An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia

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Abstract: Faunal homogenization and differentiation occur when geographic regions show increased or decreased, respectively, similarity to each other in species composition owing to introductions and extinctions or extirpations. I used species presence–absence data for "native" (i.e., estimated species compositions before European settlement) and "total" (i.e., including nonnative fishes and extinctions) faunas to examine faunal similarity of freshwater fishes among aquatic ecoregions of British Columbia and among Canadian provinces and territories. British Columbia ecoregions showed faunal differentiation as the mean Jaccard's faunal similarity coefficient for total faunas was significantly less than that for native faunas (31.4% versus 34.9%), but some ecoregions showed homogenization (e.g., Vancouver Island and Columbia River ecoregions). Comparisons across Canada showed low but significant homogenization; average pairwise Jaccard's coefficient was higher in total versus native faunas (29.1% similarity versus 27.8%, respectively). British Columbia's fish fauna increased the most in similarity to other areas (except the three territories), with an average increase of 4.9%. Native faunal similarity patterns are part of Canada's natural heritage but are threatened by human-mediated increases in nonnative species and extinctions. This analysis provides a baseline to track changes in inter-regional faunal relationships at different geographic scales.

Résumé : L'homogénéisation et la différentiation de la faune se produisent lorsque des régions géographiques présentent des compositions spécifiques respectivement plus semblables ou moins similaires à cause d'introductions ou d'extinctions ou extirpations. Des données de présence–absence sur les faunes « indigènes » (i.e., les compositions spécifiques estimées d'avant l'arrivée des européens) et « totales » (i.e., incluant les espèces introduites et les espèces disparues) m'ont permis de comparer la ressemblance des faunes de poissons d'eau douce dans les écorégions aquatiques de Colombie-Britannique et dans les provinces et territoires canadiens. Il y a de la différentiation faunique parmi les écorégions de la Colombie-Britannique puisque le coefficient de similarité de Jaccard moyen de la faune totale est significativement moins élevé que celui de la faune indigène (31,4 % par rapport à 34,9 %), mais quelques écorégions présentent une homogénéisation (e.g., les écorégions de l'île de Vancouver et du fleuve Columbia). Les comparaisons à l'échelle du Canada indiquent une homogénéisation faible, mais significative, et les coefficients de Jaccard moyens appliqués deux à deux sont plus élevés pour la faune totale que pour la faune indigène (une similarité de 29,1 % par rapport à 27,8 %). Par comparaison aux autres régions, mais à l'exception des trois territoires, c'est en Colombie-Britannique que la similarité de la faune de poissons a augmenté le plus, en moyenne de 4,9 %. Les patterns de similarité faunique indigène font partie de l'héritage naturel du Canada, mais ils sont menacés par des augmentations du nombre d'espèces non indigènes et des extinctions causées par les humains. Cette analyse fournit une base pour l'observation des changements dans les relations fauniques inter-régionales à différentes échelles géographiques.

[Traduit par la Rédaction]

Introduction

Freshwaters contain some of the most threatened faunas in the world and are estimated to have the highest recent and projected future extinction rates in North America (Riccardi and Rasumssen 1999). These faunas have generally suffered from elevated extinction rates owing to anthropogenic factors such as overexploitation, habitat degradation, so-called "chains of extinction", and the introduction of exotic species (Rhymer and Simberloff 1996). The introduction of nonnative species may result in extinctions of native species via predation, disease transmission, competition, habitat modification, or hybridization. In addition, even if nonnative species do not cause the extinction of native species, they can change the natural patterns of species diversity within geographic areas as well as the zoogeographic relationships among areas. One such change to faunal composition from the single or combined effects of introductions and extinctions or extirpations is known as "homogenization", where regional faunas become more similar to each other over time

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(Rahel 2002). A recent study of freshwater fish faunas in the United States (excluding Alaska and Hawaii) found that widespread introductions had resulted in an average increase in Jaccard's faunal similarity of 7.2% (Rahel 2000). Other studies in individual states have found similar results for fish and other aquatic taxa and also that the degree of homogenization may be dependent on the geographic scale examined (e.g., Marchetti et al. 2001; reviewed in Rahel 2002). By contrast, faunal "differentiation" may be defined as the case in which faunas become less similar to each other from the same causes, but this phenomenon has received little examination.

Homogenization is an important phenomenon to document and track because it represents a clear case of the loss of worldwide biodiversity in several ways (Wilson 1988; Marchetti et al. 2001). First, homogenization may involve extinction of species endemic to particular regions (Rahel 2002). Second, homogenization represents a loss of beta species diversity, or the turnover of species between geographic areas. The loss of beta diversity results because more species become common to different areas resulting in reduced turnover between geographic areas. Third, homogenization results in a loss of the zoogeographic "individuality" of geographic regions, as measured by native faunal uniqueness, and may change faunal relationships among areas. The natural faunal composition of a particular region results from an interplay between historical contingencies and the past and current ecological, physiological, and life history attributes of particular taxa and their interactions with other taxa. Such interactions are part of the faunal legacy of particular areas and, therefore, have inherent conservation value. The loss of diversity through homogenization also represents lost opportunities for use by humanity, as well as the potential for disruption of ecosystem services (Rahel 2002). Notwithstanding arguments concerning the potential benefits of human-induced changes in biodiversity, informed assessments of such debates cannot take place without first documenting faunal composition changes and their effects on aesthetic values and natural processes such as ecosystem stability and services.

The phenomenon of homogenization has received considerable attention in the United States (U.S.), but there have been no formal treatments of similar phenomena in Canada, despite an appreciation of the generally negative impacts of introductions and extinctions (e.g., Crossman 1991). Canada, however, is the second largest country in the world and contains over 890 000 km^2 of freshwater habitat. In particular, British Columbia (B.C.) is Canada's third largest province and has an abundance of freshwater habitats that include or form part of some of the largest drainage basins in North America (e.g., the Fraser, Mackenzie, Columbia, and Yukon river systems). These watersheds drain a vast area from the Arctic Ocean to the mid-temperate Pacific Ocean, and their sundering by extensive mountainous terrain promotes a high level of faunal distinctiveness among regions (McPhail and Carveth 1994). In addition, the freshwater fish fauna of B.C. is almost exclusively postglacial in origin, freshwater faunas having recolonized B.C. from glacial refugia located peripheral to the Wisconsinan ice sheets after they retreated beginning about 18 000 years ago (Lindsey and McPhail 1986; McPhail and Lindsey 1986). The recent origin of the B.C. freshwater fauna means that many ecosystems may not yet be at equilibrium species diversity and could be particularly sensitive to the effects of homogenization from increases in nonnative species and extinctions.

In this study, I provide a summary of fish introductions and extinctions or extirpations in B.C. by major aquatic ecoregion and conduct faunal similarity analyses to test for homogenization within B.C. I then provide a similar analysis at a larger geographic scale that includes the nine other provinces and three territories to test for homogenization for the Canadian fauna as a whole.

Materials and methods

The primary data for my analyses consisted of presence–absence information for the 82 taxonomically recognized fish species in B.C. and the 218 recognized species in Canada (i.e., native and nonnative species; presence–absence matrices are available from the Depository Unpublished Data of the National Research Council of Canada[1]). By "taxonomically recognized", I refer only to those species that have been given formal Linnaean classification. For instance, in B.C., I used "*Gasterosteus aculeatus*" (threespine stickleback) as a single species even though it is part of a complex that probably consists of several undescribed species, e.g., the benthic–limnetic species pairs (McPhail 1994). Although utilizing only formally described taxa in my analyses is an imperfect measure of fish biodiversity, there is no formal consensus on species status for such cases in sticklebacks or, indeed, for other taxa in which similar species complexes occur (e.g., sockeye salmon and kokanee (*Oncorhynchus nerka*) and normal and dwarf lake whitefish (*Coregonus clupeaformis*)), and the greatest depth of divergence in freshwater fishes is probably adequately represented by the formally described taxa. In addition, I included diadromous fishes, such as Pacific (*Oncorhynchus* spp.) and Atlantic (*Salmo salar*) salmon and American eels (*Anguilla rostrata*), which complete portions of their life history and may reside for extended periods in freshwater. I did not, however, include marine fishes that may occasionally be found in rivers that drain to the sea (e.g., fourhorn sculpin (*Myoxocephalus quadricornis*) in Ontario, Manitoba, and Quebec and Pacific staghorn sculpin (*Leptocottus armatus*) in B.C.).

