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BIODIVERSITY RESEARCH

Changes in taxonomy and species distributions and their influence on estimates of faunal homogenization and differentiation in freshwater fishes

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ABSTRACT

Aim To assess how changing taxonomy and distribution data affect estimates of faunal homogenization and differentiation as agents of global change in freshwater fishes.

Location Provinces and territories of Canada.

Methods Species presence–absence data were collated in 2000 and 2005 from regional and national lists, and faunal homogenization and differentiation were calculated using Jaccard's faunal similarity index. Differences between time periods and areas were summarized using principal coordinate analysis. Differences in faunal assemblages between native and total faunas were assessed via Whittaker's (1960) beta diversity (β_w) index and tests of differences in multivariate dispersion of fish species compositions.

Results Among aquatic ecoregions in one province (British Columbia) there were four taxonomic changes and 18 distributional changes between the 2000 and 2005 databases. Pairwise Jaccard's faunal similarity index between the eight aquatic ecoregions declined by an average of 4.8% from 35.9% in native faunas to 31.1% in total faunas (introductions – extinctions/extirpations) indicating overall faunal differentiation. Average pairwise similarity declined by 0.9% between 2000 and 2005. Across thirteen provinces and territories of Canada, there were five taxonomic changes and 61 distributional changes between the 2000 and 2005 databases. Generally, faunal homogenization increased; pairwise Jaccard's increased by an average of 1.8% from 27.1% in native faunas to 28.9% in total faunas or an average of 0.6% per comparison.

Main conclusions Despite changing taxonomy and fish distribution information, comparative analysis of 2000 and 2005 databases consistently show overall faunal differentiation at the smallest (provincial) spatial scale and homogenization at the largest scale (across Canada) and that these trends continued between time periods. Homogenization and differentiation followed expectations from conceptual models based on the relative prevalence of species invasions and extinctions within communities. General conclusions of the onset and extent of homogenization and differentiation were relatively insensitive to our changing understanding of taxonomy and distribution.

Keywords

Biodiversity, Canada, freshwater fishes, homogenization, taxonomy, zoogeography.

INTRODUCTION

Conservation of freshwater ecosystems for aesthetic, ethical, and utilitarian reasons is a top global conservation priority owing to the richness of freshwater biodiversity and the extent of threats against it (Dudgeon *et al.*, 2006). For instance, on a per unit area basis, freshwaters contain the most diversity of fishes; some 10,000 species of freshwater fishes (*c.* 40% of

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global fish diversity) occur within only 0.8% of the earth's surface area (Dudgeon *et al.*, 2006). Freshwater fishes also represent some of the most threatened faunas in the world owing to anthropogenic factors such as overexploitation, habitat degradation, so-called 'chains of extinction', and the introduction of exotic species (Rhymer & Simberloff, 1996; Ricciardi & Rasmussen, 1999; Sala *et al.*, 2000; Dudgeon *et al.*, 2006; Dextrase & Mandrak, 2006). Notwithstanding these concerns, freshwater ecosystems, in general, have received much less focus in terms of conservation prioritization exercises (e.g., Myers *et al.*, 2000; Brooks *et al.*, 2006). One of the most important threats to freshwater ecosystems is biotic composition changes owing to either biotic homogenization (when pairwise similarity between communities increases with time) or biotic differentiation (when pairwise similarity between communities decreases) as a result of human-induced species introductions/invasions and extinctions/extirpations (Sala *et al.*, 2000). The documentation of biotic homogenization has increased over the last 10 years (e.g., Olden, 2006) and its study has matured to include attempts to understand the mechanistic bases for faunal change as well as the evolutionary and ecological consequences of homogenization/differentiation (Olden & Poff, 2003; Olden *et al.*, 2004).

By definition, biotic homogenization/differentiation involves comparison of biotic composition across time periods. Typically, this involves 'historical' and 'contemporary' time frames (e.g. Rahel, 2000; Taylor, 2004; Olden *et al.*, 2008). The refinement of patterns and a better understanding of the processes contributing to biotic composition changes would, however, be facilitated by examination of homogenization and differentiation over multiple time periods. Johnston & Maceina (2008) indicated the utility of such long-term monitoring as a window on ecosystem health and also as a way of detecting more subtle changes to biotic composition, and its consequences, as they occur. The relatively recent focus on the quantification of homogenization, however, means that there have been comparatively few opportunities to monitor its dynamics over time (see Clavero & García-Berthou, 2006 for an exception) despite the importance of quantifying temporal changes (Olden, 2006).

A study of biotic homogenization and differentiation for freshwater fishes at two different spatial scales (among aquatic ecoregions within one province and among all provinces) was conducted for Canadian freshwater fishes by Taylor (2004). This study utilized a national database of presence–absence data for *c.* 200 species of freshwater fishes and compared fish distributions from 'historical' (basically pre-1900) and 'contemporary' (2000) periods. The study resolved a general pattern of faunal differentiation within British Columbia (BC), but faunal homogenization across all of Canada. As useful as such databases are, they are subject to revisions owing to new information on the distribution and taxonomy of each species – the fundamental input data upon which studies of faunal change are based. In the case of the Canadian data, a revised distributional database was released in 2005 (Wild Species 2005) and taxonomic research on several Canadian species has been completed since Taylor's (2004) analysis.

In this study, I review freshwater fish species distribution data for the 2000 and 2005 datasets to assess how earlier estimates of homogenization and differentiation might change and whether any trends in homogenization or differentiation are apparent between these two time periods owing to changes in our informational database on taxonomy and distribution. This analysis provides (1) an assessment of the effects of new taxonomic and biogeographical information on 'snapshots' of biotic change taken between any two time periods, and (2) contributes to the long-term monitoring of fish faunal changes in Canada – an important component of biodiversity monitoring and management. Although a 5-year period is short in terms of potential faunal changes, it is highly relevant to conservation of species given that recovery plans for species at risk are designed and often implemented within this time period. In addition, given increased survey efforts in the light of the initiation of recovery plans under national biodiversity programmes like Canada's *Species-at-Risk Act* (SARA), and the inherent 'fluidity' of taxonomy, it is important to gauge the influence of changes in these two kinds of data that are central to one aspect of estimating faunal change.

METHODS

Geographical context

Canada is the second largest country in the world and contains over 890,000 km^2 of freshwater habitat. British Columbia (BC) is Canada's third largest province with freshwater habitats that form, in whole or in part, some of the largest drainage basins in North America (e.g., the Fraser, Mackenzie, Columbia, and Yukon river systems). These watersheds drain an immense and nearly continuous mountainous area from the Arctic Ocean to the mid-temperate Pacific Ocean, which promotes a high level of faunal distinctiveness among regions (McPhail, 2007). In addition, the freshwater fish fauna of BC is almost exclusively post-glacial in origin; freshwater faunas recolonized BC from glacial refugia located peripheral to the Wisconsinan ice sheets after they retreated beginning about 18,000 years ago (McPhail, 2007). The recent origin of the BC freshwater fauna means that many ecosystems may not yet be at equilibrium in terms of species diversity and could be particularly sensitive to the effects of homogenization from increases in non-native species and extinctions.

