META-ANALYSIS

Patterns and repeatability of multi-ecotype assemblages of sympatric salmonids

Stephanie A. Blain[1] 🄳 | Dolph Schluter[1] | Colin E. Adams[2] | Per-Arne Amundsen[3] | Rune Knudsen[3] | Louise Chavarie[1,2,4]

[1]Department of Zoology, Biodiversity Research Center, University of British Columbia, Vancouver, British Columbia, Canada

[2]Scottish Centre for Ecology and the Natural Environment, SBOHVM, University of Glasgow, Glasgow, UK

[3]Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, University of Tromsø, Tromsø, Norway

[4]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

Correspondence
Stephanie A. Blain and Louise Chavarie, Department of Zoology, Biodiversity Research Center, University of British Columbia, Vancouver, BC, Canada.
Email: blain@zoology.ubc.ca and louise.chavarie@nmbu.no

Present address
Stephanie A. Blain, Department of Biology, Texas A&M University, College Station, Texas, USA

Abstract

Aim: High repeatability among assemblages of closely related but ecologically distinct ecotypes implies predictability in evolution and assembly of communities. The conditions under which ecotype assemblages form predictably, and the reasons, have been little investigated. Here, we test whether repeatability declines as the number of ecotypes builds.

Location: Postglacial lakes with a circumboreal distribution.

Time Period: Data were extracted from studies published between 1982 and 2019.

Major Taxa Studied: Ecotype assemblages from two Salmonid genera – *Salvelinus* and *Coregonus*. Fish in postglacial lakes commonly occur as pairs of ecotypes, typically with a pelagic and a littoral/benthic form, but in *Salvelinus* and *Coregonus*, assemblages commonly contain multiple sympatric ecotypes.

Methods: We used a meta-analysis of *Salvelinus* and *Coregonus* to empirically assess how repeatability varies across assemblages of two to seven ecotypes. We examined repeatability of use of broad niche categories as well as underlying phenotypic traits.

Results: Within *Coregonus*, repeatability across multi-ecotype assemblages did not break down with the addition of a third or fourth ecotype. However, in *Salvelinus*, repeatability was largely absent and independent of the number of ecotypes. Repeatability of trait frequency distributions was absent in both genera, yet associations between trait means and niche categories were evident, especially in *Coregonus*.

Main Conclusions: These results show that repeatability can vary greatly between lineages; that repeatability need not break down as the number of ecotypes builds; and that high repeatability of broad niche categories may result despite marked differences in the underlying frequency distribution of trait means. These findings not only affirm the presence of repeatable ecotype assembly and early stages of divergence in postglacial fishes at a global scale, but also highlight variability among taxa and underlying phenotypic traits.

KEYWORDS
Coregonus, diet, gill rakers, life history, meta-analysis, morphology, phenotype, postglacial lakes, repeatability, *Salvelinus*

1 | INTRODUCTION

Geographically distinct assemblages of coexisting ecotypes can be strikingly similar to one another (Gillespie et al., 2018; Knotek et al., 2020; Mahler et al., 2013). This suggests that the process giving rise to ecological diversity may be, to some degree, repeatable (Blount et al., 2018; Jamie & Meier, 2020; Losos et al., 1998). Ecotype assemblages, which consist of sets of co-occurring, closely related but phenotypically and ecologically distinct forms, can be established via non-random coexistence of previously evolved ecotypes, repeated divergent evolution between sympatric ecotypes or some combination thereof (Rundell & Price, 2009). Repeated evolution can result from parallel natural selection favouring similar phenotypes, or it can result from similar developmental and genetic constraints on the direction of evolution in independent ecotype assemblages (Brakefield, 2011; McGlothlin et al., 2018; Yoder et al., 2010). Additionally, for entire assemblages to resemble each other, ecological processes driving community assembly must also be repeated (Gillespie, 2004; Schluter, 1990).

A question that has been little addressed is whether repeatability of ecotype assembly changes with the number of ecotypes present within an assemblage. There are many examples of repeated ecotype pairs in nature (James et al., 2021; Saint-Laurent et al., 2003; Schluter & McPhail, 1992), but relatively few examples of repeatable multi-ecotype assemblages (Losos, 2010). We might expect increased diversity and complexity to lead to lower repeatability since each additional ecotype opens the possibility of alternate community states and presents a further opportunity for evolution or colonization to reshape the community's ecological structure (Leibold et al., 2022). Alternatively, limited niche possibilities within an environment and taxon-specific constraints on phenotypic evolution that lead to niche-tracking across lakes might reduce options for new ecotypes to colonize or evolve (Kinzig et al., 1999; MacArthur, 1969). Certain ecotypes may also be more likely to occur or co-evolve within assemblages only when others are already present, leading to nested community assemblages that could maintain repeatability despite greater diversity (Broderson et al., 2018; Gillespie, 2004; Losos, 2009).

A second question concerns how often independently assembled communities are repeatable in broad ecological niche use but not at an underlying level, such as in the traits that allow an ecotype to exploit a particular resource. Although there are many examples of repeatable ecology-associated trait differences between coexisting ecotypes (Fernandez-Mazuecos et al., 2020; Mahler et al., 2013; Riesch et al., 2014), two populations may instead exhibit dissimilar traits even if repeatability exists in broad habitat and diet categories (Blount et al., 2018; Bolnick et al., 2018). Repeatable morphological differences associated with habitat and diet have been observed in replicated ecotype assemblages, including in Caribbean *Anolis* lizards, African rift lake cichlid fish and neotropical *Viburnum* plants (Donoghue et al., 2022; Losos, 2009; Muschick et al., 2012). However, examples are few, and there are many cases of populations that have converged in broad resource use but remain distinct in the traits used to acquire those resources (Losos, 2010; Oke et al., 2017). Furthermore, it is unclear whether similarity across assemblages ever extends to repeatability of within-ecotype trait variability (Chavarie, Howland, et al., 2021).

Fish in postglacial lakes are a classic example of repeated assemblages of co-occurring ecotypes (McPhee et al., 2012; Schluter & McPhail, 1993). In many previously glaciated regions of the northern hemisphere, a number of fish species that invaded new lakes at the end of the ice age quickly gave rise to ecotypes pairs that exhibit consistent differentiation in morphology, life history and resource use (Hendry, 2009; Oke et al., 2017; Smith & Skúlason, 1996). Most of these pairs include a pelagic (sometimes termed "limnetic") ecotype that consumes zooplankton in open water regions of the lake and a benthic ecotype that occupies nearshore areas and eats primarily macroinvertebrates. The repeated occurrence of this set of ecotypes across several families of fish suggests both that there is a fundamental benthic-to-pelagic ecological gradient in postglacial lakes and that this is a gradient along which it is consistently possible for freshwater fish to adapt and coexist (Robinson & Parsons, 2002; Schluter, 2000). However, it is possible that there are multiple resource axes within a lake, such as a shallow-to-deep water axis or invertivore-to-piscivore axis, so that additional ecotypes are not constrained solely to a benthic-to-pelagic resource gradient (Recknagel et al., 2014, 2017; Wagner et al., 2014).

Here, we make use of the diversity of postglacial ecotypes in two salmonid lineages to address the two questions about repeatability raised above. *Salvelinus* and *Coregonus* are unique among salmonids in exhibiting multiple instances of assemblages of three or more ecotypes in addition to the more commonly described pairs (Schluter & McPhail, 1993; Smith & Skúlason, 1996). This allows us to address whether repeatability persists or decays in assemblages of increasing numbers of ecotypes. *Salvelinus* species have been described as exhibiting an unusually high level of phenotypic and ecological variability within and among populations spanning lacustrine, riverine and anadromous life histories, as well as diets that range from consumption of benthic invertebrates to pelagic zooplankton and to other fish (Chavarie, Adams, et al., 2021; Klemetsen, 2010; McPhee et al., 2012). *Coregonus* species have high levels of variability in habitat occupation as well as diet, ranging from zooplankton to larger freshwater invertebrates (Bernatchez et al., 2010). Different instances of ecotype assembly and evolution vary in the mechanisms underlying differentiation, being genetically based in some cases and based on phenotypic plasticity in others. Sympatric ecotypes also vary in their degree of reproductive isolation (Hendry, 2009). Here, we refer to ecologically and/or phenotypically distinct populations as ecotypes and leave open the question of mechanisms of differentiation. In most cases, phylogenetic relationships among ecotypes are unknown. In the absence of more detailed phylogenetic information, to compare trait and niche use patterns here, we treat assemblages within each genus as though they are statistically independent replicates.