The presence–absence data in B.C. were listed by the eight major aquatic ecoregions (Fig. 1) based on the classification of McPhail and Carveth (1994). These ecoregions represent the major drainage basins, or sets of smaller drainages, in B.C. defined by current or historical connectedness, isolation by saltwater barriers, and colonization from similar glacial refugia (McPhail and Carveth 1994): Vancouver Island and adjacent Strait of Georgia islands, Fraser River, Columbia River, Mackenzie River, Yukon River, North Coast (Stikine, Alsek, and Taku rivers), Queen Char-

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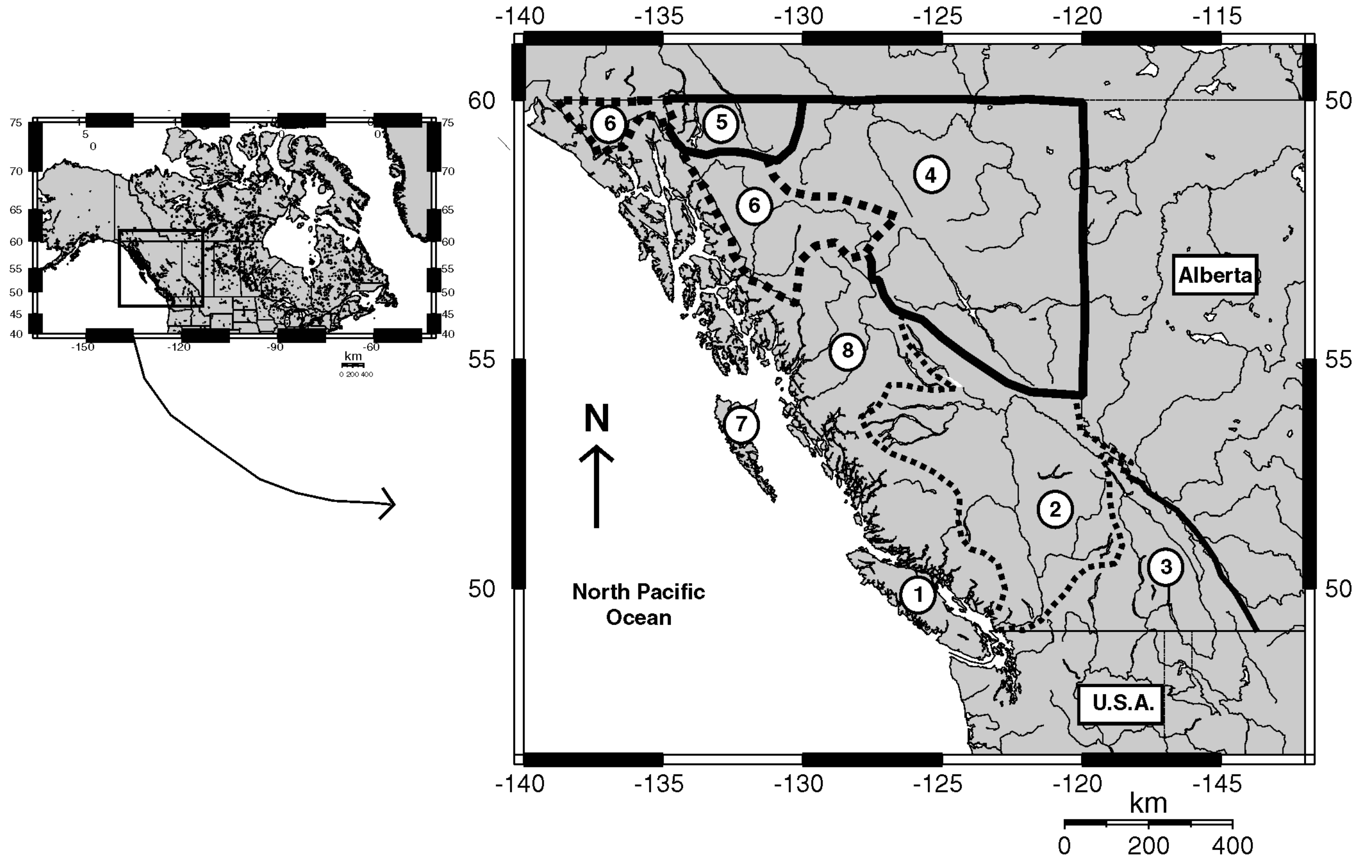
[1] Supplementary data for this article are available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada. DUD 3540. For more information on obtaining material refer to http://www.nrc-cnrc.gc.ca/cisti/irm/unpub_e.shtml.

Fig. 1. Aquatic ecoregions of British Columbia, Canada: 1, Vancouver Island; 2, Fraser River; 3, Columbia River; 4, Mackenzie River; 5, Yukon River; 6, North Coast; 7, Queen Charlotte Islands; 8, Central Coast. (Modified from McPhail and Carveth (1994).)



lotte Islands, and the Central Coast (Skeena and Nass rivers). Some of these regions are part of larger drainage systems that extend beyond the borders of B.C. (i.e., the Yukon, Columbia, and Mackenzie river ecosystems), but the current analysis refers only to those portions within B.C. Presence–absence data were obtained from McPhail and Carveth (1994) and, in some cases, records from the University of British Columbia Fish Museum (see http://www.zoology.ubc.ca/~etaylor/nfrg/fishmuseum.html) and the B.C. Ministry of Water, Land and Air Protection (BCWLAP; E. Parkinson, Biodiversity Branch, B.C. Ministry of Water Land and Air Protection, 2204 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, personal communication). Presence–absence data for the nine other provinces and three territories were based on information from the Wild Species 2000 database available at http://www.wildspecies.ca (Canadian Endangered Species Conservation Council (CESCC) 2001). The wild species database was generated by a national working group composed of representatives from all provinces and territories and two federal government agencies, Environment Canada (Canadian Wildlife Service) and Fisheries and Oceans Canada. These data were subjected to extensive review by the working group and are considered to be the result of the "best available" published and unpublished information as of 2000 (Kent Prior, Species at Risk Branch, Canadian Wildlife Service, Environment Canada, 351 St. Joseph Boulevard, Hull, QC K1A 0H3, personal communication). Other major sources of information included national and regional summaries such as Nelson and Paetz (1992) and Scott and Crossman (1998). A complete listing of authorities consulted is available from the author.