Data sources and analyses

The data used for my analyses consisted of presence–absence information for the 86 recognized freshwater and diadromous fish species in BC and the 213 species in Canada (i.e., native and non-native species (see Appendices S1 and S2). I only used data for recognized taxa (see Taylor, 2004) or for recognized species that are currently undergoing taxonomic description ($N = 1$).

Presence–absence data were assembled for each of the eight major aquatic ecoregions in BC (McPhail & Carveth, 1994) which represent major drainage basins defined by current or historical connectedness, isolation by saltwater barriers and colonization from similar glacial refugia: Vancouver Island (VI) and adjacent Strait of Georgia islands, Fraser River, Columbia River, Mackenzie River, Yukon River, North Coast (Stikine, Alsek and Taku rivers), Queen Charlotte Islands (QCI) and the Central Coast (Skeena River, Nass River). Some of these regions are part of larger drainage systems that extend beyond the borders of BC (i.e., the Yukon, Columbia and Mackenzie rivers ecosystems), but the current analysis refers only to those portions within BC. Presence–absence data were obtained from McPhail & Carveth (1994) and McPhail (2007) and, in some cases, records from the University of British Columbia Fish Museum (see http://www.zoology.ubc.ca/~etaylor/nfrg/fishmuseum.html). Presence–absence data for the nine other provinces and three territories were based on information from the Wild Species 2000 and 2005 databases available at http://www.wildspecies.ca/ [Canadian Endangered Species Conservation Council (CESCC), 2001] as described in Taylor (2004). Other major sources of information included national and regional summaries such as Nelson & Paetz (1992), Scott & Crossman (1998) and Stewart & Watkinson (2004).

I considered a ‘native’ species to be one that occurs, or occurred historically, in a defined area as a result of natural processes exclusive of any known influence from humans. By contrast, I used the term ‘non-native’ species to refer to a species 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 simplicity and because my primary interest was in assessing changes to native fish assemblages, I did not employ the terms ‘exotic’, ‘invasive’, or ‘transplanted’ to distinguish amongst the variety of processes that may have led to non-native species (Horak, 1995). A non-native species was included in the analyses only if there was at least some evidence that it had established a breeding population(s) and/or it has been repeatedly encountered in nature in the ecoregion, province or territory (e.g., from persistent introductions). ‘Taxonomic changes’ refer to new species descriptions or changes in nomenclature for existing taxa. ‘Distributional’ changes refer to the removal (or addition) of a taxon from (or to) an aquatic ecoregion or province/territory. For example, the same taxon being added to two areas is two ‘distributional changes’ as is the removal of two different taxa from a single area.

The presence–absence (1,0) data were summarized by calculating pairwise Jaccard’s coefficient of percentage faunal similarity as well as an index of faunal turnover (beta diversity) between areas within BC and between all provinces and territories. Calculation of these statistics was accomplished, in part, using EstimateS (http://viceroy.eeb.uconn.edu/estimates). Pairwise similarity and turnover indices were calculated separately for ‘native’ faunas, those representing faunas before known introductions or extinctions/extirpations associated with European settlement (cf. Rahel, 2000; Marchetti *et al.*, 2001; Taylor, 2004), and for ‘total’ faunas that include native and non-native species minus any extinctions or extirpations. Faunal similarity among areas was examined by using principal coordinate analysis (PCO) and Jaccard’s similarity coefficient using PAST version 1.9 (Hammer *et al.*, 2001). Minimal connections among ecoregions were summarized by superimposing a minimum spanning tree on the PCO ordination.

To assess differences in faunal assemblages between native and total faunas, I conducted a one sample *t*-test of Whittaker’s (1960) beta diversity (β_w) index as modified by Koleff *et al.* (2003) which measures the faunal change from one sample (native) to another (total) calculated using PAST. The value of β_w varies from 0 (two identical faunas; all species shared between both regions) to 1 (no species in common). I tested the observed mean difference between native and total faunas for the eight BC ecoregions and 13 provinces/territories against the null hypothesis value of zero. I also employed a test of differences in multivariate dispersion of fish species compositions between historical and contemporary periods using species presence–absence data as the variable and BC aquatic ecoregions and provinces/territories as sampling units (see Anderson, 2006; Olden *et al.*, 2008). Under the null hypothesis of no faunal homogenization or differentiation the average distance of each ecoregion or province/territory in multivariate space, defined by the PCO analyses, relative to the group (historical or contemporary) centroid should not differ. Statistical significance is determined by permutation analysis ($N = 1000$) of the relevant least-squares residuals employing the program PERMDISP (Anderson, 2006).

RESULTS

British Columbia freshwater fishes

The native freshwater fish fauna of BC consists of 68 taxonomically described species and varies from a low of 15 species in the QCI to a high of 41 species in the Fraser River ecoregion (see Appendix S1 in Supporting Information). Since 2000, there has been one extinction/extirpation in addition to that of chinook salmon, *Oncorhynchus tshawytscha*, from the upper Columbia River; the Pacific lamprey, *Entosphenous tridentata*, has been extirpated from the Columbia River ecoregion in BC (McPhail, 2007). There have been several taxonomic and distributional changes to the BC freshwater fish fauna since the 2000 survey. Taxonomically, two new sculpin taxa have been recognized, one sculpin taxon has been removed, there has been one name change, and there have been 20 distributional changes (Table 1, see Appendix S1). British Columbia now contains a total of 22 species that are non-native to at least one ecoregion; 18 species originated from outside the province and four species originated from one or more other BC ecoregions. Since 2000, two non-native species are now considered not to exist in BC (golden trout, *Oncorhynchus aguabonita*) or outside of their native BC

Table 1 List of species of freshwater fishes where changes in taxonomy or geographic distribution have occurred between 2000 and 2005 for the eight aquatic ecoregions of British Columbia. Underlined taxa are not native to that ecoregion, boldfaced taxa are not native to BC, those underlined and boldfaced are not native to Canada.

Taxon	Taxonomic change	Distributional change
Lampetra ayresii		Added to Queen Charlotte Islands
Alosa sapidissima		Removed from North and Central Coasts
Cyprinus carpio		Removed from Vancouver Island (VI)
Ameiurus nebulosus		Removed from Columbia River
Ameiurus natalis		Added to BC (Fraser River)
Thaleichthys pacificus		Added to VI
Oncorhynchus clarkii clarkii		Added to Columbia River
Oncorhynchus aguabonita		Removed from BC (Columbia River)
Salmo salar		Added to Fraser River and Central Coast
Prosopium coulterii		Removed from North Coast
Thymallus arcticus		Removed from Columbia River
Cottus bairdii		Removed from BC (Columbia River)
Cottus hubbsi	Replaces *C. bairdii* in BC	Added to BC (Columbia River)
Cottus sp.*	New taxon	Added to BC (Columbia River)
Lepomis macrochirus		Added to Columbia River
Micropterus dolomieu		Added to Columbia River
Perca flavescens†		Added to VI and the Fraser River
Sander vitreus	Name change from *Stizostedion vitreum*	

*Taxonomic description in progress (Neely, pers. comm., McPhail, 2007). Known by the common name 'Rocky Mountain sculpin'.

