

# Which ecological factors influence the level of intraspecific diversity within post-glacial fishes? A case study using *Coregonus* and *Salvelinus*

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## Abstract

1. While it is likely that ecological context is important, the factors that facilitate and maintain variable levels of intraspecific diversity in Salmonidae fishes across environments remain unclear.
2. Using a meta-analysis of sympatric ecotype assemblages from two salmonid genera—*Salvelinus* and *Coregonus*—we evaluated the importance of ecological factors determining the number of sympatric ecotypes (i.e. 2–7) and the level of trait divergence between them.
3. We found that ecotype diversity increased with lake depth and surface area in both *Coregonus* and *Salvelinus*. Further, diversity in *Coregonus* increased with latitude, while the number of ecotypes in *Salvelinus* assemblages was linked to climatic seasonality.
4. In comparing the two genera, we found elevated divergence in traits related to ontogeny (i.e. age and body shape) in *Salvelinus* and gill raker count in *Coregonus*. Trait divergence in life history traits (i.e. age and body length) in *Salvelinus* increased with seasonality, whereas contrasting relationships of latitude to body length and gill rakers were found in *Coregonus*. We also found similar levels of divergence in trait variance in the two genera, suggesting that among-ecotype differences in phenotypic variability are not more common in one genus than the other.
5. Overall, ecosystem characteristics, including lake location, climate and morphology, are clearly important for where these genera have diversified, but the variables that are most closely associated with intraspecific diversity differ between the two genera studied and depend on whether diversity is quantified using number of ecotypes or trait divergence.

## KEYWORDS

ecosystem, ecotype, lake, meta-analysis, Salmonidae

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## 1 | INTRODUCTION

Ecologically and phenotypically distinct ecotypes can coexist in sympatry, even at very early stages of evolutionary divergence (Schluter, 2000; Skúlason & Smith, 1995). Two or more ecotypes are usually only able to coexist if they occupy distinct ecological niches (Germain et al., 2018). Therefore, irrespective of whether ecotypes diverged in sympatry or came into secondary contact after a short period of evolution in allopatry, ecosystem characteristics are likely to be critical for where sympatric ecotype diversity can or cannot persist (Seehausen & Wagner, 2014; Skúlason & Smith, 1995). The distribution of ecotype diversity is geographically uneven, suggesting that ecotype coexistence may be possible in some environments but not others (Wagner et al., 2014). While it is likely that ecosystem characteristics are important, the specific factors that determine the level of intraspecific diversity that can arise and be maintained in one environment compared to another remain unclear.

Several explanations have been put forward to elucidate why ecological diversity evolves in some places and some lineages but not in others. Species depauperate environments and available sources of food or predator-free space are thought to facilitate in situ diversification and colonization of diverging forms of the same species, particularly in lineages with trait plasticity or sufficient standing genetic and morphological variation to exploit them (Stroud & Losos, 2016; Yoder et al., 2010). Abiotic ecosystem characteristics, such as latitude and climate, can have strong and sometimes opposing effects on rates of diversification and levels of sympatric diversity (Rabosky et al., 2018). In environments with distinct boundaries, such as lakes or islands, the size of the environment can impact both the number of intraspecific sympatric lineages and the distribution of traits within those lineages (Koene et al., 2020; Losos & Schluter, 2000; Recknagel et al., 2017; Wagner et al., 2014). Ecological diversity can be quantified in multiple ways, including the number of diverging ecotypes, divergence in trait mean values and divergence in trait variability (Violle et al., 2012). To fully understand how ecosystem characteristics shape processes of diversification and community assembly, the role of these ecological factors in facilitating different forms of diversity at early stages of divergence needs to be evaluated.

Post-glacial lakes are hotspots for recent divergent evolution and assembly of ecotypes, resulting in co-existence of ecotypes that have not fully speciated. Sympatric ecotypes in post-glacial lakes have repeatedly evolved in several families of fish, most commonly occurring as a pair of ecotypes in which one ecotype occupies a littoral (benthic) habitat and the other occupies a pelagic (limnetic) habitat (Robinson & Parsons, 2002; Schluter & McPhail, 1993). Two salmonid genera with a circumboreal distribution—*Salvelinus* and *Coregonus*—exhibit an unusual level of ecotype diversity, as they commonly occur in assemblages of up to seven sympatric ecotypes (Smith & Skúlason, 1996). These multi-ecotype assemblages are broadly distributed, occupying lakes that span temperate deciduous, boreal, subarctic and arctic biomes (Bernatchez et al., 2010; Jacobs et al., 2020; Siwertsson et al., 2010). These genera exhibit exceptional ecological and phenotypic diversity, both within and among

lakes (Chavarie, Adams, et al., 2021; Klemetsen, 2013; McPhee et al., 2012). Sympatric ecotypes in *Salvelinus* and *Coregonus* additionally vary in the mechanisms underlying ecological divergence, with trait differences arising from phenotypic plasticity in some cases, and genetic differentiation maintained by reproductive isolation in others. Therefore, they also differ in their degree of reproductive isolation (Hendry, 2009). Despite the variability in mechanisms of differentiation among ecotypes, sympatric ecotype diversity has evolved and assembled numerous times since the formation of the post-glacial lakes in which they occur (Hudson et al., 2011; Jacobs et al., 2020; Turgeon & Bernatchez, 2003). Although there are broad similarities between these genera, the traits and ecological drivers involved in ecotype divergence may differ between them.

We used the repeated evolution and assembly of varying levels of diversity in *Salvelinus* and *Coregonus* to assess what ecological factors are related to the number of sympatric ecotypes and the level of trait divergence between them. Specifically, we used a meta-analysis of morphological, life history and diet data from *Salvelinus* and *Coregonus* assemblages with a circumboreal distribution. First, we assessed whether abiotic features of lakes, including climate, location and lake dimensions, are related to the number of ecotypes that can coexist in sympatry in each genus. Second, we asked whether the extent of trait divergence among sympatric ecotypes varies with ecological factors, including ecotype richness and lake features, or between genera. Finally, we determined whether patterns of among-ecotype divergence in trait means match patterns of among-ecotype divergence in trait variance.

## 2 | METHODS

### 2.1 | Data collection

We performed a systematic literature review to identify papers with data on wild caught fish from lakes supporting two or more coexisting ecotypes, closely related species, or taxa (hereafter referred to as 'ecotypes') forming separate ecological and morphological clusters, from the genus *Salvelinus* or *Coregonus* (see details in Blain et al., 2023; Appendix S1). Following the full-text review, we retained 127 studies with data from 131 assemblages and included these in the meta-analysis (Figure S1). We extracted usable trait data for 127 assemblages (Table S4). For 124 lakes, we had both abiotic predictor variables and a count of the number of ecotypes in the lake, along with usable trait data for 91 of these lakes.

We recorded data for diet breadth, upper jaw length, lower jaw length, pectoral fin length, head length, eye diameter, snout length, body shape principal components 1 and 2, asymptotic length, depth of capture, dorsal fin length, anal fin length, gill raker length, gill raker count, gape width, caudal fin length, pelvic fin length, body length, age,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . For each of these traits, we recorded the mean, sample size and standard error for each population. We also recorded the latitude, longitude, maximum depth and surface area of each lake. Where necessary, these physical features were extracted

from additional sources such as government databases and limnology studies. To capture lake morphometry, we estimated the depth ratio as  $50 \times \text{maximum depth} \times \frac{\sqrt{\pi}}{\sqrt{\text{surface area}}}$  (Wetzel & Likens, 2000). We extracted annual mean temperature, temperature seasonality, annual mean precipitation and precipitation seasonality from the WorldClim database using each lake's latitude and longitude (Fick & Hijmans, 2017). In WorldClim, temperature seasonality is estimated as the standard deviation of annual temperature multiplied by 100 and precipitation seasonality is the coefficient of variation for precipitation. We divided the extracted temperature seasonality values by 100, so that the estimates in our data set had a similar range to those in the precipitation data set, resulting in values that ranged from 36.7 to 177. Values for precipitation seasonality in our data set ranged from 10 to 94.

## 2.2 | Effect size estimates for differences among all ecotypes

We used standardized metrics to compare ecotypes' phenotypic differentiation among lakes, as there is variation in the specific methodology with which different researchers measure traits, such as body length and gill raker counts. We calculated three effect size estimates for trait differences among ecotypes in each lake: (1) adjacent standardized mean difference (SMD; Borenstein et al., 2009), (2) outer SMD and (3) log-transformed ratio of coefficients of variation (InCVR; Senior et al., 2020). Adjacent SMD was estimated as the difference between adjacent ecotypes from the same lake, in which each ecotype was compared with the ecotype closest in value (Figure 1). To capture the full range of trait variation within each lake, outer SMD was estimated as the difference between ecotypes in the same lake with the smallest and largest values for a trait (Figure 1). InCVR was calculated as the ratio between the coefficients of variation of the two sympatric ecotypes with the smallest and largest trait values, to determine the differences in trait variance associated with the most phenotypically distinct ecotypes in a system. InCVR was used to estimate the difference between ecotypes in within-ecotype variation (O'Dea et al., 2019), while adjacent SMD and outer SMD are measures of the differences between ecotypes in trait mean values. All analyses were performed in R version 4.0.5 (R Core Team, 2021).

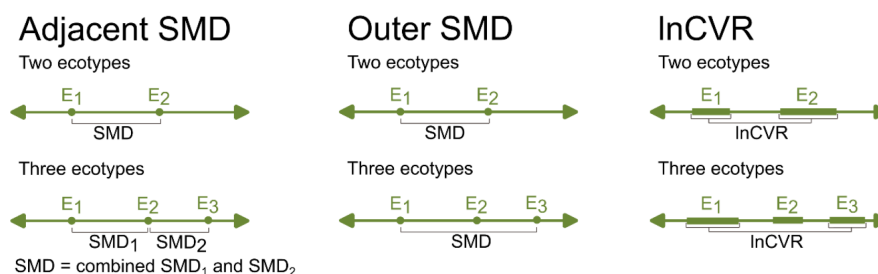
To calculate adjacent SMD's we ordered ecotypes from a lake by mean trait value, then calculated the SMD for each ecotype compared to the ones with adjacent lower and higher values. In a group with three ecotypes, for example, there would be two initial comparisons (small to medium and medium to large), from which we calculated a meta-analytic mean to estimate the adjacent SMD. For each initial comparison, an SMD was calculated using *escalc()* from the metafor R package (Viechtbauer, 2010). To allow for downstream comparisons among adjacent SMD's, we additionally used the standard error and sample size for each mean trait value to calculate the variance associated with the SMD using the *escalc()* for adjacent SMD's from two-ecotype lakes (Viechtbauer, 2010). For lakes with three or more ecotypes, the measures for some ecotypes were used in multiple pairwise comparisons. Therefore, we first calculated a variance/covariance matrix of pairwise comparisons in each lake (Gleser & Olkin, 2009, equations 19.18 and 19.19) as well as a meta-analytic mean estimate of the adjacent SMD and associated variance (Gleser & Olkin, 2009, equation 19.21).