Various definitions have been proposed to differentiate kinds of nonnative fishes, usually on the basis of geographic origin or the process of establishment (e.g., Shafland and Lewis 1984; Crossman 1991). In my analyses, a "native" species is defined as one that occurs, or occurred historically, in a defined area as a result of natural processes exclusive of any influence from humans. A "nonnative" species is defined as one that occurs in an area via the direct (e.g., via deliberate introductions) or indirect influence of humans (e.g., natural dispersal into one area as a result of introduction into an adjacent area). For instance, I included all sources of nonnative species whether they were intentionally or accidentally introduced into an area or whether their occurrence in one area is the result of dispersal from nonnative populations in an adjacent area (e.g., *Stizostedion vitreum* in the lower Columbia River basin in Canada). Because my primary interest was in testing for changes to native fish assemblages, I adopted the term "nonnative", rather than more restrictive terms such as "exotic", "invasive", or "transplanted" (see also Horak 1995) to encompass in a single term the variety of processes that may have led to nonnative species. "Introductions" or "introduced" refers to the action of becoming a nonnative fish via the direct or indirect effects of humans. A nonnative species was included in the analyses if there was at least some evidence that it had established a breeding population(s) and (or) has been repeatedly encountered in nature in the ecoregion, province, or territory (e.g., from persistent introductions). Finally, despite extensive review of the database, there will always be some uncertainty about the true absence or presence of some species in particular areas, particularly at the national level. This is largely a function of differences in opinion, even among experts (personal observation), and the inherent difficulty of proving absence of a taxon after it has been reported. The analyses that follow, however, were completed with and without these taxa ($N = 7$), and their elimination from the database did not change the general results or statistical significance of my analyses.

The presence–absence (1,0) data were summarized by calculating pairwise Jaccard's coefficient of percentage faunal similarity:

$$J = [a/(a + b + c)] \times 100\%$$

where a is the number of species shared between any two regions being compared, b is the number of species found only in the first area, and c is the number of species found only in the second area (Jaccard 1908; Rahel 2000). I also calculated an index of faunal turnover between areas within B.C. and between all provinces and territories by calculating one estimate of beta diversity (percentage faunal turnover between any two regions):

$$T = [(a + b)/c] \times 100\%$$

where a is the number of species unique to the first area, b is the number of species unique to the second area, and c is the total species pool (Rahel 2002). In the classic sense, faunal turnover refers to the change in species composition along a transect that passes through adjacent areas. In the present context, however, I employed it simply as a measure of faunal distinctiveness between areas that are not necessarily contiguous. Calculation of these statistics was accomplished, in part, using EstimateS software written by R.K. Colwell and available at http://viceroy.eeb.uconn.edu/estimates.

Pairwise similarity and turnover indices were calculated separately for native faunas, faunas before known introductions or extinctions or extirpations associated with European settlement (cf. Rahel 2000; Marchetti et al. 2001), and for total faunas, native and nonnative species minus any extinctions or extirpations. Faunal similarity among regions was summarized by clustering estimates of Jaccard's similarity coefficient (subtracted from 1.0 to generate a "distance" measure) and turnover coefficients using the neighbor-joining (NJ) algorithm (Saitou and Nei 1987). Presence–absence data, however, are an incomplete estimate of fish faunal diversity because they do not take into account the abundance of species in particular areas. In some cases, for instance, species are recorded as present in a particular area based on one or a few records only. To obtain some estimate of the robustness of ecoregion relationships based on faunal similarity, the presence–absence matrix was subjected to parsimony analysis of endemism (PAE). Rosen (1984) first applied PAE to species presence–absence data to assess area relationships based on shared presence of taxa, and it has been subsequently applied to a number of different taxa including freshwater fishes in other areas (Da Silva 1996; Watanabe 1998; Unmack 2001). Preliminary analyses indicated that applying Wagner parsimony analysis, in which species extinctions or extirpations or colonizations are equally probable, to the presence–absence matrix resolved the same topologies as NJ clustering of Jaccard's coefficient. Consequently, the presence–absence matrix was subjected to bootstrap resampling ($N = 100$) to simulate the effects of variation in species sampling on the resulting faunal similarity matrices used in the clustering analyses. These bootstrapped matrices were then used in Wagner parsimony analyses, and a consensus tree was derived using the Mix and Consense programs of Phylip (Felsenstein 1995).

Species numbers, pairwise Jaccard's and turnover coefficients, and changes in faunal similarity for B.C. were correlated with independent variables using simple parametric or rank correlations and Mantel tests (Manly 1997), as implemented in Systat (Systat Software Inc., Richmond, Calif.) and Genepop (version 3.3; Raymond and Rousset 2001). Possible explanatory variables investigated included ecoregion drainage area and geographic distance between the geographic centre of each ecoregion. These variables were estimated from topographic maps. Differences between native and total faunal pairwise Jaccard's and turnover coefficient matrices were tested by Fisher's paired comparison randomization test with 10 000 randomizations as implemented by the Rundum software package (version 1.0; Jadwiszczak 2002). In these tests, pairwise observations of Jaccard's or turnover coefficient are randomly assigned to native and total faunal groups and the difference between each pairwise comparison is computed. The mean of these randomized paired comparisons is assessed against the observed mean difference and the latter is declared significant if it is more extreme than 95% or more of the values in the randomized distribution.

Results

British Columbia freshwater fishes

The native freshwater fish fauna of B.C. consists of 66 species and varies from a low of 14 species in the Queen Charlotte Islands to a high of 42 species in the Fraser River ecoregion (Table 1). The total number of historical native species was positively correlated with drainage area ($r = 0.94$, $P = 0.001$). There is only a single recorded extinction–extirpation within any of these eight drainage areas: chinook salmon (*Oncorhynchus tshawytscha*) that once returned to spawn in tributaries of Columbia Lake in the headwaters of the Columbia River were extirpated from the Canadian portion of the Columbia drainage by the construction of the Grand Coulee Dam in Washington State in 1941. By contrast, B.C. now contains a total of 21 species that are nonnative to at least one ecoregion: 15 species originated from outside the province and six species originated from one or more other B.C. ecoregions. The Columbia River drainage has the most nonnative fishes (16) and the Queen Charlotte Islands and the Yukon River are the only B.C. aquatic ecoregions without nonnative species (Table 1). After including nonnative fishes and extinctions or extirpations, total species number was also positively correlated with drainage area ($r = 0.95$, $P < 0.001$).

Table 1. Names, approximate drainage areas, and numbers of native, nonnative, extirpated, and total freshwater fish species in the eight aquatic ecoregions of British Columbia.

Aquatic ecoregion	Drainage area (km^2)	No. of historical native species	No. of extant nonnative species	No. of extirpated species	Total no. of extant species
Queen Charlotte Islands	14 500	14	0	0	14
Yukon River	25 000	16	0	0	16
Vancouver Island	32 000	16	8	0	24
North Coast	83 800	29	1	0	30
Columbia River	116 300	27	16	1	42
Central Coast	204 900	31	1	0	32
Fraser River	233 000	42	10	0	52
Mackenzie River	285 900	39	4	0	43

Note: The total number of extant species is equal to the total number of historical native species minus any extinctions or extirpations, plus nonnative species. Species distributions and ecoregion definitions are from McPhail and Carveth (1994).

Jaccard's similarity indices of native faunas ranged from a low of 6.6% between the Yukon drainage and the Queen Charlotte Islands to a high of 76.5% between Vancouver Island and the Queen Charlotte Islands (Table 2; Fig. 2*a*). Neighbor-joining clustering of distances based on these indices revealed three major ecoregion groupings: Vancouver Island – Queen Charlotte Islands, North–Central coasts and the Fraser River, and a heterogeneous mixture of the Yukon, Mackenzie, and Columbia rivers (Fig. 3*a*). Estimates of faunal turnover ranged from a low of 13.3% between Vancouver Island and the Queen Charlotte Islands to a high of 86.5% to 87.5% between these two island ecoregions and the Yukon ecoregion. Faunal turnover coefficients resolved the same ecoregion affinities as Jaccard's coefficient (not shown). B.C. native freshwater fish faunas became less similar to one another as the distance between their geographic centres increased (r = –0.31, Mantel test, P = 0.02), and faunal turnover increased with geographic distance (r = 0.47, P = 0.02).