In this study, we assessed the repeatability of assemblages containing up to seven ecotypes in two circumpolar and circumboreal

salmonid genera, *Salvelinus* and *Coregonus*, through a meta-analysis, using published data on morphology, life history, diet and habitat use. We addressed two overarching questions. First, does repeatability occur and does it decline with increasing numbers of sympatric ecotypes? To test this, we measured the degree of repeatability from two- to multi-ecotype assemblages. Second, do sympatric ecotypes exhibit repeatable patterns of trait differentiation? We evaluated this for assemblages ranging from two to five ecotypes by using differences in trait means and trait variance among ecotypes.

2 | METHODS

2.1 | Systematic literature review

We performed a systematic literature review to identify papers with data on wild-caught fish from lakes with two or more cooccurring ecotypes, closely related species or taxa (hereafter referred to as "ecotypes") forming separate ecological and morphological clusters, from the genus *Salvelinus* or *Coregonus*, following standard systematic review guidelines (Mikolajewicz & Komarova, 2019; Moher et al., 2015). We implemented searches in Web of Science, Scopus and bioRxiv, as well as a forward search of papers citing Skulason and Smith (1995), to identify papers that potentially reported primary research on lineages at an early stage of divergence in these two genera (see Figure S1 for more details). We included studies that reported sympatric ecotypes that were considered by the authors to be intraspecific or part of a species complex of recently diverged lineages. For example, described species from the *C. artedi* and *C. lavaretus* species complexes were included (Crête-Lafrenière et al., 2012; Østbye et al., 2005). We included data from lacustrine ecotypes only, excluding riverine ecotypes even if the river was directly adjacent to a lake with ecotype diversity. Studies that provided information on sympatric *Salvelinus* or *Coregonus* ecotypes within lakes were identified by a scan of the abstract followed by a full-text review. We retained 126 studies with data from 103 assemblages following the full-text review and included these in the meta-analysis (Figure 1; Tables S2 and S3). We extracted usable trait data for 90 assemblages. For 85 lakes, all ecotypes were identified as filling a specific diet or lake habitat niche (Figure S3).

For each assemblage, we recorded the number of phenotypically distinct ecotypes described by the authors (Table S1). If the sample size was less than five individuals for a population of given ecotype, that population was excluded from our analysis due to a lack of information about those populations. In most cases, this resulted in the assemblage being excluded from the analysis because one or no populations were left in the dataset. In two cases, Ellasjoen and Kalarskii-Davatchan, we kept lakes in the analysis after removing data for one ecotype with insufficient sample size because there were still data for two or more ecotypes from the lake that did have a sufficient sample size. Population genetic analyses of both *Salvelinus* and *Coregonus* assemblages suggest that most evolved independently in situ, even among lakes in the same drainage (Jacobs

et al., 2020; Østbye et al., 2006; Pigeon et al., 1997). However, ecotypes may have evolved in one lake and then dispersed to another in a few cases. Dispersal between lakes is suggested by high genetic similarity between *Salvelinus* planktivore ecotypes in two Scottish lakes, *Salvelinus* piscivore ecotypes in two Russian lakes and *Coregonus* assemblages in adjacent lakes in Switzerland (Hudson et al., 2011; Jacobs et al., 2020). Nonetheless, these assemblages have in most cases been evolving largely independently of each other since their formation.

Mean, sample size and a measurement of error were recorded for gill raker count, body length (total, fork or standard), age (based on scales or otoliths) and stable isotopes indicative of dietary resources and habitat use (δ^{13}C and δ^{15}N). We did not require that age estimates be validated by a second method because successful age validation is relatively uncommon, although this may constitute a source of error (Beamish & Mcfarlane, 1983). These variables were selected because of their relationship to niche occupation and because they are commonly measured (Sánchez-Hernández et al., 2019). When necessary, metaDigitise was used to extract data from figures and convert standard error and 95% CI estimates to standard deviation to measure trait variability (Pick et al., 2019). All analyses were run in R, version 4.0.3 (R Core Team, 2022). All statistical tests were performed separately for *Coregonus* and *Salvelinus*. If any of mean, sample size or error were not listed or available to extract, then those values were excluded from the analysis of treat means and trait variance. For the analysis of repeatability of trait values across full assemblages, if the value for one ecotype was missing, the full assemblage was excluded.