†Some uncertainty exists as to whether or not this species is native to the Mackenzie River ecoregion (McPhail, 2007).

ecoregion (e.g., Arctic grayling, *Thymallus arcticus*, Appendix S1). In addition, three non-native species, while still present in BC, were recorded as being found in fewer ecoregions than in 2000, two others were recorded in at least one more ecoregion, and one non-native species was new to BC (see Appendix S1). The Columbia River drainage has the most non-native fishes (16) and the QCI, North Coast and the Yukon River are the only BC aquatic ecoregions without any known non-native freshwater fish species (see Appendix S1).

Jaccard's similarity indices of native faunas ranged from a low of 6.5% between the Yukon drainage and VI to a high of 88.2% between VI and the QCI (see Table S1). Principal coordinates analysis of the presence–absence matrix summarized 72% of the variation along two axes, and ecoregion affinities were similar in 2000 and 2005 (Fig. 1a). The first axis tended to separate the ecoregions into three major groups: VI – QCI, North/Central coasts and Fraser River, and the Columbia, Mackenzie and Yukon rivers (Fig. 1a). The second coordinate axis tended to separate northern ecoregions (Yukon and North Coast) from central (QCI, VI, Central Coast and Mackenzie River) and southern areas (Fraser and Columbia rivers). Estimates of faunal turnover ranged from a low of 6.3% between VI and the QCI to a high of 87.0–87.8% between these two island ecoregions and the Yukon River ecoregion. Notwithstanding the taxonomic and distributional changes summarized above (Table 1), faunal turnover was not significant between the 2000 and 2005 native fish compositions (mean $\beta_w = 0.022$, $P = 0.09$) and average pairwise native faunal similarities among ecoregions differed between 2000 (35.0%) and 2005 (35.9%) by an average of only 0.92% (Fig. 1a).

After incorporating non-native species and extinctions/extirpations based on the 2005 database, pairwise Jaccard's coefficient ranged from a low of 5.6% between VI and the Yukon ecoregions to a high of 72.2% between the North and Central coasts ecoregions (see Table S1). Ordination using principal coordinates analysis resulted in ecoregion affinities that were similar to those resolved by comparing native faunas, but with increased differentiation among some ecoregions in 2005 (Fig. 1b). For instance, the average pairwise change in Jaccard's coefficient was a decrease of 4.8% (native: 35.9% to total: 31.1%). The greatest percentage decline in similarity occurred between VI (eight non-native species) and the QCI (no non-native species) where Jaccard's index fell from 88.2% to 52.0% similarity (−41% of native value). As a measure of faunal change between native and total faunas, the average value of Whittaker's beta diversity value across all eight ecoregions was significantly greater than zero (mean $\beta_w = 0.07$, *t*-test, $P < 0.05$). Faunal differentiation was also reflected in an increase in multivariate dispersion between native and total faunas, although the change was not statistically significant (mean dispersion distances of 0.63 and 0.66, respectively, $P = 0.67$).

Some ecoregions exhibited faunal homogenization; the large number of non-native species on VI, coupled with similar species in the Columbia basin (16 non-natives) resulted in the largest percentage increase in similarity between any two regions, i.e., from 15.0% to 19.6% (+31% of native fauna value). The other pairwise comparison to show substantial faunal homogenization was that between the Columbia River and the Mackenzie River drainage where Jaccard's coefficient

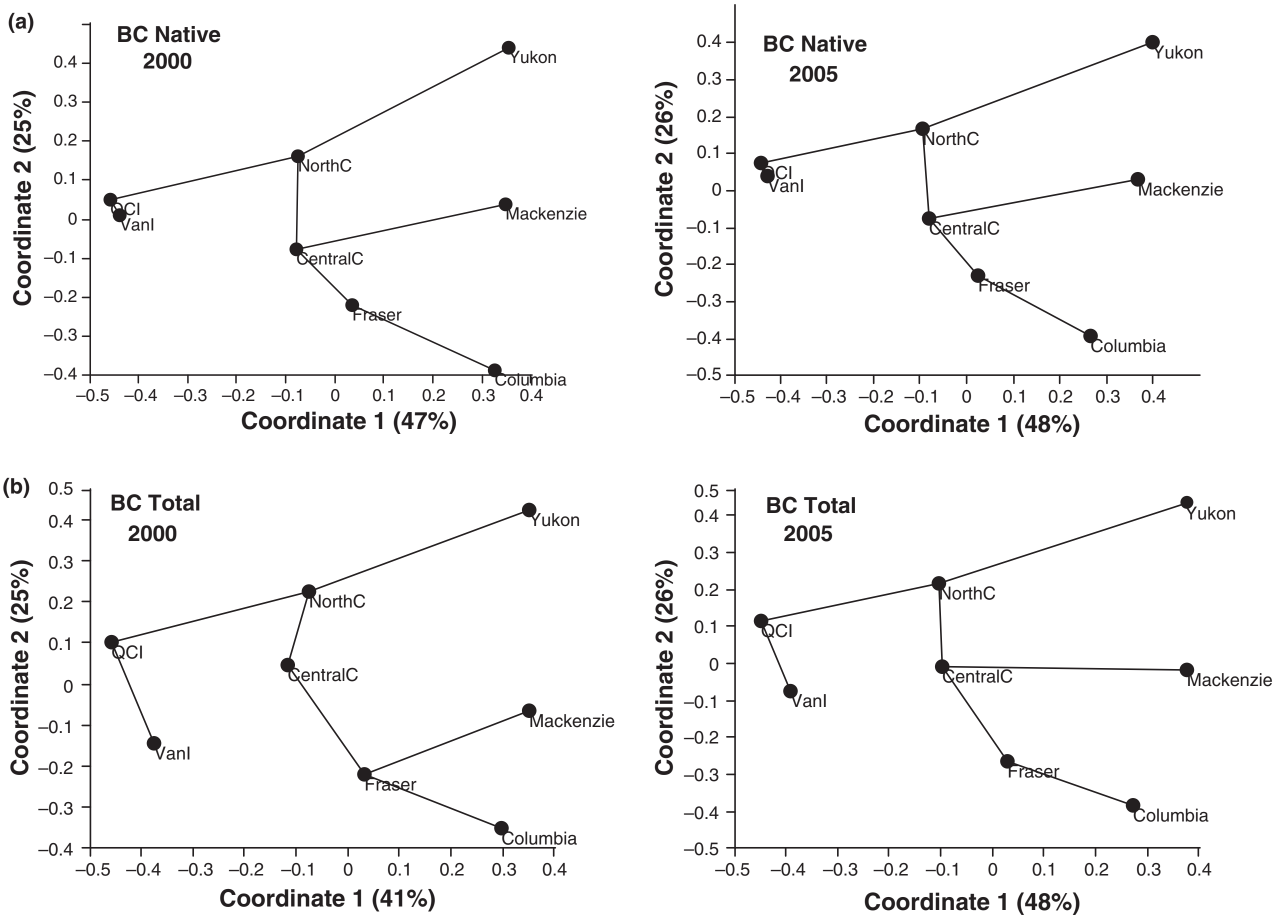

Figure 1 Relationships among eight aquatic ecoregions of British Columbia based on surveys conducted in 2000 and 2005 for (a) native and (b) total faunas. Relationships are depicted following principal coordinates ordination using Jaccard's similarity coefficient. Each ecoregion is joined using a minimum spanning tree. VanI, Vancouver Island; Fraser, Fraser River; Columbia, Columbia River; Mackenzie River, Yukon, Yukon River; NorthC, North Coast; QCI, Queen Charlotte Islands; CentralC, Central Coast.

showed an 18.1% increase relative to the native fauna value (28.3–33.4%).