After incorporating nonnative species and extinctions or extirpations, pairwise Jaccard's coefficient ranged from a low of 5.3% between Vancouver Island and the Yukon ecoregions to a high of 72.2% between the North Coast and Central Coast ecoregions (Table 2; Fig. 2*b*). Clustering these estimates resulted in ecoregion affinities similar to those resolved by comparing native faunas but revealed evidence of increased differentiation of ecoregions (Fig. 3*b*). For instance, the average pairwise change in Jaccard's coefficient was a decrease of 3.5% (34.9% to 31.4%) and the pairwise native and total Jaccard's coefficient matrices were significantly different from one another (matrix randomization test, P = 0.017; Figs. 2, 4). The greatest percentage decline in similarity occurred between Vancouver Island (eight nonnative species) and the Queen Charlotte Islands (no nonnative species), where Jaccard's index fell from 76.5% to 51.9% similarity (–23% of native value). The same large number of nonnative species on Vancouver Island, coupled with those in the Columbia basin (16 nonnative species), resulted in the largest percentage increase in similarity between any two regions, i.e., from 13.2% to 20.1% (52% of native faunal value). The only other pairwise comparison to show substantial faunal homogenization was that between the Columbia River and the Mackenzie River drainage, where Jaccard's coefficient showed a 21.1% increase relative to the native faunal value (28.8% to 34.9%). The greater differentiation of aquatic ecoregion fish faunas in B.C. was also reflected in faunal turnover, which increased from an average of 51.3% to 54.6% after incorporating nonnative species and extinctions or extirpations (matrix randomization test, $P < 0.005$). The influence of nonnative species and extirpations was detectable in the interrelationships among ecoregions (Fig. 3). For instance, bootstrap support for a tight relationship between Vancouver Island and the QCI dropped from 100% to 93% and the branch length between them increased in the total faunal tree (Fig. 3*b*). In addition, the bootstrap support for a Yukon and Columbia ecoregion group dropped from 62% to under 50% and the bootstrap support for a linking of Columbia, Yukon, and Mackenzie ecoregions dropped from 66% to 57%. Finally, the Fraser ecoregion total fauna became more distinctly separate from the Central Coast ecoregion (which grouped with the North Coast ecoregion) in the NJ tree relative to the native faunal interrelationship.

At the family level, centrarchid fishes (sunfishes and basses) were the most widely introduced taxon, accounting for nine region introductions (a combination of four different species is nonnative in up to three ecoregions each). The single most widely introduced species was the brook trout (*Salvelinus fontinalis*); it has been introduced from east of the Rocky Mountains to four of B.C.'s eight aquatic ecoregions.

Comparisons among Canada-wide fish faunas

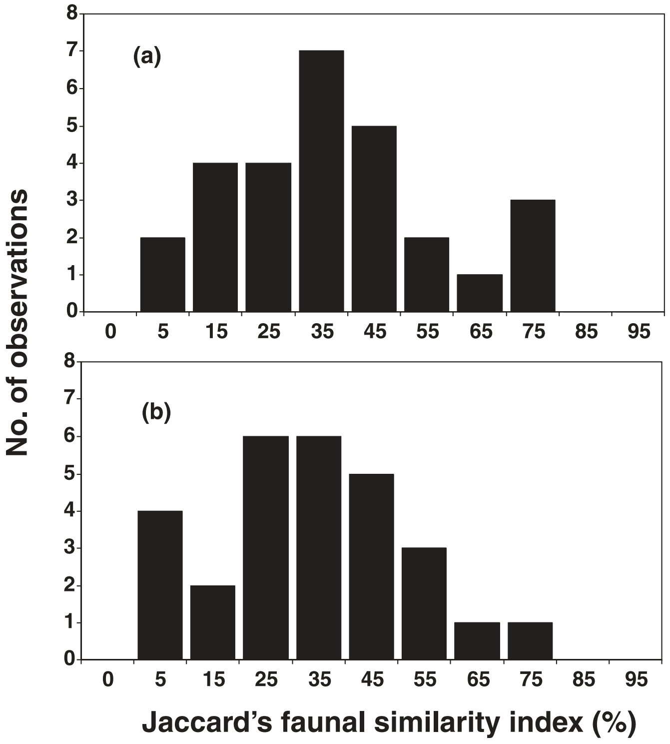
Historically, there was an estimated 197 native freshwater fishes in Canada; Ontario had the highest number (131 species) and Prince Edward Island the lowest (23 species) (Table 3). There are 48 species nonnative to Canadian freshwaters in at least one province or territory (including 21 from countries other than Canada), and four species have been declared extinct. Several nonnative species are recorded from two or more provinces or territories, and four species have been declared extirpated in more than one region. Consequently, there have been a total of 102 records of nonnative species and eight extinctions and extirpations among the 13 provinces and territories. Accounting for all nonnative species and extinction or extirpation events, Ontario still has the largest number of species (154), and Prince Edward Island, the fewest (23). Ontario has recorded the greatest number of nonnative species (28) and extinctions or extirpations (5); only Prince Edward Island has also recorded extirpations (3). Two of the territories (Yukon and Nunavut) have no recorded nonnative species (Table 3).

Table 2. Jaccard's faunal similarity coefficients for native (lower diagonal) and total (native + nonnative – extinctions or extirpations, upper diagonal) freshwater fish faunas among eight British Columbia aquatic ecoregions estimated from species presence–absence data.

	VanI	Fraser	Columbia	Mackenzie	Yukon	NorthC	QCI	CentralC
VanI	—	0.382	0.201	0.117	0.053	0.350	0.519	0.368
Fraser	0.357	—	0.492	0.338	0.172	0.491	0.269	0.615
Columbia	0.132	0.551	—	0.349	0.184	0.220	0.057	0.276
Mackenzie	0.120	0.350	0.288	—	0.283	0.306	0.096	0.339
Yukon	0.066	0.213	0.194	0.302	—	0.394	0.071	0.231
NorthC	0.452	0.591	0.244	0.327	0.406	—	0.467	0.722
QCI	0.765	0.341	0.108	0.102	0.071	0.483	—	0.438
CentralC	0.469	0.756	0.349	0.356	0.237	0.714	0.452	—

Note: VanI, Vancouver Island; Fraser, Fraser River; Columbia, Columbia River; Mackenzie, Mackenzie River; Yukon, Yukon River; NorthC, North Coast; QCI, Queen Charlotte Islands; CentralC, Central Coast.

Fig. 2. Frequency histogram of Jaccard's pairwise faunal similarity coefficients among eight British Columbia aquatic ecoregions for (*a*) native fish faunas and (*b*) total (native + nonnative – extinctions or extirpations) fish faunas.



Pairwise Jaccard's similarity matrices of native faunas averaged 27.1%, ranging from a low of 3.8–4.4% between Yukon and Northwest Territories, respectively, and Prince Edward Island to a high of 70.0% between Saskatchewan and Manitoba (Table 4). Clustering these coefficients resolved three groupings of regions: a "northwestern region" consisting of the three territories, B.C., and Alberta; a "central region" consisting of Saskatchewan through Quebec; and an "eastern region" consisting of New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland/Labrador (Fig. 5*a*). Pairwise faunal turnover between native faunas averaged 59.9%, ranging from 17.6% between Saskatchewan and Manitoba to 92.6% between Yukon and Prince Edward Island. After accounting for nonnative species and extinctions or extirpations in Canadian freshwater fish faunas, similarities averaged 28.3%, ranging from a low of 5.9–7.5% between Yukon and Northwest Territories, respectively, and Prince Edward Island to a high of 65.3–66.7% between Saskatchewan and Manitoba and New Brunswick and Nova Scotia, respectively (Table 4). Clustering these similarity coefficients resolved the same general relationships as the native faunas. The only major differences included the tighter clustering of Nova Scotia and New Brunswick (87% bootstrap support; three shared introductions) separate from Prince Edward Island and Newfoundland/Labrador, within the eastern faunal region (Fig. 5*b*). In addition, bootstrap support for a northwestern grouping (Nunavut, Yukon, and Northwest Territories, B.C., and Alberta) declined from 63% in the native faunas to less than 50% in the total faunas. There was also a slight decline in the total branch length separating the northwestern grouping from the central grouping (i.e., Saskatchewan through Quebec; Figs. 5*a*, 5*b*).