2.2 | Ecotypes

We produced four assemblage datasets: one for each *Coregonus* and *Salvelinus*, and with ecotypes defined by either diet consumed or the lake habitat occupied. We classified populations into ecotypes based on descriptions provided in each paper. If paper authors did not specifically describe an ecotype as occupying a particular habitat or diet using either their own data or by citing other primary literature, we did not assign the ecotype to a category. The ecotype habitat uses categories for both genera were "littoral/benthic", "pelagic", "profundal", "generalist" and "shallow" (Figure S2). Littoral/benthic ecotypes occupied nearshore benthic habitat, pelagic ecotypes inhabited an open-water habitat, profundal ecotypes occurred in a deep-water habitat, generalist ecotypes were found in multiple zones of a lake and shallow ecotypes were found in shallow-water but not restricted to the nearshore or open-water habitats. The diet categories were "planktivore", "benthivore" and "generalist invertivore" for *Coregonus* and "planktivore", "benthivore", "generalist invertivore", "piscivore" and "omnivore" for *Salvelinus* (Figure S2). Planktivores consumed predominantly zooplankton, benthivores specialized on benthic invertebrates, generalist invertivores consumed multiple types of invertebrate species, piscivores ate mostly other fish and omnivores preyed on a mix of invertebrates and fish. In some cases, the
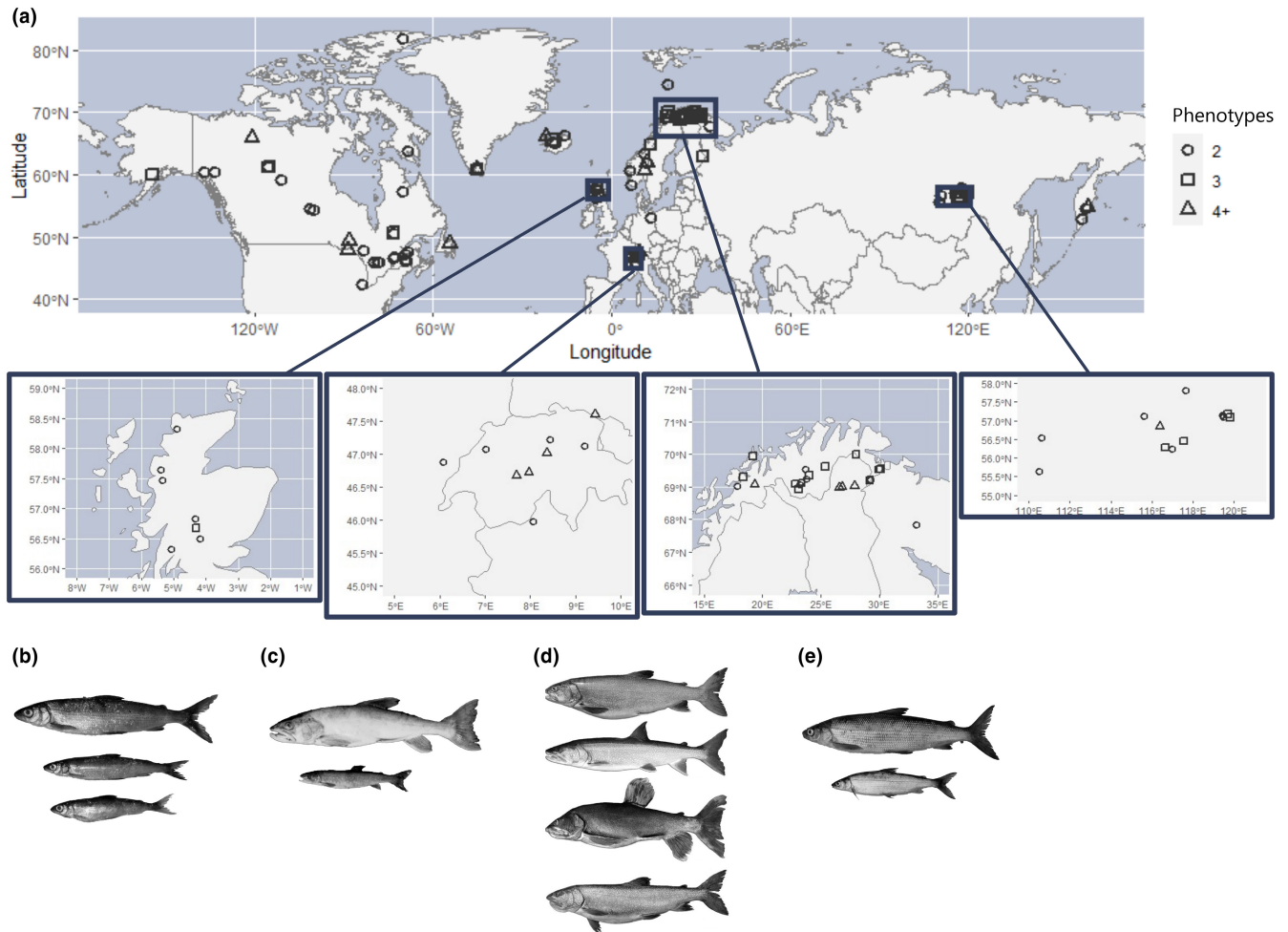
FIGURE 1 (a) Map of lakes containing two or more cooccurring ecotypes of *Salvelinus* or *Coregonus*. (b) Pelagic, littoral/benthic and profundal *Coregonus lavaretus* ecotypes from Lake Skrukkebukta (Præbel et al., 2013). (c) Piscivore and planktivore *Salvelinus alpinus* ecotypes from Loch Ericht (Maitland & Adams, 2018). (d) Three generalists and one pelagic *Salvelinus namaycush* ecotypes from Great Bear Lake (Chavarie et al., 2013). (e) Dwarf and normal *Coregonus clupeaformis* ecotypes from Cliff Lake (Bernatchez et al., 2010).

TABLE 1 Reclassification of ecotype descriptors.

Resource	Ecotype	Alternative descriptors
Habitat	Littoral/benthic	Littoral, benthic
	Pelagic	Limnetic
	Profundal	Deep, deepwater, abyssal
	Generalist	All, pelagic & littoral, pelagic & littoral & profundal, pelagic & profundal, benthic & pelagic, deep & shallow
	Shallow	Shallow littoral & pelagic
Diet	Planktivore	Zooplanktivore
	Benthivore	Gammaridivore
	Generalist invertivore	
	Piscivore	
	Omnivore	Generalist, piscivore & invertivore

documented ecotype identification was replaced with an equivalent descriptor (Table 1). For a study to be included in an analysis assessing repeatability of niche occupation, we required that all ecotypes in the assemblage be assigned to a diet or habitat category.

2.3 | Repeatability of ecotypes across lakes

Repeatability can be defined as higher similarity between assemblages than expected by chance in the frequency distribution of

ecotypes. In this case, we would expect to see matching among assemblages in the occurrence of ecotypes, non-random patterns in the frequency distribution of ecotypes and a repeatable pattern in which ecotypes additionally occur when assemblages contain more than two ecotypes. Therefore, we quantified similarity in three ways: as ecotype-for-ecotype matching, as associations in the occurrence of ecotypes within assemblages and as a pattern of nestedness among assemblages differing in the number of ecotypes.

We evaluated similarity of population assemblages using ecotype-for-ecotype matching (often referred to as "species-for-species matching"; Schluter, 1990). Ecotype-for-ecotype matching occurs when the frequency distribution of ecotypes exhibited by populations is more similar across sites compared to a null distribution where populations are assigned randomly to ecotypes while keeping the number of populations per lake and per ecotype constant. We tested for this separately in lakes with two ecotypes, three ecotypes and all ecotypes included (i.e. two to seven per lake). To test for ecotype-for-ecotype matching, we constructed contingency tables with ecological categories as columns (either diet or habitat) and lakes as rows, counting the number of ecotypes in each category (Schluter, 1990). We calculated the χ^2 statistic using the R function "chisq.test()". To generate a null distribution, we simulated contingency tables using the R function "r2dtable()", which generates tables with an algorithm that shuffles the frequencies while maintaining the observed row and column totals (Patefield, 1981). We then compared the observed χ^2 to the null distribution with a two-tailed test. To quantify whether assemblages were more similar or dissimilar than expected by chance, we calculated the ratio of the χ^2 statistic to the degrees of freedom (df). For χ^2/df, a value <1 would indicate similarity and a value >1 would indicate dissimilarity (because df is the mean of the distribution).

As a second measure of repeatability, we tested for associations among ecological categories within assemblages using the V-ratio (Schluter, 1984). V-ratios estimate whether ecotypes in particular categories are more likely to occur together (or not occur together) than expected by chance. An association would arise, for example, if ecotypes in two categories were more likely to occur in the same assemblage (positive association) or less likely to occur together (negative association) than expected by chance (Schluter, 1984). If pelagic and littoral/benthic ecotypes tend to occur together, this would be a positive association, but if planktivore and piscivore ecotypes tend to only occur in separate assemblages, this would be a negative association. A pattern of positive association would indicate similarity among assemblages in which ecotypes occur, while a pattern of negative association would imply dissimilarity among assemblages. To estimate V-ratios, we used a presence–absence matrix with ecotypes and lakes as variables, where "1" indicated that a lake contained an ecotype in a diet or habitat category and "0" indicated that it did not. These were calculated using "V.ratio()" from the package "bipartite()" (Dormann et al., 2009). To evaluate significance, we used a two-sided test compared to a null distribution generated from simulations carried out via the function "oecosimu()" (Oksanen

et al., 2020). We used the algorithm "r1" with 10,000 simulated matrices. With the r1 algorithm, row (lake) sums were fixed while column (ecological category) sums were not. Instead, the probability of occurrence in each ecological category depended on the marginal frequency of that column.

We then evaluated evidence for a pattern of nestedness of ecotype occurrence across assemblages relative to a null distribution where ecotypes are randomly distributed across lakes, with the number of ecotypes per lake held constant. This pattern would emerge if the ecotypes in lakes with few ecotypes form a subset of the categories occupied in lakes where more ecotypes are present. If ecotypes in two-ecotype assemblages are not consistently observed in three- or four-ecotype assemblages, this would be consistent with a lack of nestedness. The "NODF" score from the function "nestednodf()" in vegan version 2.5–7 was used to evaluate nestedness (Almeida-Neto et al., 2008; Oksanen et al., 2020). NODF estimates the percentage of overlap between lakes with fewer ecotypes relative to those with more, with higher NODF values indicating greater evidence for nestedness. We evaluated the null hypothesis of no nestedness against the one-sided alternative hypothesis that nestedness is greater than expected by chance. To do this, we again simulated a null distribution of 10,000 matrices with the algorithm "r1".