Outer SMD's were calculated as the SMD between ecotypes with the smallest and largest trait values within a lake that were reported in a particular paper. Both SMD and the associated variance were calculated using *escalc()* (Viechtbauer, 2010). InCVR was estimated by taking the log-transformed ratio of the coefficients of variation for the largest and smallest ecotypes in a lake. We calculated both an effect size estimate (Senior et al., 2020, equation 6) and associated variance (Senior et al., 2020, equation 16) for InCVR.

In cases where multiple studies have been performed on ecotypes from a lake, there were multiple estimates of each adjacent SMD, outer SMD and InCVR for that lake. In these cases, we performed a fixed-effects meta-analysis using *rma()* to generate one estimate per effect size for each lake (Viechtbauer, 2010).

## 2.3 | Ecological lake features

Several of the physical and ecological features of lakes that we extracted exhibited high correlations (Figure S2). To account for this when fitting traits together in a model, we first ran a principal components analysis (PCA) with eight lake features: (1) lake latitude, (2) log-transformed lake surface area, (3) log-transformed maximum



**FIGURE 1** Estimation of effect sizes. Adjacent SMD was calculated by combining the SMD estimates between ecotypes and the one immediately larger or smaller than it within an assemblage. Outer SMD and InCVR were both estimated between the ecotypes with the largest and smallest trait values within each assemblage, with outer SMD comparing ecotype trait means and InCVR comparing ecotype trait variances. SMD, standardized mean difference.

lake depth, (4) log-transformed lake depth ratio ( $Z_r$ ), (5) mean annual precipitation, (6) seasonality of annual precipitation, (8) mean annual temperature and (8) seasonality of annual temperature. We used a correlation matrix for the PCA because variables were on different scales. We retained the first four principal components, which cumulatively explained 92% of the variance. PC1 was associated with climate variables, with higher PC1 values indicating higher mean annual temperature and precipitation and lower seasonality in temperature and precipitation (Figure S3). Lake dimensions contributed most to PC2, with higher PC2 values indicating larger and deeper lakes. PC3 values decreased with depth ratio, whereas PC4 values increased with latitude.

## 2.4 | Intraspecific diversity and abiotic factors

To test whether the number of ecotypes depended on abiotic features, we used sequential ordinal regression, with three levels in our response variable (two ecotypes, three ecotypes, four or more ecotypes) and the four PC axes summarizing abiotic variation across lakes as the predictors. We fit the full model and all reduced models using *brm()* from the *brms* R package. To compare models, we estimated model weights using leave one out cross validation (LOOCV) with *loo()*, then applied model averaging via stacking with *loo\_model\_weights()*. We summed the weights of models containing each predictor variable and considered predictors with weights greater than 0.7 to have high relative importance (RI), following Wagner et al. (2014). We then re-fit the ordinal regression models including only high RI predictors to estimate effect sizes.

## 2.5 | Trait differentiation among populations

For each trait, we estimated differences in trait values among sympatric populations using separate random effects meta-analyses using the function *rma()* with restricted maximum likelihood (REML) for each of the three effect size estimates (adjacent SMD, outer SMD, and InCVR), as this approach has improved accuracy over maximum likelihood for fixed effects estimation (Luke, 2017). Adjacent SMD and outer SMD were both estimates of divergence in trait means across an assemblage, while InCVR was an estimate of divergence in trait variance. To estimate divergence for 'head lengths', we included measures for upper jaw length, lower jaw length, gape width, orbit length, head length and snout length in a multivariate random effects meta-analysis using *rma.mv()* with the trait measured and lake included as random effects. We used the same approach to estimate divergence for 'fin lengths', using lengths of pectoral, dorsal, caudal, anal and pelvic fins.

We tested the relationship between trait divergence and abiotic factors for a subset of traits that are frequently measured in each genus (i.e. body length in both genera, gill raker count in *Coregonus* and age in *Salvelinus*). For each trait, we fit a meta-analytic linear model with the four PC axes summarizing abiotic variation among

lakes as fixed effects, using maximum likelihood (ML) because likelihoods from models fit with REML would not be comparable under our AICc-based model selection approach (Luke, 2017). Using *glmulti()*, we estimated the AICc scores and weights for the full model and all reduced models (Calcagno, 2010). Following Wagner et al. (2014), we then estimated the relative importance of each effect as the sum of AICc weights of models including that effect. We then re-fitted the meta-analytic linear models with REML and included only high RI predictors to estimate effect sizes.

## 3 | RESULTS

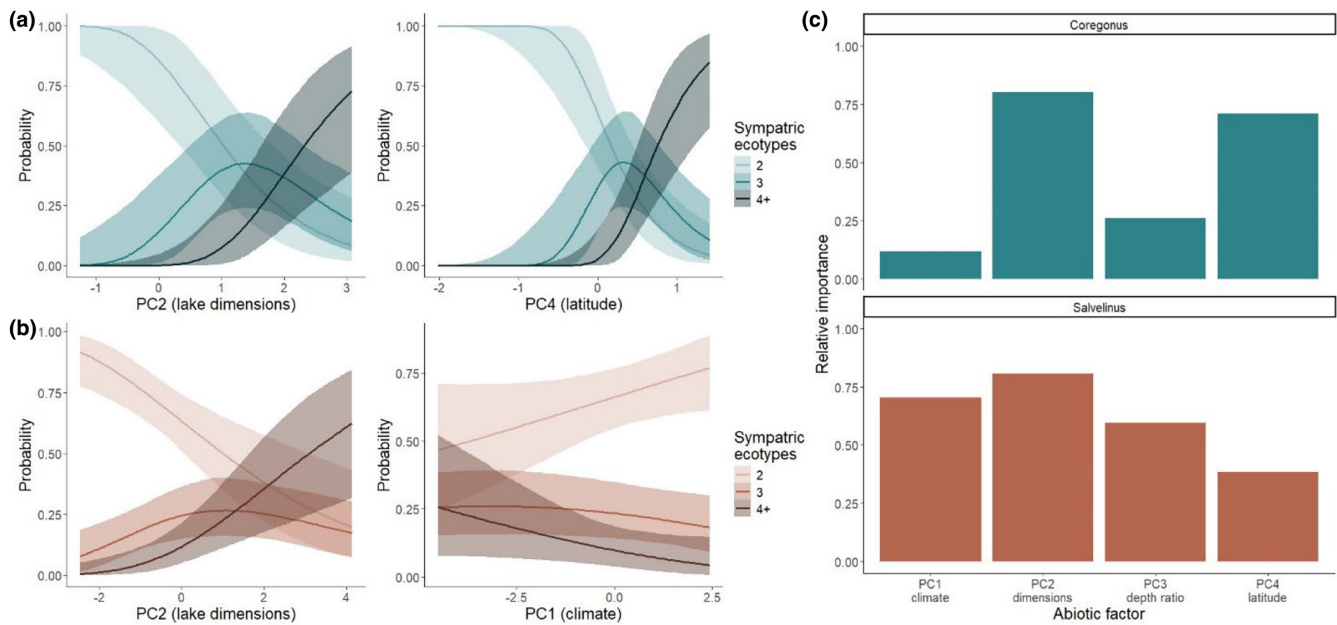
### 3.1 | Number of ecotypes and abiotic factors

In both *Coregonus* and *Salvelinus*, the number of sympatric ecotypes increased with habitat size but were differently affected by other lake features. A greater number of ecotypes in *Coregonus* assemblages increased in probability with higher values of PC2 (lake dimensions; slope=0.92, 95% CI = [0.46, 1.47]) and PC4 (latitude; slope=1.97, 95% CI = [1.00, 3.26]), whereas PC1 (climate) and PC3 (depth ratio) had low relative importance (RI) as predictors (Figure 2; Table S1). In *Salvelinus*, high ecotype diversity decreased in probability with PC1, meaning that there was a greater probability of few ecotypes in lakes with higher mean temperature and precipitation and lower seasonality (slope=-0.12, 95% CI = [-0.26, 0.01]; Figure 2). The probability of a greater number of sympatric *Salvelinus* ecotypes increased with PC2 (lake dimensions; slope=0.37, 95% CI = [0.16, 0.58]), but PC3 and PC4 had low RI as predictors (Figure 2; Table S1).

### 3.2 | Trait divergence among sympatric ecotypes

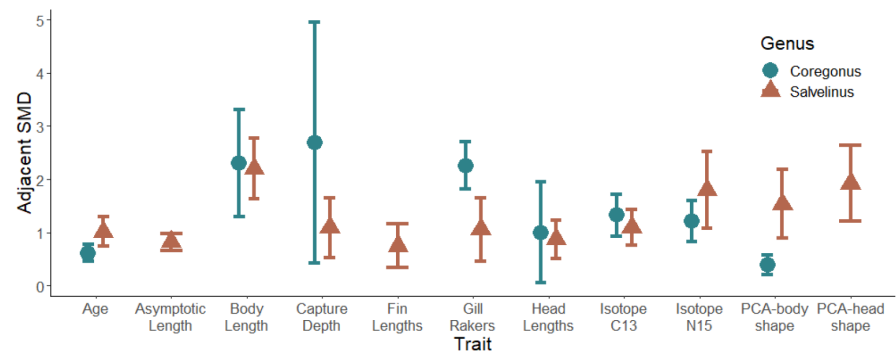
Most traits exhibited a similar extent of divergence among sympatric ecotypes in both *Coregonus* and *Salvelinus*. Mean trait divergence was similar between *Coregonus* and *Salvelinus* for most traits when quantified as adjacent SMD's (body length, capture depth,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ; Figure 3) and outer SMD's (age, body length, capture depth,  $\delta^{15}\text{N}$ ; Figure S4a). However, *Coregonus* ecotypes showed greater divergence in gill raker counts than *Salvelinus*, with higher values for both adjacent and outer SMD (adjacent SMD: 2.14x higher, outer SMD: 2.18x higher; Figure 3). Additionally, when estimated as outer SMD,  $\delta^{13}\text{C}$  exhibited more divergence in *Coregonus* than *Salvelinus* (1.93x higher; Figure S4a). On the other hand, both adjacent and outer SMD's values for overall body shape were higher in *Salvelinus* than *Coregonus* (adjacent SMD: 3.95x higher, outer SMD: 3.96x higher; Figure 2, Figure S4a), as was adjacent SMD for age (1.66x higher; Figure 3). Among-ecotype differences in trait variance (InCVR) were similar between *Coregonus* and *Salvelinus* in all traits measured (Figure S4b).