Over all pairwise comparisons, the difference between the mean native and total faunal pairwise Jaccard's coefficient matrices was small but highly significant (27.1% similarity versus 28.3%, respectively, matrix randomization test, P = 0.009; Fig. 6). As a further index of homogenization, mean pairwise faunal turnover dropped an average of 1.8% from 59.9% to 58.1% (matrix randomization test, P = 0.0004), but pairwise variation was considerable. For instance, there was a gain in turnover between Nova Scotia and Prince Edward Island from 28.6% to 39.7%, but turnover declined between B.C. and Quebec from 69.3% to 54.9% after incorporating nonnative species and extinctions or extirpations.

The B.C. freshwater fish fauna showed the greatest change in faunal similarity, with an average increase in Jaccard's similarity index of 4.9% (or an average 25.1% of the native faunal value) (Fig. 7). British Columbia's fish fauna became more similar to the faunas of all areas except the three territories, where Jaccard's similarity actually dropped an average of 5.6% (or 14.7% of the native faunal value). The greatest increase in similarity observed in comparisons with B.C. freshwater fish fauna was that with Quebec (11.0%), Nova Scotia, Ontario, and Manitoba (8.4–8.6% each). Among all regions, the largest proportional homogenization occurred between B.C. and Quebec (86.7% of native value), Alberta and Prince Edward Island (82.1%), B.C. and Nova Scotia (77.3%), Saskatchewan and Prince Edward Island (69.0%), and Yukon Territory and New Brunswick (64.1%).

Fig. 3. Relationships among eight aquatic ecoregions of British Columbia. Relationships are depicted as a neighbor-joining tree obtained by clustering pairwise values of 1.0 – Jaccard's faunal similarity coefficients for (*a*) native faunas and (*b*) total faunas (native + nonnative – extinctions or extirpations). Wagner parsimony analyses resolved the same topology as neighbor-joining clustering, and the numbers at branch points represent bootstrap support levels from 100 replicate parsimony analyses of the species presence–absence matrix. The scale bar represents 0.1 unit of 1.0 – Jaccard's faunal similarity coefficient. VanI, Vancouver Island; Fraser, Fraser River; Columbia, Columbia River; Mackenzie, Mackenzie River; Yukon, Yukon River; NorthC, North Coast; QCI, Queen Charlotte Islands; CentralC, Central Coast.

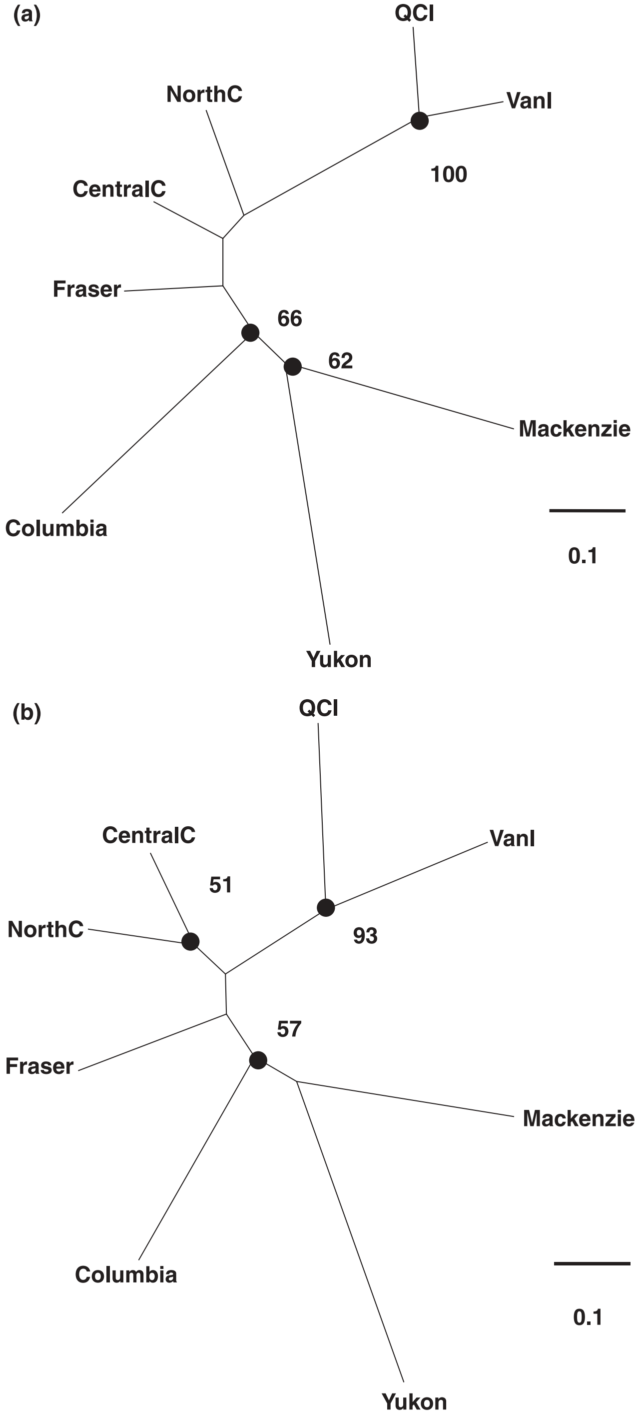
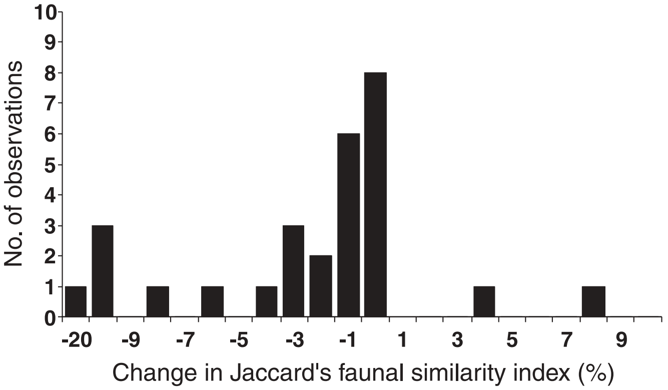


Fig. 4. Frequency histogram of the percentage change in pairwise Jaccard's faunal similarity coefficients between native and total (native + nonnative – extinctions or extirpations) freshwater fish faunas for eight aquatic ecoregions of British Columbia.



In the case of Alberta and Prince Edward Island, these two provinces went from having four species in common to having eight species in common. The largest percentage decrease in faunal similarity (55.6% to 43.2%, –22.3% from native value) occurred between Nova Scotia and Prince Edward Island, which resulted from three extirpations of shared native fauna in Prince Edward Island and six nonnative species now found in one or the other province.