2.4 | Repeatability of trait frequency distributions in ecotype assemblages

If there is repeated assemblage-wide convergence in phenotypes, then the frequency distribution of population mean trait values in assemblages would be expected to be highly similar across lakes. To test for repeatability of trait distributions for gill raker counts and total body length among ecotypes and across lakes, we evaluated whether the sets of trait values in each lake were more similar than if they were randomly drawn from the same distribution of possible values (Schluter, 1990). Alternatively, a lack of repeatability would be implicated by evidence that sets of trait values were not drawn from the same distribution or by a lack of evidence for either similarity or dissimilarity. This is a form of ecotype-for-ecotype matching, testing for matching of frequency distributions of continuous traits rather than discrete categories.

We used two-tailed k-sample Anderson–Darling tests to evaluate whether mean trait distributions were significantly similar or divergent among assemblages (Scholz & Stephens, 1987). This is a rank order test that evaluates whether samples are drawn from the same unspecified distribution. We used the function "ad.test()" from the R package "kSamples", with significance evaluated by comparing the observed AD statistic to a distribution of 10,000 simulated statistics (Scholz & Zhu, 2019). We first converted fork and standard length to total body length using conversion parameters from FishBase (Binohlan et al., 2021; Boettiger et al., 2012). For lakes with multiple and independent published estimates of mean trait values for each of the cooccurring ecotypes, a weighted mean of estimates for a particular trait value was used. Because the most common habitat categories in

both *Coregonus* and *Salvelinus* were littoral/benthic, profundal, and pelagic, we repeated the tests retaining only those ecotypes.

2.5 | Trait differences between ecological niche categories

Continuous traits might exhibit repeated differences associated with ecotype. As another test of repeatability of continuous traits, we estimated similarity among lakes in the difference in trait means among ecotypes (habitat or diet). We assessed repeatability by asking whether within-lake variation among ecotypes is large relative to the variation among lakes. Assemblages would be considered similar if ecotypes in the same ecological category (e.g., pelagic) are relatively similar among lakes but sympatric ecotypes in different ecological categories (e.g., pelagic and profundal) exhibit larger differences in a consistent direction. A lack of repeatability would emerge if trait differences among sympatric ecotypes are small or variable in direction among lakes.

To estimate repeatability of trait differences, we fit a linear model with trait value (ecotype means) for each ecological category as the response variable and lake and niche as fixed effects, weighted by the inverse of the sampling variance for each trait mean. We restricted this analysis to lakes with two or more ecotypes in different niche categories. We also limited the niche categories included to those most commonly observed: littoral/benthic, pelagic and profundal for habitat and planktivore, benthivore and piscivore for diet. We then estimated the variance explained by ecological differences among lakes (sum of squares (SS) of the interaction between ecological category and lake) relative to all variation among ecological categories. This was calculated as: $S = 1 - SS_{Niche*Lake} / (SS_{Niche} + SS_{Niche*Lake})$, where SS is calculated sequentially (type 1 sums of squares) with "Niche" entered in the model before "Lake". Possible values for S vary between 0 and 1. A value close to 1 would indicate low among-lake variability in the relationship between ecotype and traits relative to total variation among ecotypes, and therefore high similarity among lakes.

Intrapopulation trait variation, not just trait mean, has the potential to differ among sympatric ecotypes. To estimate similarity among lakes in relationships between intrapopulation variation and ecotype, we first calculated the coefficient of variation for each population. For each trait, we then fit a linear model with the coefficient of variation for each population as the response and lake, niche and their interaction as predictor variables. We then estimated similarity among lakes using the same S statistic as we used for trait means.

3 | RESULTS

3.1 | Repeatability of niche occupation across lakes

Coregonus exhibited ecotype-for-ecotype matching that was independent of ecotype number, indicating that repeatability does not decline with greater ecotype diversity. In most lakes, with ecotypes

categorized by diet, ecotype pairs tended to include one benthivore and one planktivore ecotype (Figure 2a), while trios contained two benthivore and one planktivore ecotype (Figure 2a). Four-ecotype lakes contained two benthivore ecotypes, one planktivore ecotype and a generalist invertivore ecotype (Figure 2a). Frequency distributions of populations of both habitat and diet ecotypes among two-ecotype *Coregonus* lakes were more similar than expected by chance (diet: $\chi^2/df = 0.23$, $p = 0.051$; Figure 2a; habitat: $\chi^2/df < 0.01$, $p < 0.001$; Figure 3a). In three-ecotype *Coregonus* lakes, the numbers of ecotypes in each of the diet and habitat categories were also similar across lakes (diet: $\chi^2/df = 0$, $p = 0.004$; Figure 2a; habitat: $\chi^2/df = 0$, $p < 0.001$; Figure 3a). This pattern held when all *Coregonus* lakes having two to four cooccurring ecotypes were analysed at once (diet: $\chi^2/df = 0.41$, $p < 0.001$; Figure 2a; habitat: $\chi^2/df = 0.84$, $p = 0.050$; Figure 3a).

In contrast, ecotype assemblages were highly variable for *Salvelinus*, indicating a lack of repeatability in ecotype evolution and assembly in this genus. Assemblages containing two to seven ecotypes commonly included a seemingly random combination of benthivore, planktivore and/or piscivore ecotypes (Figure 2b). Generalist invertivore and omnivore ecotypes also occurred in assemblages with varying numbers of ecotypes but were observed less frequently. In two-ecotype *Salvelinus* lakes, the frequency distributions of populations of different ecotypes showed no ecotype-for-ecotype matching (diet: $\chi^2/df = 0.90$, $p = 0.11$; Figure 2b; habitat: $\chi^2/df = 1.11$, $p = 0.79$; Figure 3b). Only three-ecotype lakes exhibited detectable diet ecotype matching (Figure 2b), but even here assemblages tended to contain either benthivore, planktivore, and piscivore ecotypes or benthivore, piscivore and omnivore ecotypes. The number of ecotypes of each diet category was overly similar ($\chi^2/df = 0.69$, $p = 0.010$; Figure 2b) but the same was not true of habitat categories ($\chi^2 = 1.11$, $p = 0.68$; Figure 3b). Across *Salvelinus* lakes with two to seven cooccurring ecotypes, no ecotype-for-ecotype matching was detected for habitat ($\chi^2 = 1.12$, $p = 0.82$; Figure 3b) or diet categories ($\chi^2 = 0.91$, $p = 0.13$; Figure 2b).

In *Coregonus*, niche categories were positively associated across lakes. Ecotypes in some diet and habitat categories were more likely to cooccur in the same assemblages than expected by chance (diet: V [95% CI] = 17.06 [2.99–14.39], $p = 0.050$; Figure S4; habitat: V [95% CI] = 20.30 [9.25–18.20], $p = 0.005$; Figure S5). Planktivore, benthivore and generalist invertivore ecotypes tended to cooccur, as did pelagic, littoral/benthic and profundal ecotypes. Conversely, for *Salvelinus*, ecotypes within an assemblage showed no evidence for associations across lakes, suggesting a random distribution of ecological category occupation across assemblages when defined by diet (V [95% CI] = 7.92 [2.73–10.93], $p = 0.458$; Figure S4) or habitat (V [95% CI] = 5.44 [2.08–8.86], $p = 0.830$; Figure S5).