The overall differentiation of aquatic ecoregion fish faunas in BC was also reflected in faunal turnover which increased from an average of 50.4% to 54.9% after incorporating non-native species and extinctions/extirpations. The biggest change in turnover occurred between VI and the North Coast where turnover increased from 6.3% to 31.5%, owing to the many introductions of fishes to VI. The influence of non-native species and extirpations was detectable in the interrelationships among ecoregions. For instance, the distance in PCO space between VI and the QCI increased substantially, and the Fraser ecoregion became more distinctly separate from the Central Coast ecoregion, and the minimum spanning tree had a direct connection between the Fraser and Mackenzie ecoregions rather than between the Central Coast and Mackenzie that characterized the native species composition in 2000, but not in 2005 (Fig. 1b). In fact, the trend towards faunal differentiation increased between 2000 and 2005; after incorporating taxonomic and distribution changes since 2000 there was a small increase in the average pairwise similarity indices of native faunas between the 2000 and 2005 surveys (2000 = 35.0% vs. 2005 = 35.9%), but a small decrease between average total faunal pairwise comparisons (2000 = 31.9%, 2005 = 31.1%). This resulted in a small increase in differentiation between native and total faunas when comparing the 2005 database (4.8%) to the 2000 database (3.1%); an average increase in differentiation of 1.7% per pairwise comparison between ecoregions (Fig. 2a).

Centrarchid fishes (sunfishes and basses) continued to be the most prevalent introduced taxa accounting for 11 region introductions (up from nine in 2000; five different species are non-native 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 BC's eight aquatic ecoregions.

Comparisons among Canada wide fish faunas

There have been some changes to the taxonomy and distribution of freshwater fishes in Canada since the 2000 Wild Species survey (Table 2); two new species have been recognized and given formal taxonomic names, one taxon has had its

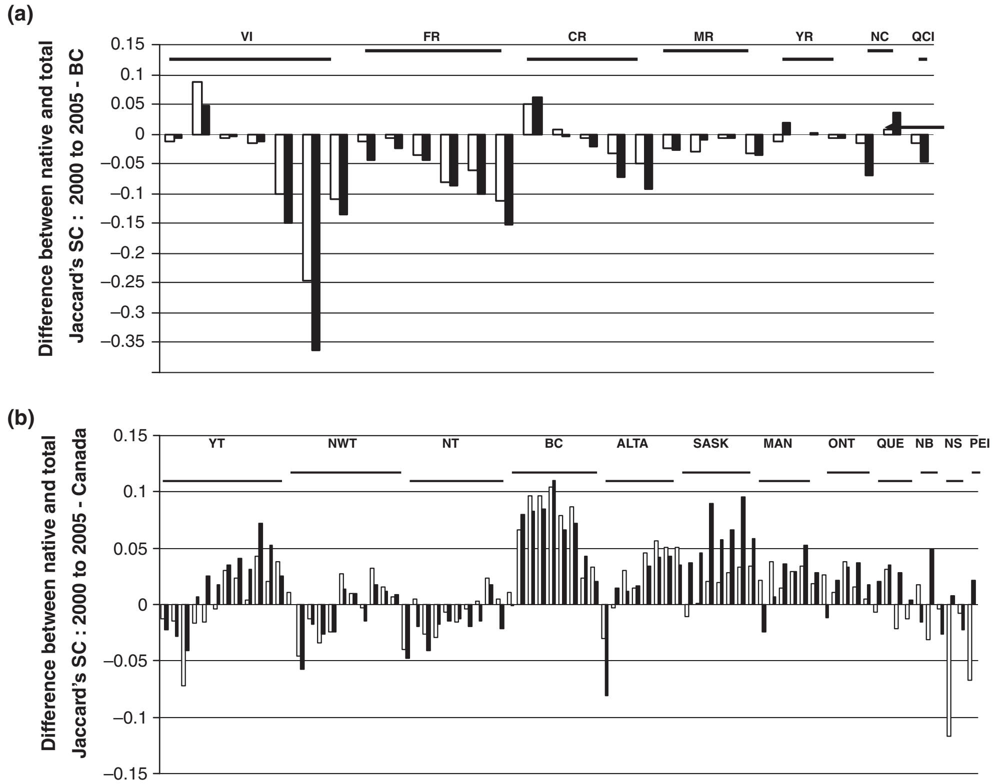

Figure 2 Frequency histogram of the difference between native and total (native + non-native − extinctions/extirpations) fish faunas' Jaccard's pairwise faunal similarity coefficients (SC) for 2000 (white bars) and 2005 (black bars) among (a) eight British Columbia aquatic ecoregions and (b) among thirteen Canadian provinces and territories. The thin horizontal bars below each area's acronym show the range of pairwise comparisons between the ecoregion or province/territory shown above the line and all subsequent ones. Values greater than zero represent homogenization; values less than zero represent differentiation. In (a) VI, Vancouver Island; FR, Fraser River; CR, Columbia River; MR, Mackenzie River; YR, Yukon River; NC, North Coast; QCI, Queen Charlotte Islands (Central Coast is the last comparison in each series and is therefore not shown). In (b) YT, Yukon Territory; NWT, Northwest Territories; NT, Nunavut Territory; BC, British Columbia; ALTA, Alberta; SASK, Saskatchewan; MAN, Manitoba; ONT, Ontario; QUE, Québec; NB, New Brunswick; NS, Nova Scotia; PEI, Prince Edward Island (Newfoundland and Labrador is the last comparison in each series and is therefore not shown).

name changed, one taxon has been removed from the list of native fishes, and a new, undescribed species of sculpin has been recognized (Table 2). In addition, there have been 61 distributional changes of taxa since the 2000 survey, including two new presumed extirpations (Table 2). These changes to the database resulted in a significant shift in native fish species composition between the 2000 and 2005 surveys (mean $\beta_w = 0.043$, $P < 0.001$). There are 200 recognized native species in Canada with Ontario having the most native species (132) and Prince Edward Island (PEI) the fewest (20, see Appendix S2).