Discussion

Faunal similarity and geographic scale

Natural levels and patterns of biodiversity of freshwater faunas worldwide are at risk of deterioration from anthropogenic activities and homogenization (the tendency for faunas to become more similar to one another over time) from the combined effects of species introductions and extinctions or extirpations. The flip side of homogenization, when faunas become more divergent from these same human activities, I have termed faunal differentiation. The present analysis has demonstrated both homogenization and differentiation in freshwater fish faunas at different geographic scales. For instance, aquatic ecoegions within B.C. have, by an average of 3.5%, become significantly less similar to one another as a result of including nonnative species and extinctions or extirpations in calculations of Jaccard's similarity coefficients and faunal turnover between ecoregions. On the other hand, comparisons between specific ecoregions indicated that some homogenization has clearly occurred (e.g., the Vancouver Island and the Columbia River ecoregions increased in similarity by 7%). At the largest geographic scale across Canada, on average, faunas have become significantly more similar by only about 1.2%, but some areas such as B.C. showed greater levels of homogenization.

The apparent dependence of homogenization and differentiation on spatial scale is probably best explained by the differing patterns of nonnative species occurrence. For instance, B.C. ecoregions have become more differentiated owing to the apparently idiosyncratic nature of most fish introductions in B.C. Of the 21 freshwater fishes nonnative to B.C., only five (brook trout (*Salvelinus fontinalis*), common carp (*Cyprinus carpio*), American shad (*Alosa sapidissima*), goldfish (*Carrasius auratus*), and brown bullhead (*Ameiurus nebulosus*))

Table 3. Numbers of native, nonnative, and total freshwater fish species in the 13 provinces and territories of Canada.

Region	No. of historical native species	No. of extant nonnative species	No. of extirpated species	Total no. of extant species
Yukon Territory	31	0	0	31
Northwest Territories	48	1	0	49
Nunavut Territory	25	0	0	25
British Columbia	67	15	0	82
Alberta	52	11	0	63
Saskatchewan	59	9	0	68
Manitoba	77	12	0	89
Ontario	131	28	5[a]	154
Quebec	102	8	0	113
New Brunswick	45	5	0	50
Nova Scotia	33	7	0	40
Prince Edward Island	23	3	3	23
Newfoundland/Labrador	25	3	0	28

Note: The total number of extant species is equal to the total number of historical native species minus any extinctions or extirpations, plus nonnative species. The table was assembled from data found in the Wild Species 2000 database (http://www.wildspecies.ca).

[a] Includes four species endemic to Ontario (= extinctions).

Table 4. Jaccard's faunal similarity coefficients for native (lower diagonal) and total (native + nonnative – extinctions or extirpations, upper diagonal) freshwater fish faunas among 13 provinces and territories of Canada estimated from species presence–absence data.

	YT	NWT	NUT	BC	ALTA	SASK	MAN	ONT	QUE	NB	NS	PEI	NFLD/LAB
YT	—	0.600	0.514	0.329	0.306	0.207	0.176	0.128	0.143	0.141	0.109	0.059	0.229
NWT	0.580	—	0.480	0.401	0.436	0.345	0.302	0.216	0.246	0.207	0.141	0.075	0.203
NUT	0.514	0.490	—	0.244	0.275	0.224	0.200	0.119	0.150	0.190	0.102	0.091	0.262
BC	0.400	0.456	0.296	—	0.465	0.339	0.326	0.242	0.291	0.234	0.184	0.082	0.183
ALTA	0.317	0.449	0.283	0.469	—	0.523	0.434	0.269	0.304	0.215	0.144	0.103	0.197
SASK	0.216	0.372	0.254	0.273	0.563	—	0.653	0.396	0.448	0.297	0.213	0.110	0.185
MAN	0.174	0.316	0.229	0.241	0.433	0.700	—	0.528	0.566	0.311	0.206	0.120	0.182
ONT	0.102	0.193	0.130	0.158	0.253	0.397	0.529	—	0.628	0.248	0.190	0.106	0.145
QUE	0.118	0.230	0.165	0.182	0.294	0.425	0.543	0.641	—	0.405	0.319	0.183	0.248
NB	0.134	0.208	0.207	0.155	0.183	0.268	0.298	0.231	0.400	—	0.667	0.404	0.529
NS	0.067	0.110	0.115	0.099	0.104	0.179	0.183	0.155	0.285	0.660	—	0.432	0.417
PEI	0.038	0.044	0.067	0.047	0.056	0.069	0.087	0.085	0.202	0.445	0.555	—	0.457
NFLD/LAB	0.191	0.177	0.250	0.136	0.149	0.135	0.159	0.130	0.245	0.522	0.415	0.500	—

Note: YT, Yukon Territory; NWT, Northwest Territories; NUT, Nunavut Territory; BC, British Columbia; ALTA, Alberta; SASK, Saskatchewan; MAN, Manitoba; ONT, Ontario; QUE, Quebec; NB, New Brunswick; NS, Nova Scotia; PEI, Prince Edward Island; NFLD/LAB, Newfoundland and Labrador.

have been introduced (or spread) to three or more ecoregions. In addition, the brook trout is the only species that is nonnative to as many as four ecoregions. There are also four species of fishes that are native to B.C. but that have been introduced or have spread to particular B.C. ecoregions in which they were historically absent: lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), Arctic grayling (*Thymallus arcticus*), walleye (*Stizostedion vitreum*), and westslope cutthroat trout (*Oncorhynchus clarki lewisi*), but none is now found in more than one new ecoregion. Consequently, the relatively limited number of introductions to multiple ecoregions has likely promoted differentiation of B.C. freshwater fish faunas rather than homogenization.

By contrast, the situation in Canada as a whole indicated a much more general trend towards homogenization, with 50 of 78 (64%) pairwise comparisons showing increasing similarity among regions. In fact, if comparisons involving the three territories are removed, 33 of 45 pairwise comparisons (73%) result in increased Jaccard's coefficients. The homogenization of the Canadian fauna is driven largely by a few species that have been introduced widely. There are, for instance, 12 species that have been introduced to three or more regions and four species (goldfish, rainbow trout (*Oncorhynchus mykiss),* brown trout (*Salmo trutta*), and smallmouth bass (*Micropterus dolomieu*)) that have been introduced to six or more of the 13 provinces or territories. Marchetti et al. (2001) also showed that the degree of homogenization in California freshwater fishes depended on spatial scale. At the smallest scale examined, that of individual watersheds, homogenization was minimal and there was evidence of faunal differentiation between some watersheds. By contrast, at the largest spatial scale examined, that of zoogeographic provinces (analogous to the B.C. ecoregions), there was clear evidence of faunal homogenization and loss of beta diversity. Similar to the proposed explanations for differing pat-

Fig. 5. Relationships among 13 provinces and territories of Canada. Relationships are depicted as a neighbor-joining tree obtained by clustering pairwise values of 1.0 – Jaccard's faunal similarity coefficients for (*a*) native faunas and (*b*) total (native + nonnative – extinctions or extirpations). Wagner parsimony analyses resolved the same topology as neighbor-joining clustering, and the numbers at branch points represent bootstrap support levels from 100 replicate parsimony analyses of the species presence–absence matrix. The scale bar represents 0.1 unit of 1.0 – Jaccard's faunal similarity coefficient. YT, Yukon Territory; NWT, Northwest Territories; NUT, Nunavut Territory; BC, British Columbia; ALTA, Alberta; SASK, Saskatchewan; MAN, Manitoba; ONT, Ontario; QUE, Quebec; NB, New Brunswick; NS, Nova Scotia; PEI, Prince Edward Island; NFLD/LAB, Newfoundland and Labrador.