Coregonus ecotypes exhibited a pattern of nestedness in diet categories, with the categories occupied in lakes with few ecotypes tending to form a subset of those with more categories occupied (NODF [95%] = 34.74 [34.63], $p = 0.027$; Figure S4). This was a consequence of the same pattern that led to ecotype-for-ecotype matching, where lakes with two ecotypes contained benthivore and
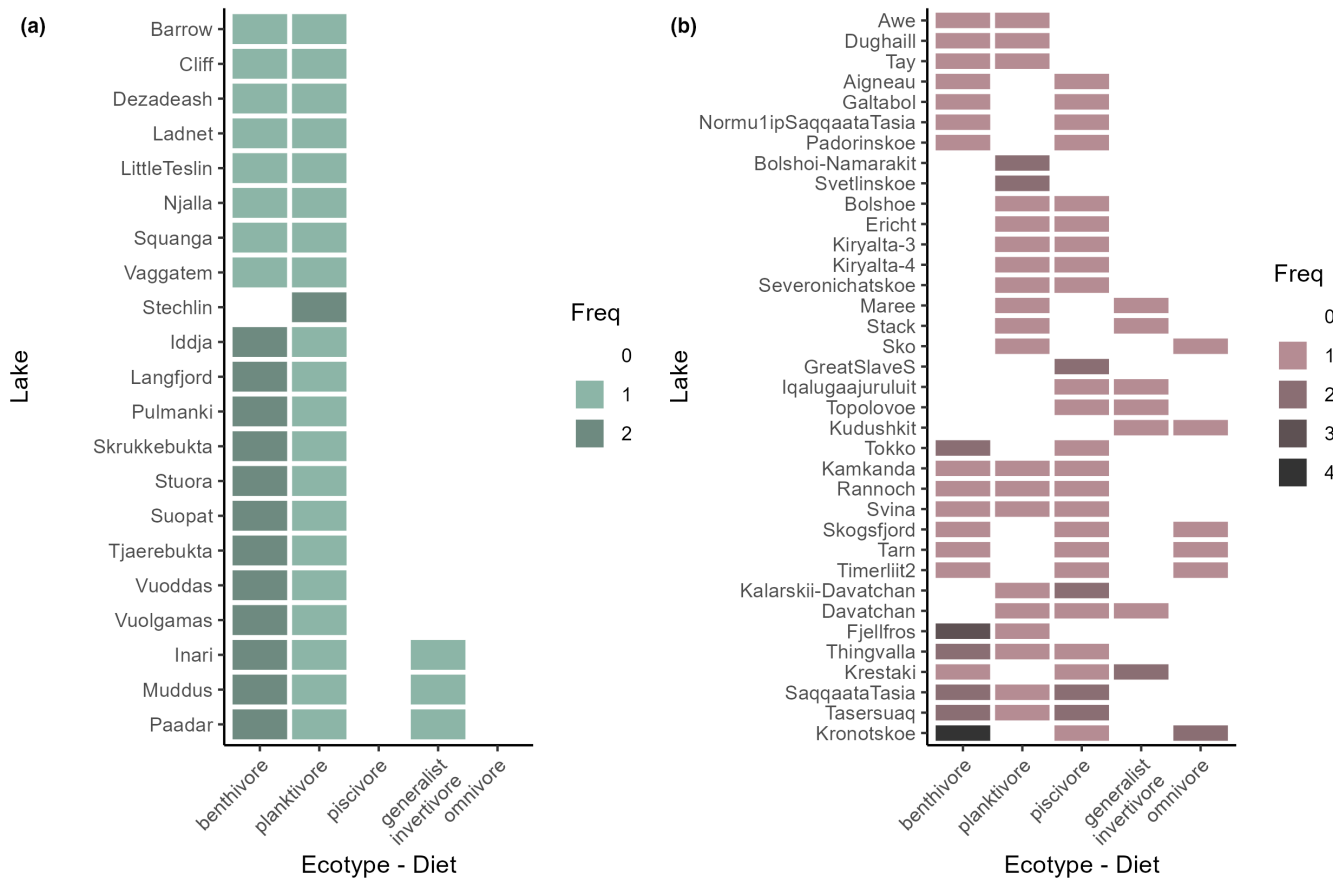
FIGURE 2 Numbers of sympatric populations grouped by diet ecotypes in lakes. Each row represents one lake, with the colour of the tiles in each row indicating the number of populations in a diet category found within a lake. (a) *Salvelinus* ecotypes and (b) *Coregonus* ecotypes.

planktivore ecotypes and lakes with a third ecotype additionally contained a generalist invertivore. However, with ecotypes defined by habitat, *Coregonus* assemblages did not exhibit a pattern of nestedness (NODF [95%]=47.15 [48.05], p=0.111; Figure S5). While littoral/benthic and pelagic ecotypes are commonly present when two categories are filled, and a profundal ecotype is often added when a third category is filled, the presence of generalist and shallow-water ecotypes in lakes with few ecotypes disrupts a pattern of nestedness. The variability in *Salvelinus* assemblages in ecotype assemblages led to an absence of nestedness when ecotypes were defined by diet (NODF [95%]=39.33 [41.53], p=0.205; Figure S4) and by habitat (NODF [95%]=22.82 [27.63], p=0.576; Figure S5).

3.2 | Repeatability of trait values across lakes

Overall, there was no support for ecotype-for-ecotype matching in continuous traits for either *Coregonus* or *Salvelinus* assemblages, reflecting the diversity in trait values among lakes and lineages. Frequency distributions of gill raker counts were divergent across lakes rather than overly similar for both *Coregonus* (AD=56.47, p<0.001; Figure 4) and *Salvelinus* (AD=13.15, p<0.001; Figure 4). Similarly, distributions of total lengths were divergent and not similar across

lakes for *Coregonus* (AD=24.5, p<0.001; Figure 4) and *Salvelinus* (AD=47.0, p<0.001; Figure 4). Distributions of total lengths of pelagic, littoral/benthic, and profundal ecotypes were also not similar for both *Coregonus* (AD=17.8, p=0.021) and *Salvelinus* (AD=9.5, p=0.073). In *Coregonus*, total length distributions of planktivore and benthivore ecotypes were divergent (AD=14.22, p=0.006), but distributions of planktivore, benthivore and piscivore ecotypes were neither divergent among assemblages nor more similar than expected by chance in *Salvelinus* (AD=14.65, p=0.707).