In *Coregonus*, adjacent SMD for body length and gill raker count declined with an increasing number of ecotypes per lake (Figure 4,



**FIGURE 2** The number of sympatric populations by abiotic variables. (a,b) Marginal effects of abiotic predictor variables on the number of sympatric ecotypes found in an assemblage. Each line shows how the posterior probability of observing a particular level of ecotype diversity varies with an abiotic predictor. Shaded regions around lines represent 95% confidence intervals. (c) Relative importance of abiotic factors for predicting the number of populations present in a lake. Relative importance was calculated as the sum of weights for all models that included a factor, based on leave one out cross-validation. PC1 primarily corresponds to variation in temperature and precipitation, PC2 to lake surface area and depth, PC3 to the ratio of lake depth to surface area and PC4 to latitude.

**FIGURE 3** Mean trait differences between phenotypically adjacent ecotypes. Each point represents the meta-analytic mean difference among sympatric ecotypes within a lake. Error bars indicate 95% confidence intervals. Results for outer SMD and InCVR are shown in Figure S1. SMD, standardized mean difference.



**FIGURE 4** Ecological factors and body length divergence. (a) Relationship between the number of ecotypes present in a lake and the adjacent SMD's (standardized mean differences) in body length between sympatric ecotypes. (b) Relative importance of abiotic factors in predicting adjacent SMD's in body length between sympatric ecotypes. PC1 primarily corresponds to variation in temperature and precipitation, PC2 to lake surface area and depth, PC3 to the ratio of lake depth to surface area and PC4 to latitude. Results for other traits, outer SMD and InCVR are in Appendix S1.

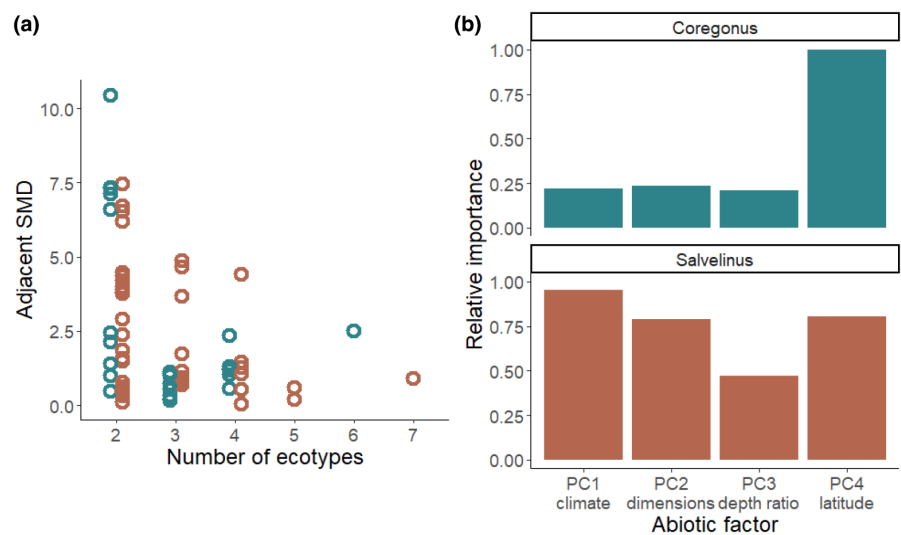


Figure S5, Table S2). Adjacent SMD for body shape PC1,  $\delta^{15}\text{N}$ , and  $\delta^{13}\text{C}$  exhibited no significant relationship to number of *Coregonus* ecotypes (Figure S5, Table S2). *Coregonus* outer SMD for gill raker count was positively related to number of ecotypes, but outer SMD was not related to number of ecotypes for body length, body shape PC1,  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  (Figure S6, Table S2). Number of ecotypes did not predict trait variance (InCVR) for any of the traits for which it was estimated in *Coregonus* (gill raker count, body length  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ; Figure S7, Table S2).

In *Salvelinus*, adjacent SMD for body length declined with number of ecotypes (Figure 4, Table S2), whereas adjacent SMD for age, asymptotic length, depth of capture,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  showed no relationship with the number of ecotypes (Figure S5, Table S2). There was no relationship in *Salvelinus* between number of ecotypes and either any of the traits quantified for outer SMD (age, asymptotic length, depth of capture,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , body shape PC1; Figure S6; Table S2) or InCVR (age, asymptotic length, depth of capture,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ; Figure S7 and Table S2).

### 3.3 | Trait divergence and abiotic factors

For *Coregonus*, PC4 (latitude) had high relative importance (RI) for body length divergence among ecotypes, with adjacent SMD, outer SMD and InCVR all decreasing at higher latitudes (adjacent SMD: slope = -2.18, 95% CI = [-2.98, -1.38]; outer SMD: slope = -1.66, 95% CI = [-2.63, -0.69]; InCVR: slope = -0.26, 95% CI = [-0.47, -0.05]; Figure 4, Figures S9 and S10). PC1, PC2 and PC3 all had low RI for adjacent SMD, outer SMD and InCVR of body length. Gill raker outer SMD increased with PC4 (latitude; slope = 1.34, 95% CI = [0.85, 1.82]), whereas PC1, PC2 and PC3 did not exhibit high RI (Figure S9). No PC axes had high RI for gill raker adjacent SMD or gill raker InCVR (Figure S8, Figure 5).

For *Salvelinus*, body length adjacent SMD declined with PC1 (climate; slope = -0.30, 95% CI = [-0.51, -0.09]), PC2 (lake dimensions; slope = -0.47, 95% CI = [-0.80, -0.14]) and PC4 (latitude; slope = -0.56, 95% CI = [-1.01, -0.11]), whereas PC3 had low RI (Figure 4, Table S3). Body length outer SMD and age outer SMD both decreased with PC1 (climate) in *Salvelinus* (body length: slope = -0.65, 95% CI = [-0.97, -0.34]; age: slope = -0.20, 95% CI = [-0.33, -0.07]), but all other PC axes had low RI for these traits (Figure S9 and Table S3). For age InCVR, PC3 (depth ratio) had high RI, with age InCVR decreasing in lakes with lower depth ratio values (slope = -0.15, 95% CI = [-0.28, -0.02]; Figure 5). For age adjacent SMD and body length InCVR, no abiotic predictor variables had high RI (Figure S8, Figure S10 and Table S3).

## 4 | DISCUSSION

We provide evidence supporting a role for lake ecosystem characteristics in determining intraspecific diversity in *Coregonus* and *Salvelinus*. Although abiotic features of lakes determined the number of ecotypes in both genera, it was lake dimensions (depth and surface area) and latitude that mattered for *Coregonus* while lake dimensions and climate variables (temperature and precipitation) were important for *Salvelinus*. A relationship of ecotype diversity to lake depth and surface area has been found previously among ecotype assemblages from a restricted geographic region and within the same species (ex. *Salvelinus alpinus*; Koene et al., 2020; Recknagel et al., 2017; Woods et al., 2012); our results show that this relationship holds on a circumboreal scale and across both genera. Both biogeographical models and empirical patterns indicate that in situ diversification should increase with habitat size in discrete systems, such as islands and lakes (Losos & Schluter, 2000; Schluter & Pennell, 2017; Valente et al., 2020;

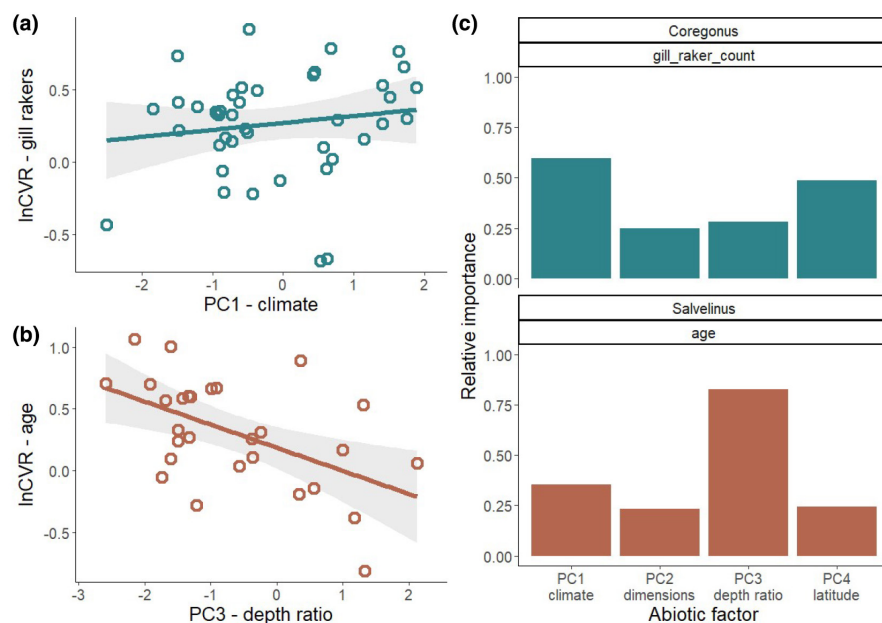


FIGURE 5 Ecological factors and divergence among sympatric ecotypes in trait variability. (a) Each point represents the InCVR in gill raker number among sympatric *Coregonus* ecotypes for one lake. (b) Each point represents the InCVR in age among sympatric *Salvelinus* ecotypes for one lake. (c) Relative importance of abiotic factors in predicting InCVR's in gill rakers (*Coregonus*) and age (*Salvelinus*) between sympatric ecotypes. PC1 primarily corresponds to variation in temperature and precipitation, PC2 to lake surface area and depth, PC3 to the ratio of lake depth to surface area and PC4 to latitude.

Wagner et al., 2014). In habitats with distinct boundaries, geographical size (surface area and depth) should be a proxy for ecological opportunity but also facilitate the evolution of reproductive isolation if larger habitats allow ecotypes to be spatially distinct during reproduction (Vonlanthen et al., 2009). The factors underlying a relationship between habitat size and diversification—opportunity for geographical isolation, availability of distinct resources, and the potential for a larger overall population size—should also enable coexistence of previously diverged ecotypes (Chesson, 2000; Losos & Ricklefs, 2009). Nonetheless, in both *Salvelinus* and *Coregonus*, multi-ecotype assemblages have evolved even in lakes that are very small, suggesting that although ecosystem size may be indicative of ecological opportunity in a lake ecosystem, these two lake traits are frequently decoupled.

The importance of lake surface area and depth for diversification and maintenance of multiple sympatric ecotypes in *Coregonus* is likely related to the presence of profundal ecotypes in the large majority of assemblages with three or more ecotypes (Blain et al., 2023; Præbel et al., 2013). Ecotype pairs in *Coregonus* may not experience the same limitations on habitat size as populations sustaining higher levels of intraspecific diversity, as they typically consist of two shallow water ecotypes—one pelagic and one littoral (Bernatchez et al., 1996; Öhlund et al., 2020; Schluter & McPhail, 1993). Thus, small and shallow lakes may lack a large enough profundal habitat for a third ecotype to evolve or establish following colonization. Habitat size may directly influence reproductive isolation, as sympatric *Coregonus* ecotypes often spawn at different depths, which has been linked to genetic divergence within multi-ecotype assemblages (Ingram et al., 2012).

