancouver Island is also home to a number of endemic species or subspecies including the critically imperiled Vancouver Island marmot (*Marmota vancouverensis*), and the Vancouver Island wolverine (*Gulo gulo vancouverensis*) which has not been observed since 1982. Bird subspecies found here include the endemic white-tailed ptarmigan and the northern goshawk subspecies that also occur in the Queen Charlotte Islands. A number of butterfly subspecies are also known to inhabit Vancouver Island, as are several endemic plants. Although genetic comparisons of species in this region remain scare, recent studies of Keen's and white-footed mice (*Peromyscus keeni* and *P. maniculatus*, respectively), resident in coastal B.C. suggest that glacial history and small effective population sizes have lead to substantial genetic differentiation between populations, raising the possibility that additional taxa remain undescribed. In particular, many sedentary species of plants, vertebrates and invertebrates may exist on islands of the B.C. coast as evolutionarily divergent lines.

3.3. Glacial Refuges

The Queen Charlotte Islands and the Brooks Peninsula on Vancouver Island are two areas in B.C. identified as glacial refuges. The Queen Charlotte archipelago includes 250 islands and has been termed "the Galapagos of the North" due to the high levels of biodiversity and relict species occurring there, including endemic species (5 vascular plant species, 3 bryophytes, 4 insects, 2 liverworts (hepatics) and 5 mosses). These areas provide homes to an important component of the genetic biodiversity of B.C. and of the planet. However, the isolation and ecological novelty which gave rise to such diversity, also makes them vulnerable to disturbance, and both the Queen Charlotte Islands and Vancouver Island have been significantly impacted by invasive species. Black-tailed deer, introduced to the Queen Charlottes, have dramatically altered the ecology of entire rainforest ecosystems, with deleterious cascading impacts to many species. Forestry, mining and tourism all have the potential to disrupt island populations by reducing historic barriers to dispersal between divergent populations or reducing and fragmenting significant habitats, and facilitating the introduction invasive species; all of these factors potentially increasing extinction risk related to demographic decline, dilution or loss of locally adapted traits.

Recent research also suggests that at least two freshwater fishes unique to B.C. and of concern to conservation, the Salish sucker (*Catostomus* sp. 4) and Nooksack dace (*Rhinichthys* sp. 4), derive from the Chehalis Refugium, centered in southern Puget Sound, during the most recent glacial maximum.[xxxv] The Salish sucker has no formal taxonomic status but is identified as an evolutionary significant unit, and both groups are of conservation concern. Various other pockets of isolation and subsequent re-colonization have contributed to differentiation in species (*e.g.*, longnose dace, *Rhinichthys cataractae*) not yet assigned formally to a taxonomic class, but that represent marked differences in life history or habitat use and, thus, are of management concern. Indeed, much diversity evident in B.C. freshwater fish below the species level is a product of range fragmentation and genetic divergence followed by recolonization from refugia.[xxxvi]

Glacial retreat, although often restoring connectivity between populations, also isolated others as the land rebounded from under the glaciers' immense weight. A rising land mass (*isostatic rebound*) also separated populations of anadramous species such as Pacific lamprey, (*Lampetra tridentata)* and longfin smelt, (*Spirinchus thaleichthys*) in fresh water, facilitating their rapid divergence. In some cases this process produced "biological species" endemic to British Columbia. A particularly well researched example involves the complex genetics of sticklebacks in B.C., wherein six lakes on three islands in the Strait of Georgia have in each lake given risen to two forms of the three-spined stickleback. 'Benthics' are stout and wide-mouthed and forage at lake margins, while 'limnetics' are slender and slim-mouthed and forage in the open waters of the lake. Studies show the two forms carry different genes, and until recent human influences altered these communities, rarely hybridized. The genetic differences evident in these species are particularly interesting because they appear to have arisen very recently (since the last ice-age) from a common ancestor, but also in parallel in each separate lake. Because these differences represent adaptive genetic variation that affects individual fitness and population persistence, each form is recognized as an endemic species.[xxxvii] Similar patterns of divergence are also noted in groups such as lampreys, smelts and sculpins, providing a remarkable snapshot of 'evolution in action'. Another example unique to B.C. is the Pygmy whitefish, also considered to be a glacial relict. Pygmy whitefish occur across northern North America in scattered populations, usually in deep, nutrient-poor lakes. However, in two nutrient-rich lakes in B.C., a 'giant' form exists that occurs nowhere else in the whitefish's range.