3.3 | Trait mean differences among ecotypes

Despite the lack of repeatability in trait means, both *Salvelinus* and *Coregonus* exhibited some evidence for among-lake similarity in the relationships between trait values and ecotypes. This suggests that there is an association between the ecotypes present in a lake and their trait values and that ecotypes with similar differences have evolved or assembled repeatedly. The index of similarity in trait–ecotype association, S, can range from 0 to 1, with values close to 1 indicating high similarity among lakes. High similarity occurs when ecotypes differ markedly in mean trait values, yet these trait differences are parallel between lakes. In *Coregonus*, the level of similarity
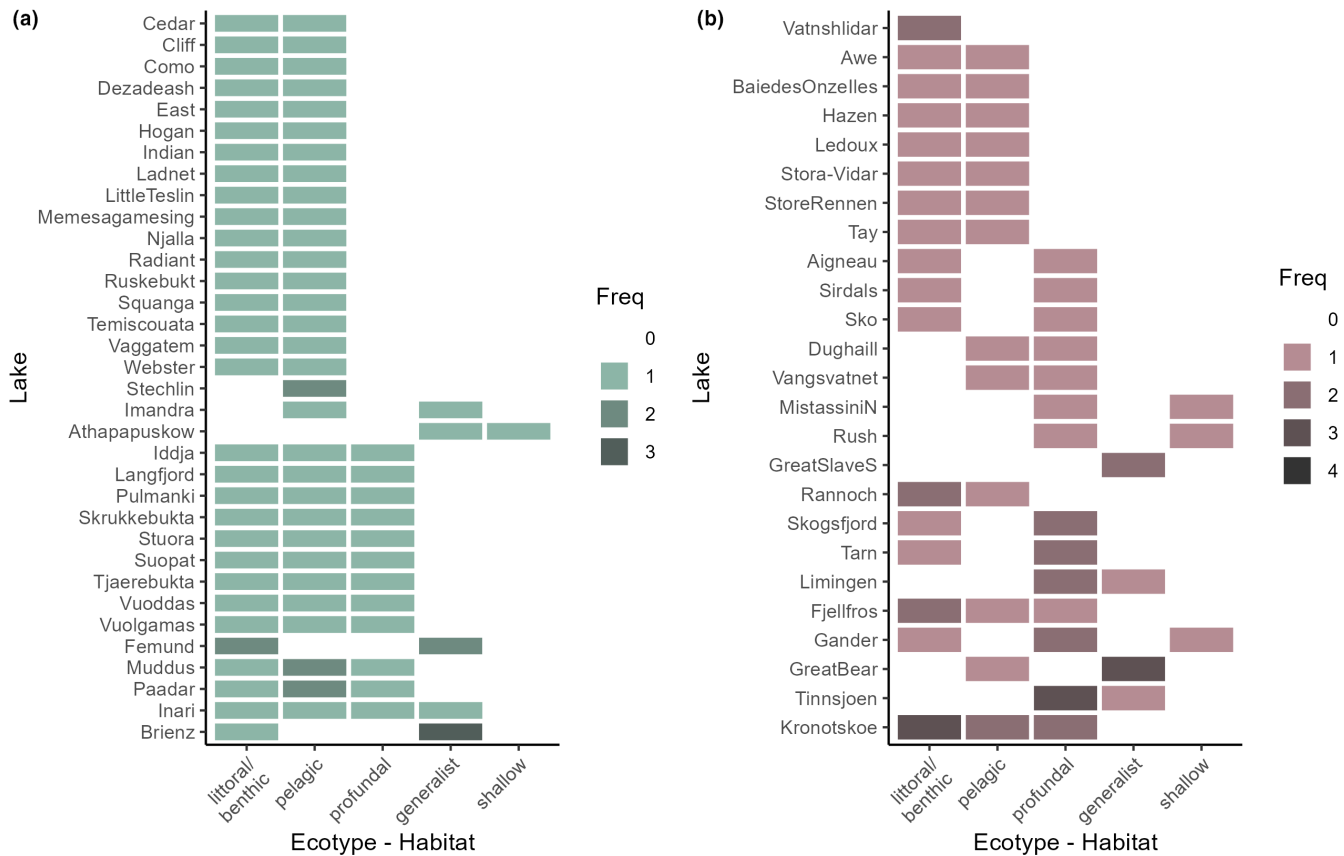
FIGURE 3 Numbers of sympatric populations grouped by habitat ecotypes across lakes. Each row represents one lake, with the colour of the tiles in each row indicating the number of populations in a habitat category found within a lake. (a) *Salvelinus* ecotypes and (b) *Coregonus* ecotypes.

was trait dependent. For gill raker counts in *Coregonus*, similarity among lakes in trait–ecotype association was relatively high (diet: S=0.885; habitat: S=0.923; Figure 4; Figure S6). Benthivore ecotypes consistently tended to have fewer gill rakers than planktivore ecotypes. Pelagic ecotypes tended to have more gill rakers than either littoral/benthic or profundal ecotypes. In contrast, similarity was low for body length (diet: S=0.482; habitat: S=0.561; Figure 5; Figure S6). Similarity among lakes for stable isotopes depended on whether δ^{13}C or δ^{15}N was measured. Similarity was high for δ^{13}C (diet: S=0.909; habitat: S=0.905; Figure S6), with littoral/benthic ecotypes tending to have higher values than pelagic or profundal ecotypes and benthivores tending to have higher values than planktivores. Similarity was moderate to low for δ^{15}N (diet: S=0.162; habitat: S=0.679; Figure S6).

In *Salvelinus*, similarity among lakes depended on which trait was measured and whether ecotypes were classified by habitat or diet. For body length, similarity among lakes was high with ecotypes categorized by diet (S=0.861; Figure 5). Across all lakes, piscivores consistently had longer bodies than sympatric planktivore or benthivore ecotypes. Similarity for body length was moderate with ecotypes categorized by habitat (S=0.540; Figure 5; Figure S7). There was a moderate-to-low level of similarity for δ^{13}C (diet: S=0.710; habitat: S=0.435; Figure S7) but high similarity for δ^{15}N (diet: S=0.970; habitat: S=0.916; Figure S7). Profundal ecotypes tended to have higher

δ^{15}N values than pelagic or littoral/benthic ecotypes that cooccur within the same lakes, while piscivore ecotypes tended to have higher δ^{15}N values than cooccurring planktivore or benthivore ecotypes. For fish age, there was high similarity with ecotypes defined by diet (S=0.907; Figure S7), with piscivores having higher ages than planktivore or benthivore ecotypes, but low similarity with ecotypes defined by habitat (S=0.039; Figure S7).

3.4 | Trait variance differences among ecotypes

Across both *Coregonus* and *Salvelinus*, there was little evidence for repeatability of relationships between within-ecotype trait variation and niche category, indicating that greater trait variability is not associated with particular niche categories across lakes. Similarity among lakes in niche category by within-ecotype variation relationships was generally low in *Coregonus*. There was low similarity for gill raker counts (diet: S=0.012; habitat: S=0.339; Figure S8) and moderate-to-low similarity for total body length (diet: S=0.259; habitat: S=0.448; Figure S8). Similarity was also moderate to low for both δ^{13}C values (diet: S=0.165; habitat: S=0.425; Figure S8) and δ^{15}N values (diet: S=0.530; habitat: S=0.182; Figure S8).

In *Salvelinus*, there was also little evidence for similarity in patterns of within-ecotype trait variation. Similarity was low for both
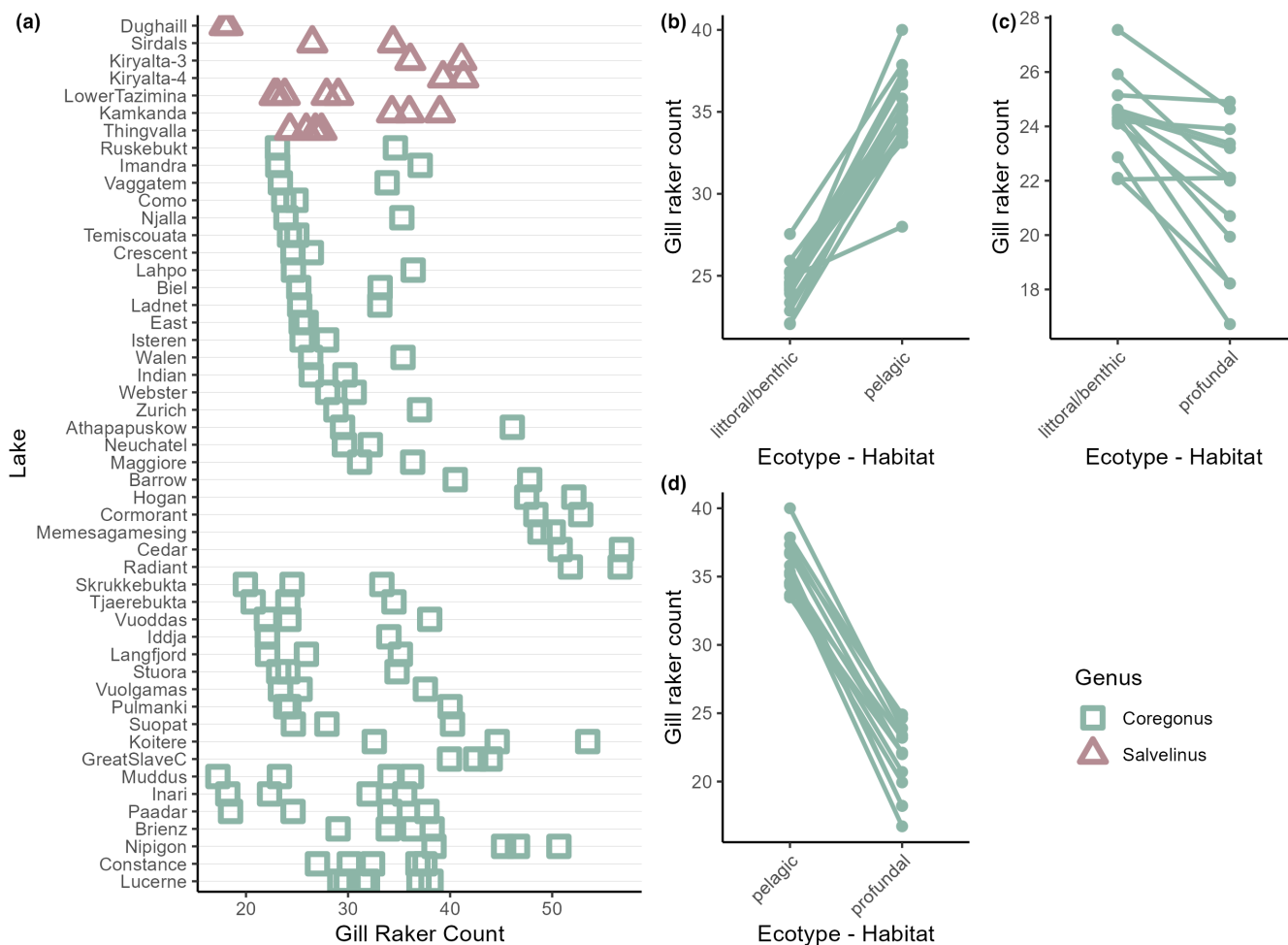
FIGURE 4 (a) Gill raker count distributions in assemblages. Each dot represents the mean gill raker count for a population, with colour and shape indicating genus. (b–d) Differences in gill raker counts between paired habitat ecotypes. Each point represents the mean of all populations in a lake from a diet or habitat category and lines connect ecotypes from the same lake. All populations are *Coregonus* because there was an insufficient sample size for comparisons in *Salvelinus*.