There are 47 species that are non-native to Canadian freshwaters in at least one province or territory (including 12 from countries other than Canada). Two more species, in addition to the four listed by Taylor (2004), have become extirpated in at least one jurisdiction (Table 2). Eight taxa listed as non-native to Canada in the 2000 database have been removed from the Wild Species Canada 2005 database as they are now considered not to have established self-sustaining populations (Table 2). Several non-native 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 103 records of non-native species and seven extinctions and extirpations among the 13 provinces and territories (see Appendix S2). Accounting for all non-native species and extinction/extirpation events, Ontario has the largest number of species (145) and Nunavut the fewest (23). Ontario and Saskatchewan have recorded the greatest number of non-native species (17) and Ontario the most extinctions/extirpations (6) while only Québec has also recorded an extirpation. Two of the territories (Northwest and Nunavut territories) have no recorded non-native species (see Appendix S2).

Pairwise Jaccard's similarity matrices of native faunas ranged from a low of 4.0% to 4.8% between Yukon and Northwest Territories, respectively, and PEI to a high of 73.3% between New Brunswick and Nova Scotia and averaged 27.1% (see Table S2). Ordination of these localities resolved the same three groupings as the 2000 database: a 'north-western region' consisting of the three territories, BC, and Alberta; a 'central region' consisting of Saskatchewan through Québec; and an 'eastern region' consisting of New Brunswick, Nova Scotia, PEI

Table 2 List of species of freshwater fishes where changes in taxonomy or geographic distribution have occurred between 2000 and 2005 for the 13 provinces and territories of Canada. Underlined taxa are not native to that province or territory and those not native to Canada are in boldface.

Taxon	Taxonomic change	Distributional change
Lampetra camtschatica	Name change from *L. japonica*	
Ichthyomyzon casteneus		Added to Quebec
Hiodon tergisus		Added to Alberta
Hiodon alosoides		Removed from Yukon
Anguilla rostrata		Added to Saskatchewan
Carassius auratus		Added to Yukon and Saskatchewan
Ameiurus nebulosus		Added to PEI
Ameiurus natalis		Added to BC
Rhinichthys obtusus	New taxon	Added to Saskatchewan, Manitoba, Ontario
Rhinichthys atratulus		Removed from Saskatchewan, Manitoba
Notropis percobromus	New taxon	Added to Manitoba
Notropis rubellus		Removed from Manitoba
Esox lucius		Added to Newfoundland
Esox masquinongy		Added to New Brunswick
Notemigonus crysoleucas		Added to PEI
Margariscus margarita		Removed from Newfoundland
Catostomus commersoni		Added to Nova Scotia
Osmerus mordax		Added to Manitoba, Saskatchewan
Oncorhynchus nerka		Added to Saskatchewan Removed from Manitoba
Oncorhynchus kisutch		Added to Saskatchewan
Oncorhynchus mykiss		Removed from Northwest Territories
Salmo salar		Removed from Ontario (extirpated)
Salvelinus alpinus		Added to Saskatchewan
Salvelinus alpinus		Added to Yukon
*Coregonus clupeaformis**		Added to Newfoundland
Coregonus laurettae		Removed from Northwest Territories
Coregonus pidschian†	Taxon not recognized	
Prosopium coulterii		Added to Northwest Territories
Prosopium williamsoni		Added to Yukon
Thymallus arcticus		Removed from Ontario
Menidia menidia		Added to New Brunswick
Gasterosteus aculeatus		Added to Yukon
Cottus bairdii		Removed from BC, Alberta
Cottus sp.‡	New taxon	Added to BC, Alberta
Cottus hubbsi	Replaces *C. bairdii* in BC	Added to BC
Myoxocephalus thompsoni		Removed from Nunavut, Québec
Myoxocephalus quadricornis		Removed from Nunavut
Lepomis macrochirus		Added to Saskatchewan
Pomoxis nigromaculatus		Added to Saskatchewan
Pomoxis annularis		Added to Saskatchewan
Morone saxatilis		Removed from Québec (extirpated)
Percina shumardi		Added to Ontario
Scardinius erythrophthalmus		Removed from Québec
Hexichromus letourneuxi	Name changed from *Hexichromis bimaculatus*	
Oncorhynchus aguabonita		Removed from Canada (BC, Alberta)
Cichlosoma managuense		Removed from Canada (Ontario)
Platichthys flesus		Removed from Canada (Ontario)
Lepisosteus platyrhincus		Removed from Canada (Ontario)
Ctenopharyngodon idella		Removed from Canada (Ontario, Saskatchewan, Alberta)

Table 2 (Continued)

Taxon	Taxonomic change	Distributional change
Colossoma bidens		Removed from Canada (Ontario)
Astronotus ocellatus		Removed from Canada (Ontario)
Dallia pectoralis		Removed from Canada (Ontario)

PEI, Prince Edward Island.

*Native to Labrador, but introduced to Newfoundland.

†Considered part of *C. clupeaformis*.

‡Taxonomic description in progress (Neely, pers. comm., McPhail, 2007). Known by the common name 'Rocky Mountain sculpin'.

and Newfoundland/Labrador (Fig. 3a). Pairwise faunal turnover between native faunas averaged 59.9% and ranged from 15.4% between New Brunswick and Nova Scotia to 92.3% between Yukon and PEI.

After accounting for non-native species and extinctions/extirpations in Canadian freshwater fish faunas in the 2005 database, similarities ranged from a low of 5.9% between the Northwest Territories and PEI, to a high of 71.7% between New