3.4. Major Hybridization Zones

Hybrids often hold a tenuous place in conservation because once detected, the appropriateness of 'species' designation is often questioned. Although hybridization is a potentially serious problem for populations with unique evolutionary histories, many naturally occurring hybrid zones are known to be stable in ecological timeframes, perhaps contributing novel lineages and species in evolutionary time. For plants in particular, hybridization has been an important process in speciation.[xxxviii, xxxix] Hybrid zones are therefore fascinating laboratories for evolutionary study and, potentially, hot spots of genetic variation and local adaptation that have as yet not received extensive study in B.C.

Research suggests that 13 ‘suture’ zones occur in North America, where overlap between divergent groups occurs and some species hybridize as a result of landscape change and the historic expansion and contraction of species ranges. A major suture zone in B.C. extends northwards from the southeast corner of the province into the central interior, representing the channeling effects of mountain ranges as species radiated across the landscape during global shifts in climate.[xl] Recent research indicates that several *superspecies*, or complexes of closely related species occur in this region, many hybridizing rarely, others extensively. For example, the northern flicker (*Colaptes*) exists across North America, but in a band stretching from B.C. down into Texas 95% of the flickers found are hybrids between the red-shafted, yellow-shafted and gilded subspecies. The Okanagan and Kootenay valleys of B.C. are also the only place in North America where two species of tiger swallowtails (*Papilio* spp.) occur together, and only in this location are two of these species known to hybridize. Overall, although the genetic diversity of closely related species in B.C. has not been well studied, recent reviews suggest that the province has the highest density of hybrid zones, significant phylogeographic breaks, and zones of secondary contact in Canada.[xli] This places increased responsibility on British Columbia for the conservation of processes related to the evolution of biodiversity.

4. Status of Genetic Data for British Columbian Taxa

At least 60 B.C. taxa have been the subject of peer-reviewed genetic studies, focusing mainly on evolutionary history, population genetic structure, phylogeography (the geography of genetic lineages), and the fine-scale effects of forest practices on genetics and hybridization (Table 2.). Eight of these studies recommend the management of evolutionarily significant taxonomic units below the species level (4 fish, 2 birds, 1 mammal, 1 invertebrate). It is apparent, however, that while some species of fish and birds have been the subject of multiple studies, genetic data are rare to nonexistent for amphibians, invertebrates, bryophytes and vascular plants other than trees. That fact that molecular markers for given species can often be readily applied to close relatives means that genetic surveys will continue to become more feasible in future. Priorities for genetic studies aimed at identifying the appropriate taxomonic units for management, cryptic species, or populations of particularly high or low genetic diversity should be guided by evaluations of species’ life history traits, phenotypic variation, geographic distribution and demographic history likely to influence N_e, divergence and/or individual and population fitness. The status of major taxomonic groups is summarized briefly below.

4.1. Vertebrates

Mammals: At least 10 species of mammals have been the subject of peer-reviewed genetic research in B.C., with some receiving repeat attention due to their key scientific relevance to the evolutionary processes of speciation and historic isolation (coastal populations of *Peromyscus maniculatus* and *P. keeni*). However, of these 10 taxa only the boreal caribou (*Rangifer tarandus*) is recognized by COSEWIC below the species level, and this group is not currently ranked as being of high global responsibility in B.C. In contrast, all 10 sub-specific taxa listed by COSEWIC and resident in B.C., including 6 for which BC has high responsibility (3 Mustelids: *M. erminea anguinae, M. e. haidarum, Gulo gulo vancouverensis*; 1 Sciurid: *Neotamias minimus selkirki*; 2 caribou *R. t. Dawsoni* [extinct] and one southern population; and 1 sub-species of mountain beaver: (*Aplodontia rufa rainieri*), are amendable to genetic study based on the availability of molecular markers for closely-related species (Table 3.) and occurrence of museum specimens in cases where live specimens are not obtainable. Further genetic study of these groups is advisable if population augmentation, translocation or re-introduction programs are anticipated. Priorities for genetic studies aimed at identifying cryptic species should focus on taxonomic groups resident in historic refugia and geographically disjunct populations that also exhibit low dispersal ability, despite moderate to large N_e. Studies aimed at establishing baselines for monitoring genetic diversity are likely to have most relevance when focused on species that display wide historic distributions in B.C., but currently exist as isolated populations of much reduced size.