total body length (diet: S=0.146; habitat: S=0.360; Figure S9) and age (diet: S=0.215; habitat: S=0.312; Figure S9). There was moderate similarity for δ^{13}C values with ecotypes defined by habitat (S=0.627; Figure S9) but low similarity with ecotypes defined by diet (D=0.195; Figure S9). For δ^{15}N values, there was low similarity with ecotypes defined by both diet (D=0.050; Figure S9) and habitat (D=0.358; Figure S9). Overall, both *Salvelinus* and *Coregonus* showed a lack of among-lake similarity in niche categories by within-ecotype variation relationships.

4 | DISCUSSION

Although high repeatability among species pairs in postglacial lakes has been well-characterized (Schluter, 2000), our meta-analysis is the first to empirically assess whether repeatability can be extended to assemblages with greater numbers of ecotypes. Postglacial lakes are known to be hot spots for ecological diversity of recently diverged lineages (Robinson & Parsons, 2002), but *Coregonus* and

Salvelinus are exceptional in their ecotypic diversity (Elmer, 2016). Repeatability across multi-ecotype assemblages was evident within *Coregonus*, suggesting that repeatability does not break down with the addition of a third or fourth ecotype in postglacial lakes. However, in *Salvelinus*, neither two-ecotype nor multi-ecotype assemblages exhibited clear patterns of repeatability. The main pattern of repeatability in two-ecotype *Coregonus* assemblages was consistent with the benthic/littoral–pelagic assemblage of other postglacial lacustrine fishes (Schluter & McPhail, 1993). In both genera, littoral/benthic, pelagic and profundal were all commonly filled habitat categories, which lends support to the idea that the profundal niche represents a third axis for divergence and coexistence that is repeated on a broad geographical scale (Præbel et al., 2013). This repeatability likely results from similarity across lakes in potential niches, but it also requires that colonizing *Coregonus* lineages contain the phenotypic variation to access those niches.

The nested pattern of diet category occupation in *Coregonus* suggests that ecotype assembly is ordered spatially, with some ecotypes occurring only when others are also present. When a
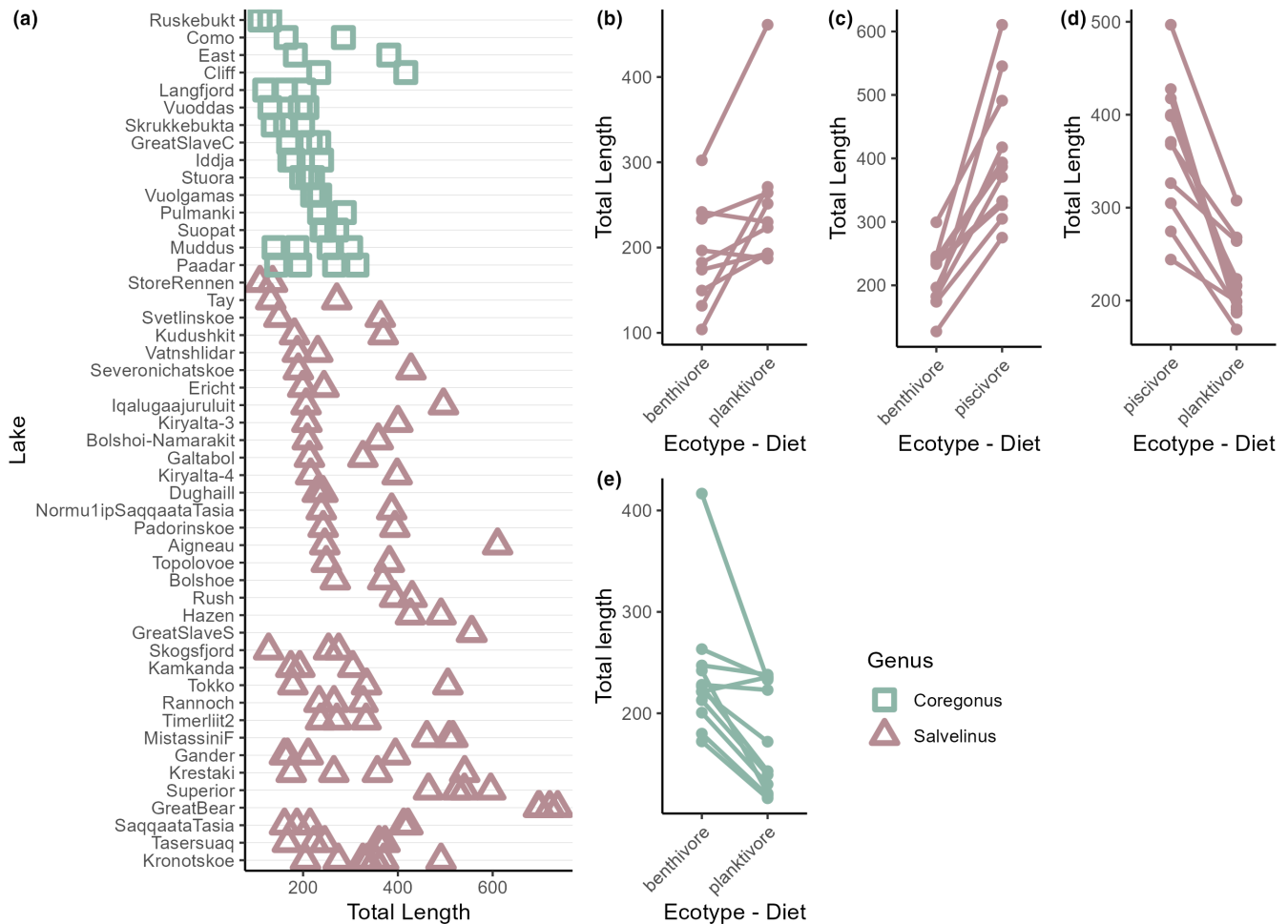
FIGURE 5 (a) Body length distributions in assemblages. Each dot represents the mean total body length of a population, with colour and shape indicating genus. (b–e) Differences in body lengths between paired habitat or diet ecotypes, for (b–d) *Salvelinus* and (e) *Coregonus*. Each point represents the mean of all populations in a lake from a diet or habitat category and lines connect ecotypes from the same lake.