Latitude emerged as an important predictor of divergence in *Coregonus*, with assemblages at higher latitudes exhibiting greater ecotype diversity, more divergence in gill rakers, and reduced divergence in body length. Patterns in ecotype diversity and gill raker divergence are likely linked, as habitat use in *Coregonus* ecotypes tends to be accompanied by diet specialization on pelagic zooplankton or benthic macroinvertebrates (Bernatchez et al., 1996; Lundsgaard-Hansen et al., 2013; Schluter & McPhail, 1993). Pelagic versus benthic resource use is reflected in  $\delta^{13}\text{C}$  isotopes and closely tied to gill raker morphology, both of which exhibited high divergence between ecotypes in this study (Figures 5 and 8; Østbye et al., 2006; Harrod et al., 2010; Siwertsson et al., 2013). Productivity and its variation across an annual cycle may drive a relationship between gill raker divergence and latitude, as pelagic zooplankton are more diverse and abundant in high productivity ecosystems and during the summer while benthic macroinvertebrates are comparatively more plentiful in low productivity ecosystems and available year-round (Hayden et al., 2019; Kahilainen et al., 2004, 2005; Sierszen et al., 2003). Perhaps higher latitude environments allow both benthic and pelagic resources to be more favourable at different times of the year (Svanbäck & Bolnick, 2007), facilitating divergence in morphology and indirectly influencing differentiation in spawning time. Whitefish species pairs exhibit greater phenotypic divergence in lakes with

greater seasonality in the community structure of benthic prey (Landry & Bernatchez, 2010). Alternatively, resource variation across the annual cycle could favour generalist tactics, and therefore, a less divergent set of sympatric phenotypes capable of exploiting resources from multiple habitats (Chavarie et al., 2016; Hayden et al., 2014). Higher temperatures are associated with shifts from food webs fueled by benthic to pelagic resources (Hayden et al., 2019), so lakes at different latitudes could vary in their source of productivity and its effect on divergence.

In contrast to trophic ecology, life history trade-offs may instead be higher at lower latitudes. Relationships among latitude, growth rates and body length are variable in Salmonids, as fish at lower latitudes might grow faster due to a longer and warmer growing season, while fish may have a counter-gradient relationship or faster annual growth rate at high latitudes (Chavarie et al., 2010; Power et al., 2005; Rypel & David, 2017). Nonetheless, it is possible that growing season constraints at higher latitudes result in fewer or more similar life history tactics within a particular lake environment, resulting in less divergence among ecotypes.

For *Salvelinus*, the number of sympatric ecotypes were best predicted by lake surface area and depth, which suggests that lake size may enhance ecological opportunity in this genus (Eloranta et al., 2015). *Salvelinus* assemblages commonly contain a combination of piscivorous, planktivorous and benthivorous ecotypes—all diets associated with distinct usage of habitat zones within a lake (Blain et al., 2023). Habitat coupling is common in *Salvelinus* and occurs when individual fish can exploit multiple habitats within a lake. Because habitat coupling can reduce specialization, this connectivity in habitat use is expected to reduce ecotype divergence (Eloranta et al., 2013; Marklund et al., 2019). Habitat coupling is most common in small lakes with a circular shape, making specialization and divergence more likely in larger lakes with reticulate coastlines (Dolson et al., 2009). Further, the number of ecotypes was higher in lakes with greater climate seasonality and lower mean temperature and precipitation, suggesting that harsher, more variable climates promote divergence in *Salvelinus*. These lakes may exhibit greater variation in resource availability, contain fewer potential competitors, and more closely match the optimal thermal environment for *Salvelinus* species—all of which have the potential to facilitate ecotype divergence.

Patterns of life history trait and body shape divergence in *Salvelinus* pointed to the importance of ontogeny in the evolution and development of *Salvelinus* ecotype diversity. *Salvelinus* ecotypes often employ alternative diet-associated life history strategies, in which fish that grow to a large size tend to be piscivorous and have a longer lifespan, while invertivores typically grow to a smaller size with a shorter lifespan (Bjorklund et al., 2003; Parsons et al., 2011). The evolution of these alternative strategies was likely driven by differing predation rates, as gape-limited predators can consume the smaller, younger invertivores but not the larger, older piscivores (Reznick et al., 1990; Smalås et al., 2013). Our results are consistent with the idea that plasticity or genetic variation in developmental trajectories is a key prerequisite for sympatric divergence in

*Salvelinus* (Parsons et al., 2011; Skúlason et al., 2019). Body lengths differ markedly among *Salvelinus* ecotypes with different life history trajectories (Alekseyev et al., 2009), and we found that divergence in this trait increased with temperature and precipitation seasonality. Annual variation in productivity, and therefore resource availability, may allow coexistence of ecotypes with alternative life history strategies. Alternatively, there may be a correlation between seasonality and another causal variable, such as reduced species richness (Jablonski et al., 2017). If seasonal environments are more species depauperate, they likely contain greater ecological opportunity (Losos, 2010), as there are likely fewer competitors of other species for both piscivorous and invertivorous *Salvelinus* ecotypes.

Phenotypic divergence was similar overall between *Salvelinus* and *Coregonus*, suggesting a degree of similarity, or similar among-lake variability, in the phenotypic effects resulting from processes driving diversification and coexistence. The consistency between genera is somewhat surprising, given prior observations that *Salvelinus* tends to be more ecologically generalist and has uniquely high phenotypic variation facilitated by exceptional levels of plasticity (Chavarie, Adams, et al., 2021; Klemetsen, 2013), and that *Coregonus* ecotypes might be more constrained in their direction of divergence (Blain et al., 2023). *Salvelinus* and *Coregonus* tend to diversify in different lakes, with only two lakes in this data set containing ecotype assemblages from both, and this geographical separation might also have been expected to lead to differences in phenotypic variability between the genera. Ecotypes can diverge in both trait means and trait variance (Chavarie, Howland, et al., 2021; Violle et al., 2012), but we found similar levels of phenotypic variability across the two genera despite more common coexistence of generalist with specialist phenotypes in *Salvelinus* (Chavarie et al., 2016). Nonetheless, *Coregonus* and *Salvelinus* exhibited a few differences in trait divergence that appear to be linked to their different patterns of resource exploitation and drivers of intraspecific diversity. *Coregonus*, which exhibited greater gill raker divergence, has a feeding ecology that is typically restricted to lower trophic level prey (i.e. zooplankton and/or benthic invertebrates), whereas *Salvelinus*, which exhibited elevated age and body shape divergence, has wider niche use as they can be piscivorous and omnivorous (Klemetsen, 2013).

In sum, we found that habitat size predicts the number of ecotypes in *Coregonus* and *Salvelinus* assemblages, while latitude and climate variables predict the level of divergence among some traits. These relationships may be critical to ecotype persistence, or lack thereof, as environments change. Ecotype diversity affects ecosystem function (Des Roches et al., 2018), and this may be especially true in high latitude and high altitude lakes that tend to be relatively species depauperate. Temperature and precipitation seasonality, which are associated with trait divergence in these genera, are expected to shift with climate. Changes in productivity may also change resources distributions across habitats in lakes of different sizes. Looking forward, it will be important to evaluate the mechanisms by which these abiotic variables facilitate the astonishing levels of intraspecific diversity expressed in *Salvelinus* and *Coregonus*.

## AUTHOR CONTRIBUTIONS

Conceptualization: SAB, CEA, PAA, RK and LC. Developing methods: SAB, CEA and LC. Data analysis, preparation of figures and tables: SAB. Conducting the research: SAB and LC. Data interpretation, writing: SAB, CEA, PAA, RK and LC.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

## DATA AVAILABILITY STATEMENT

Phenotypic traits and lake characteristic data are available on Dryad at <https://doi.org/10.5061/dryad.pg4f4qs01>. Scripts used for data analysis are available on GitHub: [https://github.com/stephblain/salmonids\\_ecological\\_factors](https://github.com/stephblain/salmonids_ecological_factors).

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## REFERENCES

- Alekseyev, S. S., Mina, M. V., Smirina, E. M., & Sokolov, A. A. (2009). Late ontogeny growth acceleration and size form transformations in Transbaikalian Arctic charr, *Salvelinus alpinus* complex: Evidence from fin ray cross section growth layers. *Environmental Biology of Fishes*, 86, 487–505.
- Bernatchez, L., Renaut, S., Whiteley, A. R., Derome, N., Jeukens, J., Landry, L., Lu, G., Nolte, A. W., Østbye, K., Rogers, S. M., & St-Cyr, J. (2010). On the origin of species: Insights from the ecological genomics of lake whitefish. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 365, 1783–1800.
- Bernatchez, L., Vuorinen, J. A., Bodaly, R. A., & Dodson, J. J. (1996). Genetic evidence for reproductive isolation and multiple origins of sympatric trophic ecotypes of whitefish (*Coregonus*). *Evolution*, 50, 624–635.
- Bjorklund, M., Hirvonen, H., Seppa, T., Peuhkuri, N., & Piironen, J. (2003). Phenotypic variation in growth trajectories in the Arctic charr *Salvelinus alpinus*. *Journal of Evolutionary Biology*, 16, 543–550.
- Blain, S. A., Schluter, D., Adams, C. E., Amundsen, P.-A., Knudsen, R., & Chavarie, L. (2023). Patterns and repeatability of multi-ecotype assemblages of sympatric salmonids. *Global Ecology and Biogeography*, 32, 2257–2270.
- Borenstein, M., Hedges, L. V., Higgins, J. P., & Rothstein, H. R. (2009). *Introduction to meta-analysis*. John Wiley & Sons, Ltd.
- Calcagno, V. (2010). Glmulti: An R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, 34, 1–29.
- Chavarie, L., Adams, C. E., Swanson, H. K., Ridgway, M. S., Tonn, W. M., & Wilson, C. C. (2021). Ecological diversity. In A. M. Muir, C. C. Krueger, M. J. Hansen, & S. C. Riley (Eds.), *The Lake Charr *Salvelinus namaycush*: Biology, ecology, distribution, and management* (pp. 69–117). Springer.