Birds: Thirteen species of birds occurring in B.C. have been the subject of peer-reviewed genetic studies, resulting in two recommendations for special recognition at the species (Timberline sparrow, *Spizella taverneri*) or subspecies level (coastal blue grouse, *Dendragapus obscurus*). However, neither the coastal blue grouse or timberline sparrow are currently ranked by the B.C. CDC or COWSEWC. By comparison, of 24 taxa identified as being of concern by the B.C. CDC, 12 are listed by COSEWIC, and for 8 of these B.C. has high global responsibility. An established history of genetic research on birds and the availability of molecular markers means that for 7 of 24 the CDC-listed taxa, publicly available genetic data (GENBANK) exists, and for 13 of these 24 taxa, molecular markers are available. Currently, several studies of birds are underway in B.C. to understand how hybrid suture zones contribute to biodiversity via speciation and the hybridization in sister taxa, [xlii] and how historic refugia and population isolation affect microgeographic variation in phenotype, genetic diversity and population persistence.[xliii] However, no peer-reviewed genetic studies of the 8 listed taxa for which B.C. has high responsibility are yet available. Applying the appropriate molecular markers to tissue from museum specimens and/or wild birds could be used to test for significant differentiation or to establish genetic baselines for monitoring in these taxa. Careful assessment of the geographic distribution of taxa inhabiting disjunct populations in known refuges, particularly those that also appear to be in population decline, could also help identify high priority genetic research.

Freshwater Fishes: Freshwater fish populations exhibit high genetic differentiation and low diversity relative to many marine populations, [xliv] and often differ in phenotype and genotype across in major drainages in B.C. due to the effects of historic isolation, founder events, high breeding site fidelity and more recent isolation in lake and/or river systems.[xlv] A long history of commercial, recreational and scientific interest has also lead to this group to be among the best-studied with respect to taxonomic and genetic diversification. Of 29 taxa recognized below the species level and identified as being of concern by the B.C. CDC, 11 are also of concern globally, 23 are listed by COSEWIC, and 25 are considered to be of high global responsibility in B.C. So far, at least 13 freshwater or anadromous species have been the subject of peer-reviewed genetic study (Table 2.), with all showing evidence of adaptive divergence, significant genetic differentiation between populations and/or being recommended for special management status. Priorities for genetic study in future are likely to be guided best by assessments based on the recent taxanomic reviews and, in the case of declining populations, the necessity to resolve uncertainty about genetic status arising in the event that translocation, augmentation or reintroductions are anticipated.

Amphibians: Of 5 B.C. species subject to genetic study in peer-reviewed literature, none was singled out for special management as a DU despite some evidence of divergence at the population level (Table 2.). In addition, no group has yet been identified as being of special conservation concern below the species level in B.C. by the CDC or COSEWIC (Table 3.). However, because meta-analysis showed that amphibian populations tend to be more differentiated than birds, [xlvi] and because some amphibians potentially share similar isolation histories to fishes, it is possible that this group incorporates higher levels of genetic differentiation in B.C. than is currently recognized. As noted above, priorities for genetic research will benefit from a careful consideration of geographic distribution and the potential for adaptive divergence based on life history.

Table 2. Summary of genetic information for B.C. native vertebrate taxa identified by the B.C. Conservation Data Centre and summarized in Table 3.