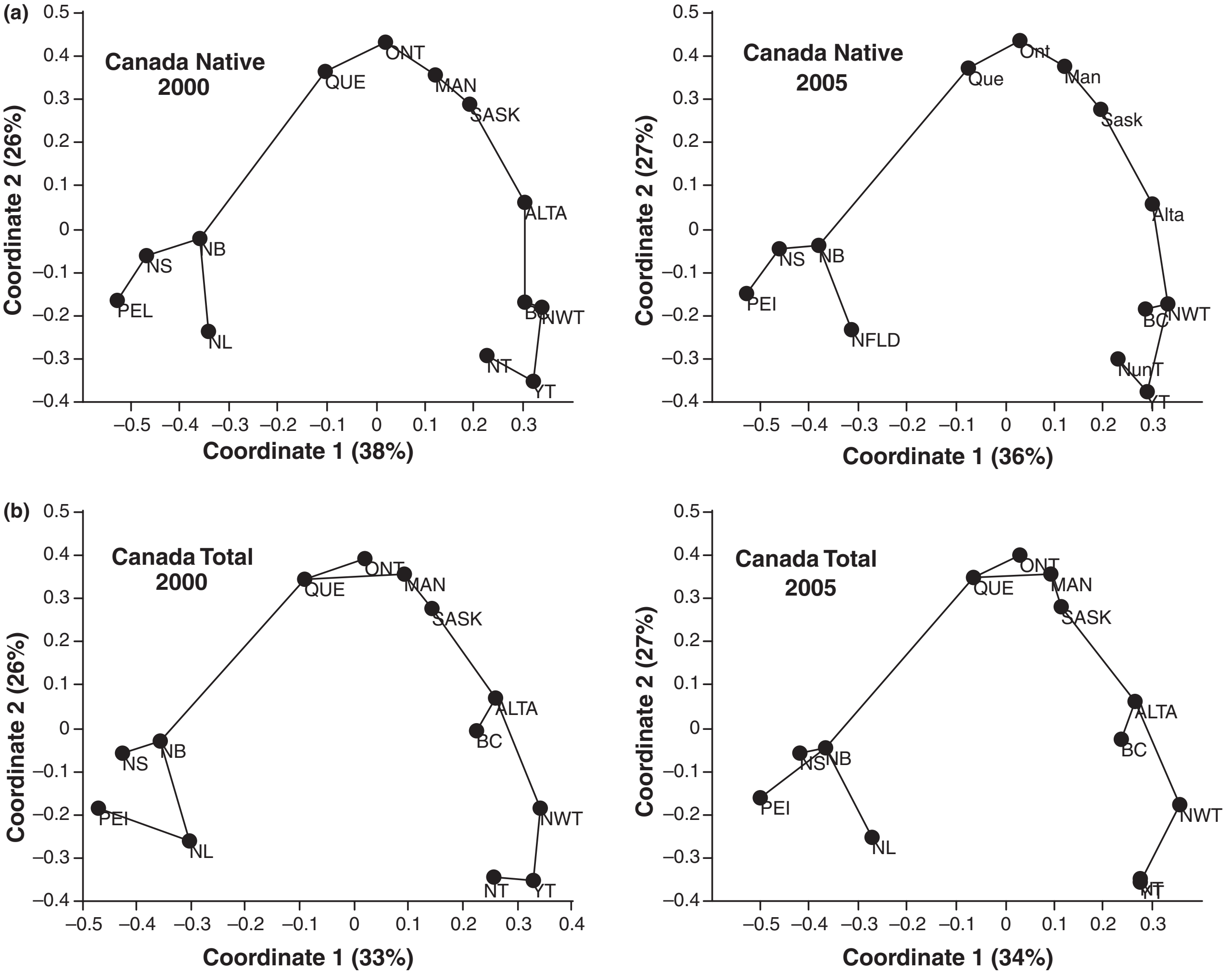

Figure 3 Relationships among thirteen provinces and territories in Canada based on surveys of freshwater fishes conducted in 2000 and 2005 for (a) native and (b) total faunas. Relationships are depicted following principal coordinates ordination using Jaccard's similarity coefficient. Each province/territory is joined using a minimum spanning tree. YT, Yukon Territory; NWT, Northwest Territories; NT, Nunavut Territory; BC, British Columbia; Alta, Alberta; Sask, Saskatchewan; Man, Manitoba; Ont, Ontario; Que, Québec; NB, New Brunswick; NS, Nova Scotia; PEI, Prince Edward Island; NFLD/LAB, Newfoundland and Labrador.

Brunswick and Nova Scotia and averaged 28.9% (see Table S2). Across all provinces and territories, there was a significant shift in 2005 faunal distributions between native and total faunas as measured by beta diversity which was significantly greater than zero ($\beta_w = 0.07$, $P < 0.001$). Ordination of localities resolved the same general relationships as the native faunas except that there was a tighter clustering between Nova Scotia and New Brunswick, and Newfoundland/Labrador was more distinct from the remainder of the eastern faunal region (Fig. 3b). In addition, closer faunal relationships were observed between Ontario and Québec, and between these two provinces and Saskatchewan and Manitoba, and between BC and Alberta (Fig. 3b). Overall pairwise comparisons, there was a small increase in the average native and total faunal pairwise Jaccard's coefficient matrices in 2005 (27.1% similarity versus 28.9%, respectively). A trend of homogenization was also apparent in the lower average multivariate dispersions among areas in 2005 (native = 0.722, total = 0.703), although this difference was not statistically significant ($P = 0.5$).

As a further index of homogenization, mean pairwise faunal turnover between provinces and territories dropped an average of 1.8% from 59.9% to 57.2% in the 2005 database, but pairwise variation was considerable. For instance, there was a gain in turnover between Nova Scotia and PEI from 28.6% to 39.7%, but turnover declined between BC and Québec from 69.3% to 54.9% after incorporating non-native species and extinctions/extirpations. The greatest changes in faunal similarity occurred in three provinces: PEI, Saskatchewan and British Columbia where pairwise similarities increased by an average of 3.8%, 3.4% and 3.4%, respectively. Three jurisdictions showed slight faunal differentiation: Nunavut, Alberta, Northwest Territories and Nunavut where pairwise faunal similarities decreased by an average of 1.8%, 1.3% and 0.8%, respectively, with the least faunal change between native and total faunas in 2005 being shown by the Northwest Territories.

After incorporating taxonomic and distribution changes since 2000, there was a small decrease in the pairwise similarity indices of native faunas between the 2000 and 2005 surveys (2000 = 27.9% vs. 2005 = 27.1%) and between total faunal pairwise comparisons (2000 = 29.1%, 2005 = 28.9%). There was, however, a slight increase in homogenization between native and total faunas based on the 2005 database (1.8%) compared to the 2000 database (1.2%); an average of 0.6% homogenization per pairwise comparison (Fig. 2b).

Across Canada, the goldfish (*Carassius auratus*, eight provinces and territories) and two salmonids, the brown trout (*Salmo trutta*, 10 provinces and territories) and rainbow trout (*Oncorhynchus mykiss*, eight provinces and territories) were the most widely introduced fishes (see Appendix S2).

DISCUSSION

In this study, I examined the effects of changing taxonomy and information on the geographic distribution of Canadian freshwater fishes on estimates of faunal homogenization and differentiation (faunal change). Despite numerous changes in taxonomy and distribution of native and exotic fishes across a 5-year time period, estimates of homogenization and differentiation were consistent between the two time periods; there was a slightly increasing trend towards faunal homogenization across Canada as a whole and small increase in the trend of faunal differentiation within British Columbia. Because taxonomic and geographic distribution data are fundamental to the study of faunal change, it is important to assess how uncertainty or instability in these sources of data could affect our point estimates of faunal change. Also, and as expected, most of the changes in input data were related to changes in species distributions rather than to taxonomy (81 vs. 8, respectively). This study demonstrates that over a relatively short time period, but one that is highly relevant to relevant to national species conservation assessments and recovery actions, estimates of faunal change are relatively insensitive to changes in taxonomy and information on species distributions. Consequently, at least in this study system, conservation monitoring and action plans can proceed with some confidence that faunal change is detectable and tractable under some uncertainty.

Conservation monitoring

The *raison d'être* of biological conservation has been described as the maintenance of the *status quo* or the manipulation of a biological system to achieve some predetermined target in terms of species presence, abundance, levels of genetic diversity, or other aspects of ecosystem structure and/or function (Legg & Nagy, 2006). Monitoring is integral to determine the state of ecosystem structure and/or function, or the degree to which it departs from a predetermined standard, as well as for detecting responses to management actions and/or disturbances (Hellawell, 1991; Yoccoz *et al.*, 2001; Legg & Nagy, 2006). Monitoring efforts have increased over the last 20 years and, in fact, efforts to assess the effectiveness of monitoring programmes themselves have received increased attention (Legg & Nagy, 2006). Biotic homogenization and differentiation are considered principle aspects of global change and threats to biodiversity (Olden, 2006; Rahel, 2007). Consequently, the regular assessment of species composition within and among geographic areas is essential to detect homogenization or differentiation and also to detect any responses by ecosystems to actions undertaken to manage biotic homogenization/differentiation. This study had as its principle aim the assessment of influences of our changing knowledge of taxonomy and species distributions on estimates of biotic homogenization/differentiation across different spatial scales and provides a first 'gauge' on the stability of such estimates under taxonomic and distributional uncertainty.