- Chavarie, L., Dempson, J. B., Schwarz, C. J., Reist, J. D., Power, G., & Power, M. (2010). Latitudinal variation in growth among Arctic charr in eastern North America: Evidence for countergradient variation? *Hydrobiologia*, 650, 161–177.
- Chavarie, L., Harford, W. J., Howland, K. L., Fitzsimons, J., Muir, A. M., Krueger, C. C., & Tonn, W. M. (2016). Multiple generalist morphs of Lake trout: Avoiding constraints on the evolution of intraspecific divergence? *Ecology and Evolution*, 6, 7727–7741.
- Chavarie, L., Howland, K. L., Harris, L. N., Gallagher, C. P., Hansen, M. J., Tonn, W. M., Muir, A. M., & Krueger, C. C. (2021). Among-individual diet variation within a lake trout ecotype: Lack of stability of niche use. *Ecology and Evolution*, 11, 1457–1475.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–358.
- Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, 2, 57–64.
- Dolson, R., McCann, K., Rooney, N., & Ridgway, M. (2009). Lake morphometry predicts the degree of habitat coupling by a mobile predator. *Oikos*, 118, 1230–1238.
- Eloranta, A. P., Kahilainen, K. K., Amundsen, P. A., Knudsen, R., Harrod, C., & Jones, R. I. (2015). Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. *Ecology and Evolution*, 5, 1664–1675.
- Eloranta, A. P., Knudsen, R., & Amundsen, P.-A. (2013). Niche segregation of coexisting Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) constrains food web coupling in subarctic lakes. *Freshwater Biology*, 58, 207–221.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.
- Germain, R. M., Williams, J. L., Schluter, D., & Angert, A. L. (2018). Moving character displacement beyond characters using contemporary coexistence theory. *Trends in Ecology & Evolution*, 33, 74–84.
- Gleser, L. J., & Olkin, I. (2009). Stochastically dependent effect sizes. In H. Cooper, L. V. Hedges, & J. C. Valentine (Eds.), *The handbook of research synthesis and meta-analysis* (pp. 357–376). Russell Sage Foundation.
- Harrod, C., Mallela, J., & Kahilainen, K. K. (2010). Phenotype-environment correlations in a putative whitefish adaptive radiation. *Journal of Animal Ecology*, 79, 1057–1068.
- Hayden, B., Harrod, C., & Kahilainen, K. K. (2014). Dual fuels: Intra-annual variation in the relative importance of benthic and pelagic resources to maintenance, growth and reproduction in a generalist salmonid fish. *Journal of Animal Ecology*, 83, 1501–1512.
- Hayden, B., Harrod, C., Thomas, S. M., Eloranta, A. P., Myllykangas, J. P., Siwertsson, A., Præbel, K., Knudsen, R., Amundsen, P. A., & Kahilainen, K. K. (2019). From clear lakes to murky waters—Tracing the functional response of high-latitude lake communities to concurrent ‘greening’ and ‘browning’. *Ecology Letters*, 22, 807–816.
- Hendry, A. P. (2009). Ecological speciation! Or the lack thereof? *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 1383–1398.
- Hudson, A. G., Vonlanthen, P., & Seehausen, O. (2011). Rapid parallel adaptive radiations from a single hybridogenetic ancestral population. *Proceedings of the Royal Society B: Biological Sciences*, 278, 58–66.
- Ingram, T., Hudson, A. G., Vonlanthen, P., & Seehausen, O. (2012). Does water depth or diet divergence predict progress towards ecological speciation in whitefish radiations? *Evolutionary Ecology Research*, 14, 487–502.
- Jablonski, D., Huang, S., Roy, K., & Valentine, J. W. (2017). Shaping the latitudinal diversity gradient: New perspectives from a synthesis of paleobiology and biogeography. *American Naturalist*, 189, 1–12.
- Jacobs, A., Carruthers, M., Yurchenko, A., Gordeeva, N. V., Alekseyev, S. S., Hooker, O., Leong, J. S., Minkley, D. R., Rondeau, E. B., Koop, B. F., Adams, C. E., & Elmer, K. R. (2020). Parallelism in eco-morphology and gene expression despite variable evolutionary and genomic backgrounds in a Holarctic fish. *PLoS Genetics*, 16, e1008658.
- Kahilainen, K., Alajärvi, E., & Lehtonen, H. (2005). Planktivory and diet overlap of densely raked whitefish (*Coregonus lavaretus* [L.]) in a subarctic lake. *Ecology of Freshwater Fish*, 14, 50–58.
- Kahilainen, K., Malinen, T., Tuomaala, A., & Lehtonen, H. (2004). Diel and seasonal habitat and food segregation of three sympatric *Coregonus lavaretus* forms in a subarctic lake. *Journal of Fish Biology*, 64, 418–434.
- Klemetsen, A. (2013). The most variable vertebrate on earth. *Journal of Ichthyology*, 53, 781–791.
- Koene, J. P., Elmer, K. R., & Adams, C. E. (2020). Intraspecific variation and structuring of phenotype in a lake-dwelling species are driven by lake size and elevation. *Biological Journal of the Linnean Society*, 131, 585–599.
- Landry, L., & Bernatchez, L. (2010). Role of epibenthic resource opportunities in the parallel evolution of lake whitefish species pairs (*Coregonus* sp.). *Journal of Evolutionary Biology*, 23, 2602–2613.
- Losos, J. B. (2010). Adaptive radiation, ecological opportunity, and evolutionary determinism. *The American Naturalist*, 175, 623–639.
- Losos, J. B., & Ricklefs, R. E. (2009). Adaptation and diversification on islands. *Nature*, 457, 830–836.
- Losos, J. B., & Schluter, D. (2000). Analysis of an evolutionary species-area relationship. *Nature*, 408, 847–850.
- Luke, S. G. (2017). Evaluating significance in linear mixed-effects models in R. *Behavior Research Methods*, 49, 1494–1502.
- Lundsgaard-Hansen, B., Matthews, B., Vonlanthen, P., Taverna, A., & Seehausen, O. (2013). Adaptive plasticity and genetic divergence in feeding efficiency during parallel adaptive radiation of whitefish (*Coregonus* spp.). *Journal of Evolutionary Biology*, 26, 483–498.
- Marklund, M. H. K., Svanbäck, R., Faulks, L., Breed, M. F., Scharnweber, K., Zha, Y., & Eklöv, P. (2019). Asymmetrical habitat coupling of an aquatic predator—The importance of individual specialization. *Ecology and Evolution*, 9, 3405–3415.
- McPhee, M. V., Noakes, D. L. G., & Allendorf, F. W. (2012). Developmental rate: A unifying mechanism for sympatric divergence in postglacial fishes? *Current Zoology*, 58, 21–35.
- O’Dea, R. E., Lagisz, M., Hendry, A. P., & Nakagawa, S. (2019). Developmental temperature affects phenotypic means and variability: A meta-analysis of fish data. *Fish and Fisheries*, 20, 1005–1022.
- Öhlund, G., Bodin, M., Nilsson, K. A., Öhlund, S., Mobley, K. B., Hudson, A. G., Peedu, M., Brännström, Å., Bartels, P., Præbel, K., Hein, C. L., Johansson, P., & Englund, G. (2020). Ecological Speciation in European Whitefish Is Driven by a Large-Gaped Predator. *Evolution Letters*, 4, 243–256.
- Østbye, K., Amundsen, P.-A., Bernatchez, L., Klemetsen, A., Knudsen, R., Kristoffersen, R., Næsje, T. F., & Hindar, K. (2006). Parallel Evolution of Ecomorphological Traits in the European Whitefish *Coregonus lavaretus* (L.) Species Complex During Postglacial Times. *Molecular Ecology*, 15, 3983–4001.
- Parsons, K. J., Sheets, H. D., Skúlason, S., & Ferguson, M. M. (2011). Phenotypic plasticity, heterochrony and ontogenetic repatterning during juvenile development of divergent arctic charr (*Salvelinus alpinus*). *Journal of Evolutionary Biology*, 24, 1640–1652.
- Power, M., Dempson, J. B., Reist, J. D., Schwarz, C. J., & Power, G. (2005). Latitudinal variation in fecundity among Arctic charr populations in eastern North America. *Journal of Fish Biology*, 67, 255–273.
- Præbel, K., Knudsen, R., Siwertsson, A., Karhunen, M., Kahilainen, K. K., Ovaskainen, O., Østbye, K., Peruzzi, S., Fevolden, S. E., & Amundsen, P.-A. (2013). Ecological speciation in postglacial European whitefish: Rapid adaptive radiations into the littoral, pelagic, and profundal lake habitats. *Ecology and Evolution*, 3, 4970–4986.
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

- Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., Kaschner, K., Garilao, C., Near, T. J., Coll, M., & Alfaro, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, *599*, 392–395.
- Recknagel, H., Hooker, O. E., Adams, C. E., & Elmer, K. R. (2017). Ecosystem size predicts eco-morphological variability in a postglacial diversification. *Ecology and Evolution*, *7*, 5560–5570.
- Reznick, D. A., Bryga, H., & Endler, J. A. (1990). Experimentally induced life-history evolution in a natural population. *Nature*, *346*, 357–359.
- Robinson, B. W., & Parsons, K. J. (2002). Changing times, spaces, and faces: Tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 1819–1833.
- Rypel, A. L., & David, S. R. (2017). Pattern and scale in latitude–Production relationships for freshwater fishes. *Ecosphere*, *8*, e01660.
- Schluter, D. (2000). *The ecology of adaptive radiation*. OUP.
- Schluter, D., & McPhail, J. D. (1993). Character displacement and replicate adaptive radiation. *Trends in Ecology & Evolution*, *8*, 197–200.
- Schluter, D., & Pennell, M. W. (2017). Speciation gradients and the distribution of biodiversity. *Nature*, *546*, 48–55.
- Seehausen, O., & Wagner, C. E. (2014). Speciation in freshwater fishes. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 621–651.
- Senior, A. M., Viechtbauer, W., & Nakagawa, S. (2020). Revisiting and expanding the meta-analysis of variation: The log coefficient of variation ratio. *Research Synthesis Methods*, *11*, 553–567.
- Sierszen, M. E., McDonald, M. E., & Jensen, D. A. (2003). Benthos as the basis for arctic lake food webs. *Aquatic Ecology*, *37*, 437–445.
- Siwertsson, A., Knudsen, R., Kahilainen, K. K., Præbel, K., Primicerio, R., & Amundsen, P.-A. (2010). Sympatric diversification as influenced by ecological opportunity and historical contingency in a young species lineage of whitefish. *Evolutionary Ecology Research*, *12*, 929–947.
- Siwertsson, A., Knudsen, R., Præbel, K., Adams, C. E., Newton, J., & Amundsen, P.-A. (2013). Discrete foraging niches promote ecological, phenotypic, and genetic divergence in sympatric whitefish (*Coregonus lavaretus*). *Evolutionary Ecology*, *27*, 547–564.
- Skúlason, S., Parsons, K. J., Svanbäck, R., Räsänen, K., Ferguson, M. M., Adams, C. E., Amundsen, P.-A., Bartels, P., Bean, C. W., Boughman, J. W., Englund, G., Guðbrandsson, J., Hooker, O. E., Hudson, A. G., Kahilainen, K. K., Knudsen, R., Kristjánsson, B. K., Leblanc, C. A. L., Jónsson, Z., ... Snorrason, S. S. (2019). A way forward with eco evo devo: An extended theory of resource polymorphism with postglacial fishes as model systems. *Biological Reviews*, *94*, 1786–1808.
- Skúlason, S., & Smith, T. B. (1995). Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution*, *10*, 366–370.
- Smalås, A., Amundsen, P. A., & Knudsen, R. (2013). Contrasting life history strategies of sympatric Arctic charr morphs, *Salvelinus alpinus*. *Journal of Ichthyology*, *53*, 856–866.
- Smith, T. B., & Skúlason, S. (1996). Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics*, *27*, 111–133.
- Stroud, J. T., & Losos, J. B. (2016). Ecological opportunity and adaptive radiation. *The Annual Review of Ecology, Evolution, and Systematics*, *47*, 507–532.
- Svanbäck, R., & Bolnick, D. I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 839–844.
- Turgeon, J., & Bernatchez, L. (2003). Reticulate evolution and phenotypic diversity in north American ciscoes, *Coregonus* ssp. (Teleostei: Salmonidae): Implications for the conservation of an evolutionary legacy. *Conservation Genetics*, *4*, 67–81.
- Valente, L., Phillimore, A. B., Melo, M., Warren, B. H., Clegg, S. M., Havenstein, K., Tiedemann, R., Illera, J. C., Thébaud, C., Aschenbach, T., & Etienne, R. S. (2020). A simple dynamic model explains the diversity of Island birds worldwide. *Nature*, *579*, 92–96.
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*, 1–48.
- Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V., & Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution*, *27*, 244–252.
- Vonlanthen, P., Roy, D., Hudson, A. G., LargiadÈr, C. R., Bittner, D., & Seehausen, O. (2009). Divergence along a steep ecological gradient in lake whitefish (*Coregonus* sp.). *Journal of Evolutionary Biology*, *22*, 498–514.
- Wagner, C. E., Harmon, L. J., & Seehausen, O. (2014). Cichlid species-area relationships are shaped by adaptive radiations that scale with area. *Ecology Letters*, *17*, 583–592.
- Wetzel, R. G., & Likens, G. (2000). *Limnological analyses (third.)*. Springer Science & Business Media.
- Woods, P. J., Skúlason, S., Snorrason, S. S., Kristjánsson, B. K., Malmquist, H. J., & Quinn, T. P. (2012). Intraspecific diversity in Arctic charr, *Salvelinus alpinus*, in Iceland: II. Which environmental factors influence resource polymorphism in lakes? *Evolutionary Ecology Research*, *14*, 993–1013.
- Yoder, J. B., Clancey, E., Des Roches, S., Eastman, J. M., Gentry, L., Godsoe, W., Hagey, T. J., Jochimsen, D., Oswald, B. P., Robertson, J. B. A. J., Sarver, B. A. J., Schenk, J. J., Spear, S. F., & Harmon, L. J. (2010). Ecological Opportunity and the Origin of Adaptive Radiations. *Journal of Evolutionary Biology*, *23*, 1581–1596.