benthivore and a planktivore coexist, it appears that a second benthivore ecotype may be the most likely to invade or evolve and a generalist invertivore is the most likely to be the fourth ecotype. This contrasts with the non-nested pattern in *Salvelinus*, where each possible ecotype occurs in two-ecotype assemblages, and piscivore ecotypes co-occurred with planktivore and benthivore ecotypes at similar frequencies. Nestedness in these assemblages indicates that the processes driving divergent adaptation and coexistence among ecotypes are, to some extent, deterministic and able to produce similar ecological outcomes even when local climates and species communities vary substantially (Losos et al., 1998; Mahler et al., 2013). Comparative studies in *Coregonus* have suggested that interspecific predation on *Coregonus* may make it possible for ecotypes to evolve and persist by creating a trade-off between alternate habitat-specific life-history strategies (Öhlund et al., 2020), while others have implicated competition by linking divergence to restricted habitat and prey availability (Landry et al., 2007). Presence/absence of specific ecotypes may also be nested among lakes if there are abiotic features that tend to provide the necessary ecological opportunity for the assembly and evolution of a particular set and number of

ecotypes (Losos & Schluter, 2000; Wagner et al., 2014). Biotic communities may act in a similar way through priority effects (Fukami et al., 2007; Grainger et al., 2019; Lindsey, 1981). For example, competitor species may prevent an ecotype from establishing in a lake while prey community structure may facilitate evolution of a set of ecotypes (Fukami, 2015).

The different results for *Coregonus* and *Salvelinus* indicate that repeatability is likely to be taxon specific and the reasons in this case are unclear. It is possible that higher repeatability in *Coregonus* than in *Salvelinus* is a consequence of greater developmental or physiological constraint, as evidenced by the greater phenotypic and ecological variability in *Salvelinus* than *Coregonus* (Chavarie, Adams, et al., 2021; Klemetsen, 2013). In contrast to *Coregonus* ecotypes, which consistently consume zooplankton and/or benthic invertebrates, we found that ecotypes in *Salvelinus* are commonly also piscivorous and omnivorous. However, a recently expanded *Coregonus* population in Lake Michigan was found to consume predominantly invasive fish species, suggesting that constraints on *Coregonus* ecotypes may shift with changing environments (Breaker et al., 2020). The context-dependent use of multiple food sources or habitats

("habitat coupling"), as in omnivorous or habitat generalist ecotypes, tends to be associated with higher trophic levels in aquatic ecosystems and is relatively common in *Salvelinus* (Amundsen, 1995; Cavalli et al., 1997; Dolson et al., 2009; McMeans et al., 2016). This greater ecological flexibility could allow *Salvelinus* ecotypes to exploit the best available resources, resulting in the evolution of different ecotypes in variable ecological contexts, rather than being constrained to a limited number of divergence axes. Furthermore, cannibalism is common in *Salvelinus* and may make it possible for ecotypes to coexist. Cannibalism of small, planktivorous fish reduces competition for zooplankton, thereby making the availability and profitability of pelagic and littoral/benthic resources comparable and allowing coexistence of pelagic and littoral/benthic ecotypes (Andersson et al., 2007). If cannibalism and resource competition are alternative possible ecological interactions driving ecotype evolution and coexistence in *Salvelinus*, this could generate variability among lakes. Alternatively, biogeography could play a role, as *Salvelinus* ecotypes could experience less consistency between lakes in ecological filtering and selective landscapes. Repeatability is most likely to be seen where resource distributions are similar between lakes, and this may be truer for lakes inhabited by *Coregonus* than by *Salvelinus*, although we have no evidence of this. The two genera only occasionally exhibit ecotype diversity in the same lakes, with only two lakes from our dataset containing two or more ecotypes from both *Coregonus* and *Salvelinus*. Thus, environmental and/or intrinsic differences have led to lower repeatability in ecotype assembly in *Salvelinus* than in *Coregonus*, but we are unable to say which.

Even when lakes contained sets of ecotypes with repeatable niche occupations, they were not matched in their distribution of trait means, indicating that communities of ecotypes can be similar ecologically even if their specific traits differ. Limited repeatability in mean trait distributions across *Salvelinus* and *Coregonus* is unsurprising, given the large spatial and taxonomic scale of sympatric ecotypes in the genera. Even if a broad ecological gradient is repeated across lakes, the productivity, water chemistry and prey community composition may vary substantially (Hayden et al., 2019), with potential effects on which ecotypes can invade or evolve. Additionally, the genetic variation and propensity for phenotypic plasticity present in founding populations will affect which trait means are able to evolve in an assemblage (Ghalambor et al., 2007; Landry et al., 2007).

Although distributions of trait means exhibited low repeatability, differences between sympatric ecotypes in their trait means exhibited high similarity across lakes in both genera. Patterns aligned with prior expectations (Schluter & McPhail, 1993), such as higher gill raker numbers in planktivore than benthivore ecotypes in *Coregonus* and larger body sizes in piscivore ecotypes than others in *Salvelinus*. For *Coregonus*, repeatability of trait-by-ecotype relationships emerged when ecotypes were defined by either habitat or diet. However, for *Salvelinus*, there was greater similarity with ecotypes defined by diet. This may result because unlike in *Coregonus*, *Salvelinus* ecotypes that occupy similar habitats can have different diets. For example, pelagic *Salvelinus alpinus* ecotypes may be either planktivorous or piscivorous (Snorrason et al., 1994). Several

traits not included in our study, including fin shape, jaw morphology and body proportions, have been associated with each habitat and diet in each *Coregonus* and *Salvelinus* (McPhee et al., 2012; Smith & Skúlason, 1996; Taylor, 1999). Therefore, it is possible that a more extensive suite of traits may characterize among-ecotype niche differences in these genera, similar to what has been observed in other systems with repeatable ecotype assemblages.

Differences between ecotypes in intrapopulation trait variation were not repeatable across assemblages in either *Salvelinus* or *Coregonus*. Populations of some ecotypes were not consistently more or less variable phenotypically than others. There can be high variability among individuals within an ecotype (Chavarie, Howland, et al., 2021; Skúlason et al., 2019). Repeatable differences in trait variation would have been expected to emerge if certain ecotypes consistently accessed a broader range of resources than others (Svanbäck & Schluter, 2012) or were consistently more sexually dimorphic. Perhaps, morphological variation does not correspond to niche width in these assemblages. Additionally, lakes might vary in the range of resources available in different habitats, dissociating niche breadth from ecotype when compared across assemblages.

Salmonids in postglacial lakes are a valuable model system for investigating community assembly of ecotypes at an early stage of diversification. We provided empirical evidence for an intermediate degree of repeatability across *Coregonus* and *Salvelinus*. In these genera, repeatability of ecotype community structure did not break down with increasing diversity but was instead dependent on other, lineage-specific factors. To better understand what drives repeatability or its absence in *Coregonus* and *Salvelinus* inhabiting postglacial lakes, future studies will be needed to investigate associations between repeatability and among-assemblage variability in ecological context as well as genetic differentiation and reproductive isolation (Hendry, 2009; Parsons et al., 2011). Furthermore, it remains unclear whether ecotypes evolve in situ or if patterns of co-occurrence result from ecological filtering of previously evolved ecotypes.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data have been deposited in Dryad and are accessible at https://doi.org/10.5061/dryad.kd51c5bcb. Scripts used for plotting and analysis are publicly available at https://github.com/stephblain/salmonids_repeatability.

ORCID

Stephanie A. Blain https://orcid.org/0000-0002-4977-191X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.