Taxonomy and biogeography

Monitoring of phenomena like homogenization/differentiation is important because of the dynamic nature of the fundamental components of biotic homogenization. First, 'the species' is the principle taxon upon which studies of homogenization/differentiation are based, but our taxonomic understanding and, therefore, our species composition databases change with time. This is especially true in the era of molecular biology where taxonomy can be now be based on both morphological and molecular data, and re-analysis of an established taxon using molecular data can reveal the presence of multiple cryptic species (Mallet & Willmott, 2003; Hebert *et al.*, 2004). In this study, examples of changes to taxonomy between 2000 and 2005 were apparent both at the within BC level and across Canada. For example, the mottled sculpin, *Cottus bairdii*, was recorded in 2000 as being present in five provinces: BC (one ecoregion), Alberta, Manitoba, Ontario and Québec. Recent molecular analysis, however, has indicated that *C. bairdii* does not exist in BC or Alberta and that these provinces contain a new taxon, commonly known as the Rocky Mountain sculpin, that is undergoing formal taxonomic description (McPhail, 2007). Consequently, instead of one taxon being shared amongst five provinces, there are now two taxa: one endemic to BC and Alberta and one endemic to the three other provinces.

Second, the biogeography of taxa changes with new information. Following the example above, taxonomic changes can change biogeography; the mottled sculpin is now recorded in three provinces, not five. In addition, even without taxonomic changes, our understanding of animal and plant distributions changes with time. This is especially evident when conservation concern precipitates increased survey efforts for species assessments, such as by Canada's Committee on the Status of Endangered Wildlife in Canada (COSEWIC), or subsequent recovery actions. These activities result in established distributions being confirmed, extended or reduced. Within Canada, one example involves the striped bass, *Morone saxatilis*, which was native to Québec in 2000, but is now considered extirpated. By contrast, the Arctic char, *Salvelinus alpinus*, was not recorded as being present in Yukon in 2000, but it is considered native (to north-west portions of Yukon) in the 2005 database. There are also changes in the distributions of non-native species; some are new records within Canada (e.g., yellow bullhead, *Ameiurus natalis*, in BC), others are now no longer considered present at least as self-sustaining populations in nature (e.g., grass carp, *Ctenopharyngodon idella*).

Third, the homogenization/differentiation process itself is dynamic, potentially shifting with the changing strengths and directionality of human and natural phenomena that influence species introductions, establishment, spread and extinction (Clavero & García-Berthou, 2006; Marchetti *et al.*, 2006; McKinney, 2006; Olden, 2006). Urbanization and related land use changes, for instance, influence extent and rates of species invasions and biotic homogenization/differentiation and they vary temporally and spatially (Marchetti *et al.*, 2006; McKinney, 2006; Ficetola *et al.*, 2010). In addition, climate change is thought to be an important factor influencing faunal and floral change by introduced and invasive species (Stachowicz *et al.*, 2002; Sharma *et al.*, 2007), and it varies spatially and temporally. The dynamic nature of these factors that can influence homogenization/differentiation indicate the need for regular monitoring over appropriate time and spatial scales. Clearly, the 5-year time frame between the 2000 and 2005 databases is a relatively short one. Nevertheless, many changes to taxonomy and species distribution information accumulated over this time, yet initial estimates of homogenization/differentiation in made in 2000 were substantiated in the 2005 database and subtle increases were detected across only 5 years.

The current analyses point to two important implications for conservation. First, estimates of faunal change depend fundamentally and critically on taxonomy and geographic distribution as data inputs. Given new information and techniques, however, these input data, like all biological data, are subject to some uncertainty and change as described herein. Despite such uncertainty and potential biases, estimates of faunal change were consistent across time periods suggesting that we can have confidence in 'snapshots' of measures of homogenization and differentiation under what are presumably typical levels of uncertainty and change. Consequently, conservation assessments and programmes incorporating or based on estimates of faunal change can proceed with some confidence under uncertainty. Second, notwithstanding the relatively short time frame between faunal surveys (5 years), slight increases in faunal change were detected which was a combination of better information as well as actual geographic spread of certain invasive species (cf. Clavero & García-Berthou, 2006). Thus, while longer time frame studies often detect the greatest absolute change between two time periods, the design of serially repeated surveys across shorter appropriate time frames can help better resolve (1) the rate of faunal change (Clavero & García-Berthou, 2006), and (2) the relative contributions of faunal change stemming from invasions, changes in taxonomy and better information on geographic distributions.

Temporal patterns in homogenization/differentiation in Canada

The choice of monitoring time frame for this study was driven by the availability of distinct 2000 and 2005 Wild Species databases. The update in 2005 was important as a first assessment of the consistency and veracity of patterns resolved by Taylor (2004). Analysis using the 2005 database presents the first opportunity to assess the magnitude of impact on initial results in the light of the taxonomic and geographic distributional changes between the 2000 and 2005 databases. In general, the impact of some database 'instability' was minimal; the same basic patterns of faunal differentiation in BC and homogenization across Canada were resolved using the 2005 database. In addition, the ecoregion or provincial/territorial relationships resolved in 2000 where largely unchanged in 2005. What the new analysis also showed, however, was that both trends in biotic faunal change continued in 2005; biotic differentiation in BC increased by 1.7% and homogenization across Canada as a whole increased, albeit marginally, by 0.6%.

These results indicate that the changes to Canada's freshwater fish faunal composition driven by non-native species introductions continued between 2000 and 2005. While trends resolved between 2000 and 2005 are slight (< 2%), they occurred over only a 5-year time period. Looking forward, it will be important to decide upon an appropriate time frame to monitor faunal change and to employ it consistently because changes to faunal composition may be driven, in part, by different time frames chosen for analysis (Olden & Poff, 2003; Olden *et al.*, 2006). The 5-year interval of Wild Species Canada updates coupled with increasing monitoring activities associated with Canada's *Species at Risk Act* (SARA) should help to facilitate such monitoring.