## REFERENCES USED FOR DATA

- Adams, C., Fraser, D., McCarthy, I., Shields, S., Waldron, S., & Alexander, G. (2003). Stable isotope analysis reveals ecological segregation in a bimodal size polymorphism in Arctic charr from loch Tay, Scotland. *Journal of Fish Biology*, *62*, 474–481.
- Adams, C. E., Fraser, D., Huntingford, F. A., Greer, R. B., Askew, C. M., & Walker, A. F. (1998). Trophic polymorphism among Arctic charr from loch Rannoch, Scotland. *Journal of Fish Biology*, *52*, 1259–1271.
- Adams, C. E., & Huntingford, F. A. (2004). Incipient speciation driven by phenotypic plasticity? Evidence from sympatric populations of Arctic charr. *Biological Journal of the Linnean Society*, *81*, 611–618.
- Adams, C. E., Wilson, A. J., & Ferguson, M. M. (2008). Parallel divergence of sympatric genetic and body size forms of Arctic charr, *Salvelinus alpinus*, from two Scottish lakes. *Biological Journal of the Linnean Society*, *95*, 748–757.
- Alekseyev, S. S., Gordeeva, N. V., Matveev, A. N., Samusenok, V. P., Vokin, A. I., & Yur'ev, A. L. (2014). Three sympatric forms of Arctic charr *Salvelinus alpinus* complex (Salmoniformes, Salmonidae) from Lake Kamkanda, northern Transbaikalia. *Journal of Ichthyology*, *54*, 384–408.
- Alekseyev, S. S., Mina, M. V., Smirina, E. M., & Sokolov, A. A. (2009). Late ontogeny growth acceleration and size form transformations in Transbaikalian Arctic charr, *Salvelinus alpinus* complex: Evidence from fin ray cross section growth layers. *Environmental Biology of Fishes*, *86*, 487–505.
- Alekseyev, S. S., Pichugin, M. Y., Samusenok, V. P., Gordeeva, N. V., Yur'ev, A. L., Khlystov, V. S., & Matveev, A. N. (2019). Reproductive strategies of Arctic charr *Salvelinus alpinus* (L.) forms in Kiryalta lakes, Transbaikalia, Russia. *Hydrobiologia*, *840*, 113–136.
- Alekseyev, S. S., Samusenok, V. P., Matveev, A. N., & Pichugin, M. Y. (2002). Diversification, sympatric speciation, and trophic polymorphism of Arctic charr, *Salvelinus alpinus* complex, in Transbaikalia. *Environmental Biology of Fishes*, *64*, 97–114.
- Alfonso, N. R. (2004). Evidence for two morphotypes of lake charr, *Salvelinus namaycush*, from Great Bear Lake, Northwest Territories, Canada. *Environmental Biology of Fishes*, *71*, 21–32.
- Amundsen, P.-A., Knudsen, R., & Klemetsen, A. (2008). Seasonal and ontogenetic variations in resource use by two sympatric Arctic charr morphs. *Environmental Biology of Fishes*, *83*, 45–55.
- Amundsen, P.-A., Knudsen, R., Klemetsen, A., & Kristoffersen, R. (2004). Resource competition and interactive segregation between sympatric whitefish morphs. *Annales Zoologici Fennici*, *41*, 301–307.
- Aoki, K. A. A., & Bodaly, R. A. (2003). Sympatric presence of low and high gill-raker forms of cisco, *Coregonus artedii*, in Lake Athapapuskow, Manitoba. *The Canadian Field-Naturalist*, *117*, 49–52.