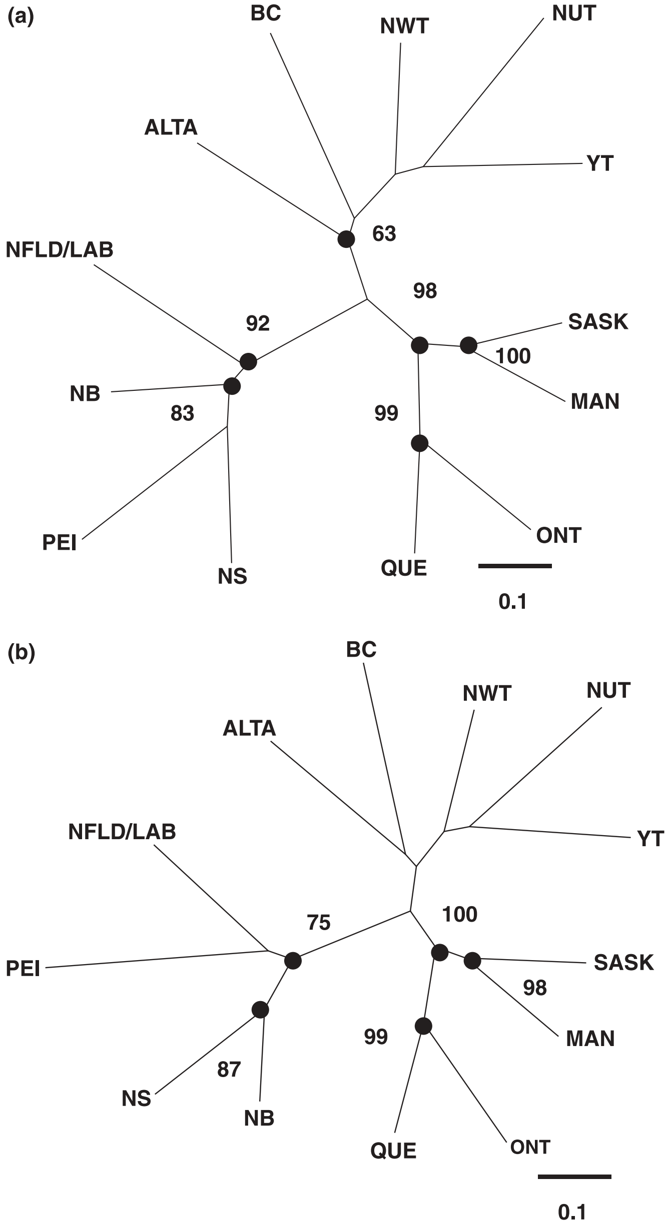


Fig. 6. Frequency histogram of Jaccard's pairwise faunal similarity coefficients among 13 provinces and territories of Canada for (*a*) native fish faunas and (*b*) total (native + nonnative – extinctions or extirpations) fish faunas.

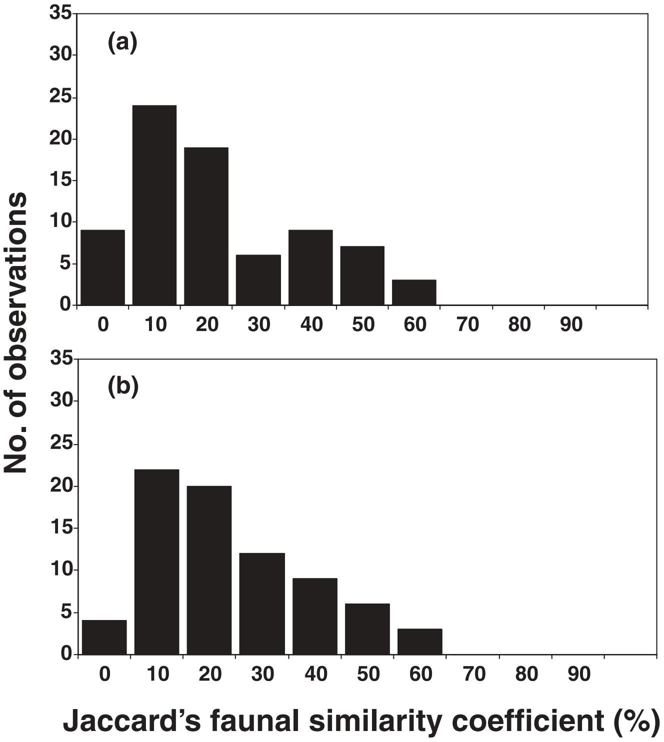
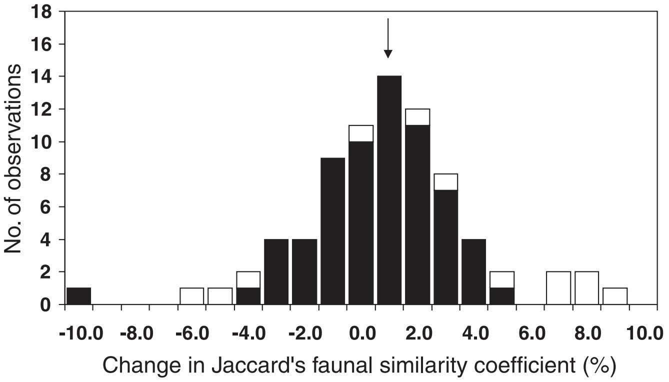


Fig. 7. Frequency histogram of the percentage change in pairwise Jaccard's faunal similarity coefficients between native and total (native + nonnative – extinctions or extirpations) freshwater fish faunas for 13 provinces and territories of Canada. Open bars are for comparisons involving British Columbia. The arrow represents the mean difference between all 78 pairwise comparisons of native and total Jaccard's coefficients.



terns within B.C. and across Canada, Marchetti et al. (2001) suggested that faunal differentiation at small spatial scales was due to the haphazard nature of fish introductions among individual watersheds, whereas homogenization at larger scales was due to greater commonality in the taxonomic composition of nonnative species. These similar observations in independent studies highlight the importance of considering spatial scale in assessments of faunal homogenization and differentiation in conservation.

Losses of native fauna can also clearly play a role in homogenization, but they cannot explain the homogenization resolved here. For instance, introductions have been much more common than extinctions or extirpation in terms of both the number of events and their geographic scope. There have been only eight recorded extinctions or extirpations in Canada with most (5) occurring in Ontario and the rest (3) confined to a single other province, Prince Edward Island. Nevertheless, within specific comparisons, extinctions and extirpations have been important factors in homogenization. For instance, for a variety of reasons, including predation by introduced sea lamprey (*Petromyzon marinus*), the native salmonid fauna of the Great Lakes region of Ontario was decimated, including the extinction of several species of endemic whitefishes, *Coregonus* (see Smith 1980). The extinction or extirpation of much of the Great Lakes salmonid fauna precipitated a program of introductions of salmonid fishes from Canada's west coast (e.g., coho (*Oncorhynchus kisutch*) and chinook salmon and rainbow trout) to rehabilitate the sport fishery (Bureau of Sport Fisheries and Wildlife 1973). This combination of extinctions of fishes endemic to Ontario, introductions of native B.C. fishes to Ontario, as well as introductions to B.C. of fishes found in Ontario (e.g., brook trout, various centrarchids, and two catfishes) has clearly made the faunas of these two areas more similar. Rahel (2000) also found that introductions, rather than extinctions or extirpations, caused homogenization of the U.S. freshwater fish fauna.

Comparative analysis of homogenization

The pattern of homogenization across Canada is similar to the pattern reported by Rahel (2000) for U.S. continental freshwaters, but the mean increase in Jaccard's similarity in Canada was considerably lower (1.2% versus 7.2%). The evidence for lower homogenization in Canadian freshwater fishes occurs even though Canada has a much lower diversity of native species than the U.S. (with an estimated 800 native species versus 197 in Canada) and a similar rate of introductions should have a greater effect in Canada. In fact, there have been proportionally more introduction events in the U.S. than in Canada. Rahel (2000) reported 901 introduction events in the U.S. across 48 states or an average of 18.8 events per state, whereas in Canada there have been only 102 across the 13 provinces and territories or an average of 7.8 introduction events. In addition, extinctions and extirpations have been more common in the U.S.; Rahel (2000) reported 196 extinction or extirpation events (4.1 per state), whereas there have been only eight in Canada (0.62 per province or territory). Both the greater rate of introductions and extinctions or extirpations in the U.S. should promote greater homogenization of freshwater fish faunas. A possible instigating factor in the greater rate of homogenization in U.S. freshwaters is the fact that management of freshwater fisheries are subdivided into 48 distinct jurisdictional units (i.e., state fish and game departments) vs. only 13 in Canada (provincial and territorial governments). Consequently, there are many more potential pairwise interactions (1128 vs. 78, respectively) and potentially different management attitudes among states that could lead to introduction or extinction or extirpation events.