At the scale of British Columbia aquatic ecoregions, there were six instances of non-native species removed from species composition lists as new information suggests that they are 'accidental' or temporary occurrences that have not established self-sustaining populations. By contrast, in the 2005 survey there were eight occurrences of species being newly recorded in an ecoregion to which they were not native. Five of these eight occurrences involved species that are not native to BC at all, and occurrences of non-native species within ecoregions tend to be idiosyncratic, i.e., they do not occur across all ecoregions. At least two of these non-native species occurrences probably represent newly established non-native species since 2000 rather than being a result of increased survey effort. For instance, the Atlantic salmon, *Salmo salar*, is the focus of intensive marine fish-farming in the south-central and south-western coast of BC. Escapes of Atlantic salmon from sea net pens represents a form of 'propagule pressure' that would be expected to increase occurrences of the species in nearby rivers (e.g., Volpe *et al.*, 2000; Naylor *et al.*, 2003). This kind of pressure is persistent enough to result in the species being considered present in two new ecoregions (Fraser River and Central Coast) when in 2000 it was considered present only in VI streams (McPhail, 2007). Another species, the yellow bullhead (*Ameiurus natalis*) has only recently (post-2002) been recorded in several tributaries of the lower Fraser River despite intensive collections in this area since the 1980s (McPhail, 2007; E.B. Taylor, pers. obs.). Consequently, these cases suggest that increasing faunal change in BC is not simply a case of better data documenting the presence of long-established non-native species, but that the *processes* that lead to the establishment of new non-native species are continuing. In addition, the taxonomic changes resulted in the new occurrences of two native species that are endemic to a single ecoregion in BC (the Columbia River) which would also contribute to the observed increase in differentiation among ecoregions. By contrast, in Canada, there were 14 occurrences of non-native species removed from the Wild Species 2005 list and seven of these fish that were once recorded as present in Canada were restricted to Ontario. Twenty-three species, however, were added to provinces/territories where they were not native and all of these were either found in other provinces naturally or had been widely introduced across Canada previously (e.g., the goldfish). Both of these events would contribute to the observed trend of increased homogenization in Canada.

Processes and future biotic change in BC and Canada's freshwater fish fauna

Olden & Poff (2003) articulated 14 scenarios involving species introductions and extinctions that could explain patterns of homogenization and differentiation, and the present study provides one of the few assessments of the applicability of these scenarios. For BC ecoregions, overall differentiation appears to result largely from 'introduction/invasion only' scenarios because species extirpations are limited in number (2) and to a single ecoregion (Columbia River). Non-native species in BC were introduced into an average of only 1.8 (of 8) ecoregions which suggests that the overall differentiation of BC ecoregions follows scenario I2 ('different species invade, no extinctions of resident species') of Olden & Poff (2003). For the Columbia River ecoregion, overall faunal differentiation relative to other ecoregions appears to follow scenarios IE7/8 ('Different species invade, extinction in one community of a species that was originally shared/not shared by both communities') of Olden & Poff (2003). In two cases, however, the Columbia River ecoregion showed faunal homogenization relative to the VI and Mackenzie River ecoregions and here scenario IE3 held ('Same species invade, extinction in one community of a species that was originally shared by both communities').

Across Canada, non-native species were introduced to an average of 2.2 provinces/territories (out of 13) and the seven extinctions/extirpations are unique to single areas. The overall trend towards homogenization in Canada, therefore, stems largely from scenario I1 ('same species invade, no extinctions of resident species') or in the relatively few cases of differentiation, scenario I2 ('different species invade, no extinctions of resident species'). The major exception was Ontario where the six extinctions/extirpations unique to Ontario, including four taxa endemic to Ontario, increased the importance of Olden & Poff's (2003) scenario IE4 ('same species invade, extinction in one community of a species that was originally not shared by both communities'). Overall, the empirical observations in BC and across Canada are consistent with community responses (homogenization or differentiation) predicted from the scenarios of Olden & Poff (2003).

The current analyses have documented that the extent of fish faunal homogenization and differentiation at different spatial scales are relatively stable in the face of taxonomic and distributional changes. It is remarkable that the most common species introduced that lead to homogenization and differentiation in BC and Canada (e.g., goldfish, carp, various salmonids, mosquitofish), respectively, are almost identical to those responsible for the same patterns in another continent in the Southern Hemisphere – Australia (Olden *et al.*, 2008). This suggests that the factors that initiate and promote faunal change are globally general ones, although they are still largely unquantified. It is clear, however, that specific commercial and recreational pressures (aquaculture, sportsfishing, aquarium trade) are important drivers of initial species introductions in Canada and elsewhere (e.g., Dextrase & Mandrak, 2006; Rahel, 2007), but the specific environmental and biological factors that promote the persistence and spread of non-native species are largely unknown. One notable exception is the process of urbanization which appears to be very important in promoting faunal changes that contribute to faunal homogenization or differentiation (Marchetti *et al.*, 2006; Johnston & Maceina, 2008; Olden *et al.*, 2008). This inference is supported by the pattern in BC where the three ecoregions showing the highest levels of homogenization/differentiation, and the most consistent increases in these phenomena between 2000 and 2005, where VI and the Fraser and Columbia rivers – areas of the highest population density and growth in BC (Stats BC, 2009). These areas, along with the Mackenzie River ecoregion, also show the greatest levels of ecosystem conversion from natural states to landscapes for human uses (e.g., buildings, agricultural and commercial uses, reservoirs, Austin *et al.*, 2008). Across Canadian provinces and territories, regions with high levels of homogenization/differentiation both in 2000 and 2005 (Yukon Territory, BC, Alberta, Saskatchewan) tend to show higher than average human population growth rates (Statistics Canada, 2009). It seems likely that these spatial trends in faunal change will continue both within BC and in Canada as human population size increases are projected to continue in these particular jurisdictions, especially if the biological factors contributing to homogenization/differentiation continue to operate. For instance, Canada has 44 freshwater fish species at risk and protected under SARA with many more under consideration for listing (COSEWIC 2009; DFO 2009). Should any of these species become extirpated or extinct and are endemics, then homogenization, by definition, will increase. Even if they are not endemics, their loss could provide opportunities for non-native species to become established. Second, global climate change may facilitate extinctions of native fishes and/or establishment of non-native species (Stachowicz *et al.*, 2002; Sharma *et al.*, 2007) and contribute to homogenization or differentiation. Future trends may be especially important in northern areas of Canada where biotic change has been relatively low for the 2000 and 2005 surveys (see also Dextrase & Mandrak, 2006), but where increased human development coupled with projections for substantial climate changes and relatively low fish faunal diversity may promote rapid increases in homogenization/differentiation (Olden & Poff, 2003; Olden *et al.*, 2006). Understanding the shifting distributions of both native and non-native freshwater fishes, and what anthropogenic and natural ecological processes contribute to these changes is necessary to help develop predictive models of faunal changes (e.g., Xenopoulos *et al.*, 2005; Sharma *et al.*, 2007). Documenting the presence and dynamics of existing homogenization/differentiation, developing predictive models of faunal change, implementation of steps to prevent native fish from becoming at risk and recovering those already at risk, coupled with increased vigilance against and prevention of the introduction of non-native species are all necessary to limit faunal homogenization/differentiation from increasing. Although these are not insignificant tasks in-and-of-themselves, they are paramount in the face of increasing urbanization and global climate change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Freshwater fish species presence–absence data for aquatic ecoregions in British Columbia.

Appendix S2 Freshwater fish species presence–absence data for Canadian provinces and territories.

Table S1 Jaccard's faunal similarity coefficients for freshwater fish faunas in British Columbia.

Table S2 Jaccard's faunal similarity coefficients for freshwater fish faunas in Canada.

BIOSKETCH

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