- Arbour, J. H., Hardie, D. C., & Hutchings, J. A. (2011). Morphometric and genetic analyses of two sympatric morphs of arctic char (*Salvelinus alpinus*) in the Canadian high arctic. *Canadian Journal of Zoology*, 89, 19–30.
- Baillie, S. M., Muir, A. M., Hansen, M. J., Krueger, C. C., & Bentzen, P. (2016). Genetic and phenotypic variation along an ecological gradient in lake trout *Salvelinus namaycush*. *BMC Evolutionary Biology*, 16, 1–16.
- Bernatchez, L., Chouinard, A., & Lu, G. (1999). Integrating molecular genetics and ecology in studies of adaptive radiation: Whitefish, *Coregonus* sp., as a case study. *Biological Journal of the Linnean Society*, 68, 173–194.
- Bernatchez, L., Vuorinen, J. A., Bodaly, R. A., & Dodson, J. J. (1996). Genetic evidence for reproductive isolation and multiple origins of sympatric trophic ecotypes of whitefish (*Coregonus*). *Evolution*, 50, 624–635.
- Bertrand, M., Marcogliese, D. J., & Magnan, P. (2008). Trophic polymorphism in brook charr revealed by diet, parasites and morphometrics. *Journal of Fish Biology*, 72, 555–572.
- Bittner, D., Excoffier, L., & Largiadere, C. R. (2010). Patterns of morphological changes and hybridization between sympatric whitefish morphs (*Coregonus* spp.) in a Swiss lake: A role for eutrophication? *Molecular Ecology*, 19, 2152–2167.
- Bjorv, B., & Sandlund, O. T. (1995). Differences in morphology and ecology within a stunted Arctic char population. *Nordic Journal of Freshwater Research*, 71, 163–172.
- Blackie, C. T., Weese, D. J., & Noakes, D. L. G. (2003). Evidence for resource polymorphism in the lake charr (*Salvelinus namaycush*) population of Great Bear Lake, Northwest Territories, Canada. *Ecoscience*, 10, 509–514.
- Bourke, P., Magnan, P., & Rodriguez, M. A. (1997). Individual variations in habitat use and morphology in brook char. *Journal of Fish Biology*, 51, 783–794.
- Bryce, C., Fraser, A., Knudsen, R., Greer, R., & Adams, C. (2016). Divergent functional traits in three sympatric Arctic charr *Salvelinus alpinus* morphs are not coupled with the age of the lineage divergence. *Hydrobiologia*, 783, 177–189.
- Chavarie, L., Harford, W. J., Howland, K. L., Fitzsimons, J., Muir, A. M., Krueger, C. C., & Tonn, W. M. (2016). Multiple generalist morphs of Lake trout: Avoiding constraints on the evolution of intraspecific divergence? *Ecology and Evolution*, 6, 7727–7741.
- Chavarie, L., Howland, K., Gallagher, C., & Tonn, W. (2016). Fatty acid signatures and stomach contents of four sympatric Lake trout: Assessment of trophic patterns among morphotypes in Great Bear Lake. *Ecology of Freshwater Fish*, 25, 109–124.
- Chavarie, L., Howland, K., Harris, L., & Tonn, W. (2015). Polymorphism in lake trout in Great Bear Lake: Intra-lake morphological diversification at two spatial scales. *Biological Journal of the Linnean Society*, 114, 109–125.
- Chavarie, L., Howland, K., Venturelli, P., Kissinger, B. C., Tallman, R., & Tonn, W. (2016). Life-history variation among four shallow-water morphotypes of lake trout from Great Bear Lake, Canada. *Journal of Great Lakes Research*, 42, 193–203.
- Chavarie, L., Howland, K. L., & Tonn, W. M. (2013). Sympatric polymorphism in Lake trout: The coexistence of multiple shallow-water morphotypes in Great Bear Lake. *Transactions of the American Fisheries Society*, 142, 814–823.
- Chavarie, L., Muir, A. M., Zimmerman, M. S., Baillie, S. M., Hansen, M. J., Nate, N. A., Yule, D. L., Middel, T., Bentzen, P., & Krueger, C. C. (2017). Challenge to the Model of Lake Charr Evolution: Shallow and Deep-Water Morphs Exist Within a Small Postglacial Lake. *Biological Journal of the Linnean Society*, 120, 578–603.
- Chouinard, A., Pigeon, D., & Bernatchez, L. (1996). Lack of specialization in trophic morphology between genetically differentiated dwarf and normal forms of lake whitefish (*Coregonus clupeaformis* Mitchell) in lac de l'Est, Quebec. *Canadian Journal of Zoology*, 74, 1989–1998.
- Conejeros, P., Phan, A., Power, M., O'Connell, M., Alekseyev, S., Salinas, I., & Dixon, B. (2014). Differentiation of sympatric arctic char morphotypes using major histocompatibility class II genes. *Transactions of the American Fisheries Society*, 143, 586–594.
- Dion-Côté, A. M., Symonová, R., Lamaze, F. C., Pelikánová, Š., Ráb, P., & Bernatchez, L. (2017). Standing chromosomal variation in Lake whitefish species pairs: The role of historical contingency and relevance for speciation. *Molecular Ecology*, 26, 178–192.
- Doenz, C. J., Bittner, D., Vonlanthen, P., Wagner, C. E., & Seehausen, O. (2018). Rapid buildup of sympatric species diversity in alpine whitefish. *Ecology and Evolution*, 8, 9398–9412.
- Doenz, C. J., Krähnenbühl, A. K., Walker, J., Seehausen, O., & Brodersen, J. (2019). Ecological opportunity shapes a large Arctic charr species radiation. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191992.
- Dorucu, M., Adams, C. E., Huntingford, F. A., & Crompton, D. W. T. (1995). How fish-helminth associations arise: An example from Arctic charr in loch Rannoch. *Journal of Fish Biology*, 47, 1038–1043.
- Dynes, J., Magnan, P., Bernatchez, L., & Rodriguez, M. A. (1999). Genetic and morphological variation between two forms of lacustrine brook charr. *Journal of Fish Biology*, 54, 955–972.
- Esin, E. V., & Markevich, G. N. (2019). Parallel late ontogeny transformations in contrasting landlocked phenotypes of *Salvelinus malma* (Salmonidae) from small volcanic lakes. *Ecology of Freshwater Fish*, 28, 624–638.
- Franklin, O. D., Skúlason, S., Morrissey, M. B., & Ferguson, M. M. (2018). Natural selection for body shape in resource polymorphic Icelandic Arctic charr. *Journal of Evolutionary Biology*, 31, 1498–1512.
- Fraser, D., Adams, C. E., & Huntingford, F. A. (1998). Trophic polymorphism among Arctic charr *Salvelinus alpinus* L., from loch Ericht, Scotland. *Ecology of Freshwater Fish*, 7, 184–191.
- Fraser, D., Huntingford, F. A., & Adams, C. E. (2008). Foraging specialisms, prey size and life-history patterns: A test of predictions using sympatric polymorphic Arctic charr (*Salvelinus alpinus*). *Ecology of Freshwater Fish*, 17, 1–9.
- Fraser, D. J., Calvert, A. M., Bernatchez, L., & Coon, A. (2013). Multidisciplinary population monitoring when demographic data are sparse: A case study of remote trout populations. *Ecology and Evolution*, 3, 4954–4969.
- Gallagher, C. P., & Dick, T. A. (2010). Trophic structure of a landlocked Arctic char *Salvelinus alpinus* population from southern Baffin Island, Canada. *Ecology of Freshwater Fish*, 19, 39–50.
- Garduño-Paz, M. V., Adams, C. E., Verspoor, E., Knox, D., & Harrod, C. (2012). Convergent evolutionary processes driven by foraging opportunity in two sympatric morph pairs of Arctic charr with contrasting post-glacial origins. *Biological Journal of the Linnean Society*, 106, 794–806.
- Gislason, D., Ferguson, M. M., Skúlason, S., & Snorrason, S. S. (1999). Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 2229–2234.
- Gordeeva, N. V., Alekseyev, S. S., Matveev, A. N., & Samusenok, V. P. (2014). Parallel evolutionary divergence in arctic char *salvelinus* alpines complex from transbaikalia: Variation in differentiation degree and segregation of genetic diversity among sympatric forms. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 96–115.
- Guiguer, K. R. R. A., Reist, J. D., Power, M., & Babaluk, J. A. (2002). Using stable isotopes to confirm the trophic ecology of Arctic charr morphotypes from Lake Hazen, Nunavut, Canada. *Journal of Fish Biology*, 60, 348–362.
- Häkli, K., Østbye, K., Kahilainen, K. K., Amundsen, P.-A., & Præbel, K. (2018). Diversifying selection drives parallel evolution of gill raker number and body size along the speciation continuum of European whitefish. *Ecology and Evolution*, 8, 2617–2631.
- Harrod, C., Mallela, J., & Kahilainen, K. K. (2010). Phenotype-environment correlations in a putative whitefish adaptive radiation. *Journal of Animal Ecology*, 79, 1057–1068.
- Hawley, K. L., Rosten, C. M., Christensen, G., & Lucas, M. C. (2016). Fine-scale behavioural differences distinguish resource use by ecomorphs in a closed ecosystem. *Scientific Reports*, 6, 1–12.
- Helland, I. P., Vållestad, L. A., Freyhof, J., & Mehner, T. (2009). Morphological differences between two ecologically similar sympatric fishes. *Journal of Fish Biology*, 75, 2756–2767.
- Henderson, B. A., & Anderson, D. M. (2002). Phenotypic differences in buoyancy and energetics of lean and siscowet lake charr in Lake Superior. *Environmental Biology of Fishes*, 64, 203–209.
- Hesthagen, T., Hindar, K., Jonsson, B., Ousdal, J. O., & Holthe, H. (1995). Effects of acidification on normal and dwarf Arctic charr *Salvelinus alpinus* (L.) in a Norwegian lake. *Biological Conservation*, 74, 115–123.
- Hindar, K., & Jonsson, B. (1982). Habitat and food segregation of dwarf and normal arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 1030–1045.
- Hooker, O. E., Barry, J., van Leeuwen, T. E., Lyle, A., Newton, J., Cunningham, P., & Adams, C. E. (2016). Morphological, ecological and behavioural differentiation of sympatric profundal and pelagic Arctic charr (*Salvelinus alpinus*) in loch Dughail Scotland. *Hydrobiologia*, 783, 209–221.
- Hudson, A. G., Lundsgaard-Hansen, B., Lucek, K., Vonlanthen, P., & Seehausen, O. (2017). Managing cryptic biodiversity: Fine-scale intralacustrine speciation along a benthic gradient in alpine whitefish (*Coregonus* spp.). *Evolutionary Applications*, 10, 251–266.
- Hudson, A. G., Vonlanthen, P., Bezault, E., & Seehausen, O. (2013). Genomic signatures of relaxed disruptive selection associated with speciation reversal in whitefish. *BMC Evolutionary Biology*, 13, 108.
- Huuskonen, H., Shikano, T., Mehtätalo, L., Kettunen, J., Eronen, R., Toivainen, A., & Kekäläinen, J. (2017). Anthropogenic environmental changes induce