SPECIES GROUP	Species with genetic data for B.C. Populations	Established molecular markers
Birds	7	13
Freshwater Fishes	6	12
Mammals	1	10
Non-marine molluscs	0	0
Reptiles and turtles	0	2

Reptiles and Turtles: No species in this group has yet been the subject of peer reviewed genetic study in B.C. despite the fact that 4 are listed as being of conservation concern provincially and by COSEWIC (Table 2. ,Table 3.). In contrast, many detailed studies of genetic differentiation in adaptive traits related to predation and coloration have focused on the garter snakes (*Thamnophis* spp.) including species common in B.C. and on coastal islands. Priorities for genetic studies of reptiles and turtles in B.C. will depend on assessments of population trend, proposals for reintroduction or translocation, and on the perceived need to understand better patterns of divergence in geographically isolated populations.

4.2. Invertebrates

Butterflies and Skippers: Of 35 taxa identified below the species level in B.C., 3 are listed by COSEWIC, and 8 are considered to be of high global responsibility in B.C. (Table 3.). Four species in this group have also been the subject of peer-reviewed genetic studies in B.C., with 3 of these displaying genetic and/or adaptive divergence at the population level, and 1 being recommended for special management (*Nebria charlotte, N. haida*; Table 2.). Genetic studies of species in this group elsewhere in the world often report strong differentiation within species based on geographic distribution and food-plant specialization, suggesting that as yet undescribed genetic variants may also exist in B.C. Priorities for future genetic studies in this group will benefit from careful assessments of variation in life history and geographic distribution to identify candidate groups likely to represent high levels of genetic diversity below the species level.

Dragonflies and Damselflies: No B.C. taxa in this group have been recognized for special conservation concern below the species level by COSEWIC or the B.C. CDC, and no peer-reviewed genetic studies of B.C. have yet appeared in the literature. The potential value of genetic study in this group requires further expert input.

Non-marine molluscs: Two species have been recognized in B.C. by the CDC at levels below species. One of these is of provincial conservation concern, but no peer-reviewed genetic studies are available for this group in B.C., despite its high profile in parts of the United States, where species diversity is also often high relative to B.C. The potential value of genetic study in this group requires further expert input.

Table 3. Summary of conservation status and global responsibility for B.C. native taxa below species level identified by the B.C. Conservation Data Centre.

SPECIES GROUP	Number of Taxa of Global Conservation Concern (GX,GH, G1-G3)[1]	Number of Taxa of Provincial Conservation Concern (SX,SH,S1-S3)[2]	Number of Taxa of Important Global Responsibility[3] (Responsibility Classes 1-3)	Number of Taxa Listed by COSEWIC[4]
VERTEBRATES				
Amphibians	0	0	0	0
Birds	0	24	8	12
Freshwater Fishes	11	29	25	23
Mammals (excluding cetaceans)	0	20	6	10
Reptiles and Turtles	0	4	0	4
INVERTEBRATES				
Butterflies and Skippers	1	32	8	3
Dragonflies and Damselflies	0	0	0	0
Non-marine Molluscs	0	1	0	0
VASCULAR PLANTS				
Ferns and Fern Allies	1	8	0	0
Conifers	0	0	0	0
Monocots	0	43	3	0
Dicots	2	220	16	8
NON-VASCULAR PLANTS				
Mosses	0	76	not assessed	2
TOTAL	**15**	**457**	**66**	**64**

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[1] Global Conservation Concern=ranked by the B.C. Conservation Data Centre as extinct or extirpated (GX), known only from historical records (GH), critically imperiled (G1), imperiled (G2), or vulnerable (G3) within British Columbia.

[2] Provincial Conservation Concern=ranked by the B.C. Conservation Data Centre as extinct or extirpated (SX), known only from historical records (SH), critically imperiled (S1), imperiled (S2), or vulnerable (S3) within British Columbia.

[3] Global Responsibility=>50% of range, distribution or population is within B.C.

[4] Taxa ranked by the Committee on the Status Of Endangered Wildlife in Canada as extinct (XX), extirpated (XT), endangered (E), Threatened (T), or Special Concern (SC). A number of the rankings reflect the COSEWIC ranking for the full species and not for the individual subspecies. See database for these.