The evidence for faunal differentiation in B.C. and homogenization across Canada is generated by sets of commonly introduced species that are remarkably similar to each other and to fish species that dominate introductions in the U.S. In fact, the top five species introduced in Canada (common carp, brown trout, goldfish, rainbow tout, and smallmouth bass) are the same as in the U.S. (Rahel 2000). Further, with the exception of the striped bass (*Morone saxatilis*), the top 17 species introduced in the U.S. have all been introduced to at least one region in Canada as well (Rahel 2000). Most of these commonly introduced species across Canada and the U.S. have also been introduced into B.C., but only a few (common carp, goldfish, brown bullhead, American shad, and brook trout) have been introduced to more than two ecoregions. This reflects the more haphazard pattern of introductions in B.C. and contributes to the differentiation of faunas within B.C.

These commonly introduced freshwater fishes also reflect the important and common motivating forces of introductions in Canada and the U.S. — for the purposes of recreational fishing (e.g., brown and rainbow trout, smallmouth bass) and aquaculture (rainbow trout, common carp) and by accidental releases from aquaria (e.g., goldfish). These pressures have, however, resulted in greater average changes to the fish faunas of the U.S. than Canada. In the former, 17 states have over 25% of their contemporary fish faunas consisting of introduced species (and three are over 50%), whereas Ontario, B.C., Alberta, and Nova Scotia have the highest proportions of nonnative faunas (all from 21–22%) and the average across Canada is "only" 12.5 (standard deviation (SD) = 6.5%).

Consequences of faunal change

Several issues should be considered in light of the current analysis of differentiation and homogenization in Canadian freshwater fish faunas. First, the primary data consist of presence–absence information only and, consequently, do not take relative abundance into account in calculating faunal similarity. Although such measures are available for smaller scale analyses of biodiversity (e.g., within individual lakes or river reaches), the number of individuals of each fish species across broad geographic regions cannot generally be determined. An alternative may be to record presence or absence of populations within individual water bodies or major drainages to produce more detailed estimates of faunal diversity within provinces and territories. The collection of data by ecoregion for B.C. (McPhail and Carveth 1994) is a step in this direction and more detailed "extent of occurrence" measures are needed for more biologically realistic assessments of faunal homogenization. A further refinement may be to extend the approach adopted by McPhail and Carveth (1994) to include faunal surveys for aquatic ecoregions that transcend political boundaries and better reflect the natural faunal boundaries for all of Canada. There is a current attempt to define a workable number of aquatic ecoregions for all of Canada (N. Mandrak, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, P.O. Box 5050, 867 Lakeshore Road, Burlington, ON L7R 4A6, personal communication), and this may form the basis for assessments of homogenization and differentiation for natural aquatic groups.

Second, the current analysis neglects faunal homogenization and differentiation within ecoregions. Again, this is largely an issue of current limitations on data collection and analysis. For instance, rainbow trout have been introduced among multiple watersheds within individual ecoregions in

B.C., and this results in some level of homogenization (or differentiation) on very small scales that can have the same consequences as at the level of aquatic ecoregions within the province as a whole (e.g., see Scott and Helfman 2001). Third, analyses of homogenization and differentiation reflect the situation at a particular time only, and updates should be regularly performed. For instance, increases in nonnative species via introductions, transplants, and invasions may result in short-term increases in biodiversity in the narrow sense (i.e., there are more species in a particular place). The eventual consequences of introductions, however, may result in lowered native biodiversity if the extinction process runs its course and nonnative species replace native species (Scott and Helfman 2001). This process may result from a "relaxation" of species diversity, raised artificially by human activities, towards levels before human-induced changes. Because many introduced species are either chosen for their broad environmental tolerances or are the "survivors" from accidental introductions, such faunal relaxation could result in a subset of widely distributed species increasing homogenization, and reducing biodiversity, over the longer term (Rahel 2002). Such faunal relaxation may become common in the future because intentional introductions are no longer permitted or are discouraged in most Canadian jurisdictions. In addition, virtually all of Canada's freshwater fish fauna is postglacial in origin. Consequently, species diversity in postglacial environments may not be at equilibrium levels and, over the short term, may be able to "absorb" introduced species resulting in short-term increases in biodiversity (Brown and Lomolino 1998; Rahel 2002). Two issues, however, argue that the apparent benefits of such increased biodiversity are illusionary. First, it is difficult to predict the eventual outcome of introductions on native fauna, and if introductions result in the extinction of endemic fauna, then no matter how much total biodiversity has increased, the loss of endemics results in permanent losses of biodiversity worldwide. Second, both homogenization and differentiation from the combined effects of introductions and extinctions or extirpations may result in altered faunal and zoogeographic "relationships" among watersheds and larger geographic units (e.g., the relative similarities among areas). The major grouping of provinces and territories into northwestern, central, and eastern faunal regions likely reflects the postglacial recolonization of constituent provinces and territories from distinct sets of Wisconsinan glacial refugia. The northwestern grouping was predominantly recolonized from the Bering, Pacific, and Mississippi refugia, the central grouping from the Bering, Mississippi, and Atlantic refugia, and the eastern grouping was predominantly colonized from the Mississippi, Atlantic, and Acadian refugia (McPhail and Lindsey 1970; Schmidt 1986; Scott and Crossman 1998). Such relationships are part of the faunal legacy of Canada and are of inherent and perhaps under appreciated conservation value. My analyses, both for B.C. and for Canada as a whole, revealed slight but detectable changes in ecoregion interrelationships of native faunas after accounting for nonnative species and extirpations or extinctions. The changes in relationships reflect relatively minor rearrangements of component groups nested within larger regional units (e.g., relative position of the Columbia ecoregion within the Mackenzie–Yukon–Columbia grouping in B.C., the position of P.E.I. within the eastern grouping of provinces) and degrees of differentiation among faunal groups. Both the kinds and magnitudes of these topological changes are consistent with the relatively small but significant changes in Jaccard's indices between native and total faunas. Although the detected changes were small, the NJ analyses provide a necessary baseline and a convenient method to visualize changes in regional relationships in the future. Finally, the differentiation and homogenization of diversity can also occur in terms of within-species genetic diversity. This topic has received considerable attention in terms of its relevance to within-species biodiversity conservation in fishes (e.g., Hindar et al. 1991; Ryman et al. 1995), but large-scale geographic studies of anthropogenic-based genetic differentiation or homogenization are lacking for the relevant Canadian fishes (e.g., salmonid fishes subject to hatchery or aquacultural production; cf. Reisenbichler et al. 1989).

In conclusion, Rahel (2002) outlined several steps to help reduce the rate of biotic homogenization: reducing or eliminating intentional and accidental introductions, reducing the rate of native species extinctions or extirpations, reducing habitat changes that result in abiotic homogenization which indirectly promotes biotic homogenization, and rehabilitating native faunas through exotic species removal. The results of studies such as the current analyses can hopefully also contribute by establishing a baseline to help track future changes in faunal composition and ecoregion relationships in B.C. and in Canada as a whole.

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