4.3. Vascular Plants

Ferns and Fern Allies, Conifers, Monocots, Dicots: The extent of genetic structure in plant populations, especially among subspecies, has been shown via meta-analysis to often be linked to traits such as mating system, pollinators and seed dispersal mechanisms[xlvii], but also to various proximate factors.[xlviii] To date, 9 coniferous and 2 deciduous tree species have been the subjects of detailed genetic study in B.C., aimed mainly at identifying relict populations, rare genotypes, hotspots of genetic diversity, and population structure related to geographic distribution and historic isolation. Overall, 22 peer-reviewed studies have considered the population genetics of 1 fern, 2 monocots, 10 dicots, and 9 conifers (Table 2.). Although just one of these studies reports evidence of adaptive divergence of populations, and none include recommendations for the special management of DUs, 11 do report significant genetic divergence among at least some of the populations sampled. By contrast, as long history of 'common garden' studies has demonstrated pronounced adaptive divergence among conifer populations in B.C., and more recently among iconic plants of Garry Oak meadows (e.g., *Plectritis congesta*, *Sedum spathulifolium* [xlix]and Collinsia spp.[l]). What is not yet understood, however, is the degree to which phenotypic differences between populations result as a consequence of proximate factors affecting micro-evolution, present-day gene flow and natural selection versus those related to historic isolation. Resolving this question is essential to facilitating propagation programs in support of species and ecosystem restoration. For example, the high value of conifers to the B.C. economy has fueled extensive genetic and common garden (also referred to as 'provenance trials') research aimed at identifying appropriate limits to seed and seedling transfer for the purposed of reforestation. This work serves as a potential model for future work on the genetics of vascular plants of concern to conservation.

To date, of 16 ferns and allies identified below the level of species in B.C., 8 have been identified as being of concern to conservation, but for none of these is B.C. identified as having high global responsibility (Table 3.). Of 5 conifers so identified, none are identified as being of concern to conservation. In contrast, 43 of 170 monocots (3 of which B.C. has high responsibility for) and 220 of 589 dicots have been identified as being of concern in B.C. Although COSEWIC lists no monocots and just 8 dicots as being of concern to conservation, B.C. has high global responsibility for 16 dicots and 3 monocots listed as being of provincial concern. It is highly likely that further genetic studies of listed vascular plants could help identify populations of high conservation value. However, because of the large number of candidates, expert assessments based on life history, geographic distribution and existing evidence of phenotypic and adaptive divergence are necessary to insure funds are invested effectively.

4.4. Non-Vascular Plants

Mosses: Of 130 mosses identified below the species level, 76 are listed as being of provincial conservation concern, and 2 of these are also listed by COSEWIC. B.C.'s global responsibility has not yet been assessed and peer-reviewed genetic studies of these taxa in B.C. have yet to appear. As for other poorly described groups with respect to the potential for adaptive divergence below the species level, expert assessment is required to consider the potential value of genetic research in this group.

5. Conclusions

Genetic information has great potential to inform conservation management beyond just documenting genetic diversity and divergence. In particular, identifying uniquely adapted genetic taxa is likely to enhance efforts to conserve species by emphasizing the maintenance of locally adapted types and thus the persistence of local populations. Efforts to identify hotspots of genetic distinctiveness [li] and divergent populations identified by phenotype provide potential models for the development genetic monitoring in B.C., but many cases also indicate that some DUs are cryptic and require genetic markers for identification.[lii] In this case, careful assessment of geographic distribution in relation to glacial refugia, hybrid zones and highly disjunct populations with moderate to large N_e should offer useful guidance to managers wishing to prioritize investments in genetic research. Genetic analyses can also provide information on the significance of historic and recent fluctuations in population size to population viability, migration routes, dispersal barriers, and even sex ratio skews potentially of interest to conservation.[liii] For example, uncertainty about the potential value of dispersal corridors might be resolved by genetic analyses to identify whether or not a species' historic dispersal patterns have been interrupted by habitat fragmentation, and whether re-established corridors are actually used.[liv] Overall, genetic analysis is likely to benefit conservation most when the study designs, taxa and objectives are carefully evaluated in relation to management concerns.

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