- introgression in sympatric whitefish ecotypes. *Biological Journal of the Linnean Society*, 121, 613–626.
- Ingram, T., Hudson, A. G., Vonlanthen, P., & Seehausen, O. (2012). Does water depth or diet divergence predict progress towards ecological speciation in whitefish radiations? *Evolutionary Ecology Research*, 14, 487–502.
- Jonsson, B. (2002). Parallel sympatric segregation in arctic charr and threespined stickleback in Lake Galtaból, Iceland. *Fisheries Science*, 68, 459–460.
- Jonsson, B., & Hindar, K. (1982). Reproductive strategy of dwarf and normal arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, Western Norway. *Canadian Journal of Fisheries and Aquatic Sciences*, 39, 1404–1413.
- Jónsson, B., & Skúlason, S. (2000). Polymorphic segregation in Arctic charr *Salvelinus alpinus* (L.) from Vatnshlíðarvatn, a shallow Icelandic lake. *Biological Journal of the Linnean Society*, 69, 55–74.
- Kahilainen, K., Lehtonen, H., & Könönen, K. (2003). Consequence of habitat segregation to growth rate of two sparsely raked whitefish (*Coregonus lavaretus* (L.)) forms in a subarctic lake. *Ecology of Freshwater Fish*, 12, 275–285.
- Kahilainen, K., & Østbye, K. (2006). Morphological differentiation and resource polymorphism in three sympatric whitefish *Coregonus lavaretus* (L.) forms in a subarctic lake. *Journal of Fish Biology*, 68, 63–79.
- Kahilainen, K. K., Malinen, T., Tuomaala, A., Alajärvi, E., Tolonen, A., & Lehtonen, H. (2007). Empirical evaluation of phenotype-environment correlation and trait utility with allopatric and sympatric whitefish, *Coregonus lavaretus* (L.), populations in subarctic lakes. *Biological Journal of the Linnean Society*, 92, 561–572.
- Kahilainen, K. K., Smura, T., Knudsen, R., Amundsen, P.-A., Jokela-Määttä, M., & Donner, K. (2016). Visual pigments of Arctic charr (*Salvelinus alpinus* (L.)) and whitefish (*Coregonus lavaretus* (L.)) morphs in subarctic lakes. *Hydrobiologia*, 783, 223–237.
- Kahilainen, K. K., Thomas, S. M., Nystedt, E. K. M., Keva, O., Malinen, T., & Hayden, B. (2017). Ecomorphological divergence drives differential mercury bioaccumulation in polymorphic European whitefish (*Coregonus lavaretus*) populations of subarctic lakes. *Science of the Total Environment*, 599–600, 1768–1778.
- Kapralova, K. H., Gudbrandsson, J., Reynisdóttir, S., Santos, C. B., Baltanás, V. C., Maier, V. H., Snorrason, S. S., & Palsson, A. (2013). Differentiation at the MHCIIa and Cath2 loci in sympatric *Salvelinus alpinus* resource morphs in Lake Thingvallavatn. *PLoS One*, 8, e69402.
- Karvonen, A., Lundsgaard-Hansen, B., Jokela, J., & Seehausen, O. (2013). Differentiation in parasitism among ecotypes of whitefish segregating along depth gradients. *Oikos*, 122, 122–128.
- Klemetsen, A. (2002). Evidence for genetic differences in the offspring of two sympatric morphs of Arctic charr. *Journal of Fish Biology*, 60, 933–950.
- Knudsen, R., Amundsen, P.-A., Jobling, M., & Klemetsen, A. (2008). Differences in pyloric caeca morphology between Arctic charr *Salvelinus alpinus* ecotypes: Adaptation to trophic specialization or parasite-induced phenotypic modifications? *Journal of Fish Biology*, 73, 275–287.
- Knudsen, R., Amundsen, P.-A., & Klemetsen, A. (2003). Inter- and intra-morph patterns in helminth communities of sympatric whitefish morphs. *Journal of Fish Biology*, 62, 847–859.
- Knudsen, R., Amundsen, P.-A., Primicerio, R., Klemetsen, A., & Sørensen, P. (2007). Contrasting niche-based variation in trophic morphology within Arctic charr populations. *Evolutionary Ecology Research*, 9, 1005–1021.
- Knudsen, R., Eloranta, A. P., Siwertsson, A., Paterson, R. A., Power, M., & Sandlund, O. T. (2019). Introduction of *Mysis relicta* (Mysida) reduces niche segregation between deep-water Arctic charr morphs. *Hydrobiologia*, 840, 245–260.
- Knudsen, R., Gjelland, K. Ø., Eloranta, A. P., Hayden, B., Siwertsson, A., Amundsen, P.-A., & Klemetsen, A. (2016). A specialised cannibalistic Arctic charr morph in the piscivore guild of a subarctic lake. *Hydrobiologia*, 783, 65–78.
- Knudsen, R., Klemetsen, A., Amundsen, P.-A., & Hermansen, B. (2006). Incipient speciation through niche expansion: An example from the Arctic charr in a subarctic lake. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2291–2298.
- Knudsen, R., Primicerio, R., Amundsen, P.-A., & Klemetsen, A. (2010). Temporal stability of individual feeding specialization may promote speciation. *Journal of Animal Ecology*, 79, 161–168.
- Knudsen, R., Siwertsson, A., Adams, C. E., Garduño-Paz, M., Newton, J., & Amundsen, P.-A. (2011). Temporal stability of niche use exposes sympatric Arctic charr to alternative selection pressures. *Evolutionary Ecology*, 25, 589–604.
- Knudsen, R., Siwertsson, A., Adams, C. E., Newton, J., & Amundsen, P.-A. (2014). Similar patterns of individual niche use are revealed by different time-integrated trophic tracers (stable isotopes and parasites). *Ecology of Freshwater Fish*, 23, 259–268.
- Laporte, M., Rogers, S. M., Dion-Côté, A. M., Normandeau, E., Gagnaire, P. A., Dalziel, A. C., Chebib, J., & Bernatchez, L. (2015). RAD-QTL mapping reveals both genome-level parallelism and different genetic architecture underlying the evolution of body shape in lake whitefish (*Coregonus clupeaformis*) species pairs. *G3: Genes, Genomes, Genetics*, 5, 1481–1491.
- Liso, S., Gjelland, K., & Amundsen, P.-A. (2013). Resource partitioning between pelagic coregonids in a subarctic watercourse following a biological invasion. *Journal of Ichthyology*, 53, 101–110.
- Lu, G., & Bernatchez, L. (1999). Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): Support for the ecological speciation hypothesis. *Evolution*, 53, 1491–1505.
- Markevich, G., Esin, E., & Anisimova, L. (2018). Basic description and some notes on the evolution of seven sympatric morphs of Dolly Varden *Salvelinus malma* from the Lake Kronotskoe Basin. *Ecology and Evolution*, 8, 2554–2567.
- Markevich, G. N., Esin, E. V., Busarova, O. Y., Knudsen, R., & Anisimova, L. A. (2017). Diversity of nosed charrs *Salvelinus malma* (Salmonidae) of Lake Kronotskoe (Kamchatka). *Journal of Ichthyology*, 57, 675–687.
- May-McNally, S. L., Quinn, T. P., Woods, P. J., & Taylor, E. B. (2015). Evidence for genetic distinction among sympatric ecotypes of Arctic char (*Salvelinus alpinus*) in south-western Alaskan lakes. *Ecology of Freshwater Fish*, 24, 562–574.
- McCarthy, I. D., Fraser, D., Waldron, S., & Adams, C. E. (2004). A stable isotope analysis of trophic polymorphism among Arctic charr from loch Erich, Scotland. *Journal of Fish Biology*, 65, 1435–1440.
- Mocetti, P., Siwertsson, A., Kjær, R., Amundsen, P.-A., Præbel, K., Tamayo, A. M. P., Power, M., & Knudsen, R. (2019). Contrasting patterns in trophic niche evolution of polymorphic Arctic charr populations in two subarctic Norwegian lakes. *Hydrobiologia*, 840, 281–299.
- Muir, A. M., Bronte, C. R., Zimmerman, M. S., Quinlan, H. R., Glase, J. D., & Krueger, C. C. (2014a). Ecomorphological diversity of Lake trout at Isle Royale, Lake Superior. *Transactions of the American Fisheries Society*, 143, 972–987.
- Muir, A. M., Vecsei, P., Power, M., Krueger, C. C., & Reist, J. D. (2014b). Morphology and life history of the Great Slave Lake ciscoes (Salmoniformes: Coregonidae). *Ecology of Freshwater Fish*, 23, 453–469.
- Næsje, T. F., Vuorinen, J. A., & Sandlund, O. T. (2004). Genetic and morphometric differentiation among sympatric spawning stocks of whitefish (*Coregonus lavaretus* L.) in Lake Femund, Norway. *Journal of Limnology*, 63, 233–243.
- Østbye, K., Amundsen, P.-A., Bernatchez, L., Klemetsen, A., Knudsen, R., Kristoffersen, R., Næsje, T. F., & Hindar, K. (2006). Parallel evolution of ecomorphological traits in the European whitefish *Coregonus lavaretus* (L.) species complex during postglacial times. *Molecular Ecology*, 15, 3983–4001.
- Østbye, K., Hagen Hassve, M., Peris Tamayo, A. M., Hagenlund, M., Vogler, T., & Præbel, K. (2020). "And if you gaze long into an abyss, the abyss gazes also into thee": Four morphs of Arctic charr adapting to a depth gradient in Lake Tinnsjøen. *Evolutionary Applications*, 13, 1240–1261.
- Østbye, K., Næsje, T. F., Bernatchez, L., Sandlund, O. T., & Hindar, K. (2005). Morphological divergence and origin of sympatric populations of European whitefish (*Coregonus lavaretus* L.) in Lake Femund, Norway. *Journal of Evolutionary Biology*, 18, 683–702.
- Pavlov, S. D., Kuzishchin, K. V., Gruzdeva, M. A., Senchukova, A. L., & Pivovarov, E. A. (2013). Phenetic diversity and spatial structure of charrs (*Salvelinus*) of the Kronotskaya riverine-lacustrine system (eastern Kamchatka). *Journal of Ichthyology*, 53, 662–686.
- Perreault-Payette, A., Muir, A. M., Goetz, F., Perrier, C., Normandeau, E., Sirois, P., & Bernatchez, L. (2017). Investigating the extent of parallelism in morphological and genomic divergence among lake trout ecotypes in Lake Superior. *Molecular Ecology*, 26, 1477–1497.
- Piette-Lauzière, G., Bell, A. H., Ridgway, M. S., & Turgeon, J. (2019). Evolution and diversity of two cisco forms in an outlet of glacial Lake Algonquin. *Ecology and Evolution*, 9, 9654–9670.
- Power, M., O'Connell, M. F., & Dempson, B. (2012). Determining the consistency of thermal habitat segregation within and among Arctic charr morphotypes in Gander Lake, Newfoundland. *Ecology of Freshwater Fish*, 21, 245–254.
- Power, M., O'Connell, M. F., & Dempson, J. B. (2005). Ecological segregation within and among Arctic charr morphotypes in Gander Lake, Newfoundland. *Environmental Biology of Fishes*, 73, 263–274.
- Power, M., Power, G., Reist, J. D., & Bajno, R. (2009). Ecological and genetic differentiation among the Arctic charr of lake Aigueau, northern Québec. *Ecology of Freshwater Fish*, 18, 445–460.
- Præbel, K., Knudsen, R., Siwertsson, A., Karhunen, M., Kahilainen, K. K., Ovaskainen, O., Østbye, K., Peruzzi, S., Fevolden, S. E., & Amundsen, P. A. (2013). Ecological speciation in postglacial European whitefish: Rapid adaptive

- radiations into the littoral, pelagic, and profundal lake habitats. *Ecology and Evolution*, 3, 4970–4986.
- Reid, S. M., Parna, M., & Reist, J. D. (2017). Collapse of Lake whitefish *Coregonus clupeaformis* (Mitchill, 1818) species pair in Como Lake, Ontario. *Journal of Applied Ichthyology*, 33, 933–939.
- Saltykova, E., Markevich, G., & Kuzishchin, K. (2015). Divergent skull morphology between trophic separated lacustrine forms of Dolly Varden charr from Lake Kronotskoe, Kamchatka, Russia. *Environmental Biology of Fishes*, 98, 559–570.
- Saltykova, E., Siwertsson, A., & Knudsen, R. (2017). Parallel phenotypic evolution of skull-bone structures and head measurements of Arctic charr morphs in two subarctic lakes. *Environmental Biology of Fishes*, 100, 137–148.
- Samways, K. M., Leavitt, P. R., Magnan, P., Rodríguez, M. A., & Peres-Neto, P. R. (2015). Convergent polymorphism between stream and lake habitats: The case of brook char. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 1406–1414.
- Sandlund, O. T., Gjelland, K. Ø., Bøhn, T., Knudsen, R., & Amundsen, P.-A. (2013). Contrasting population and life history responses of a young morph-pair of European whitefish to the invasion of a specialised Coregonid competitor, Vendace. *PLoS One*, 8, e68156.
- Sandlund, O. T., Gunnarsson, K., Jonasson, P. M., Jonsson, B., Lindem, T., Magnusson, K. P., Malmquist, H. J., Sigurjónsdóttir, H., Skúlason, S., & Snorrason, S. S. (1992). The Arctic Charr *Salvelinus Alpinus* in Thingvallavatn. *Oikos*, 64, 305–351.
- Sandlund, O. T., Jonsson, B., Malmquist, H. J., Gydemo, R., Lindem, T., Skúlason, S., Snorrason, S. S., & Jónasson, P. M. (1987). Habitat Use of Arctic Charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Environmental Biology of Fishes*, 20, 263–274.
- Sandlund, O. T., Naesje, T. F., & Saksgard, R. (1995). Ecological diversity in whitefish *Coregonus lavaretus*: Ontogenetic niche shifts and polymorphism. *Archiv Für Hydrobiologie Special Issues Advances Limnology*, 46, 49–59.
- Sigursteinsdóttir, R. J., & Kristjánsson, B. K. (2005). Parallel evolution, not always so parallel: Comparison of small benthic charr, *Salvelinus alpinus*, from Grímsnes and Thingvallavatn, Iceland. *Environmental Biology of Fishes*, 74, 239–244.
- Simonsen, M. K., Siwertsson, A., Adams, C. E., Amundsen, P.-A., Præbel, K., & Knudsen, R. (2017). Allometric trajectories of body and head morphology in three sympatric Arctic charr (*Salvelinus alpinus* (L.)) morphs. *Ecology and Evolution*, 7, 7277–7289.
- Sitar, S. P., & Traynor, D. J. (2018). Differences in pyloric caeca counts between lean and siscowet lake trout (*Salvelinus namaycush*) in southern Lake Superior. *Journal of Great Lakes Research*, 44, 352–356.
- Siwertsson, A., Knudsen, R., Adams, C. E., Præbel, K., & Amundsen, P.-A. (2013). Parallel and non-parallel morphological divergence among foraging specialists in European whitefish (*Coregonus lavaretus*). *Ecology and Evolution*, 3, 1590–1602.
- Siwertsson, A., Knudsen, R., & Amundsen, P.-A. (2012). Temporal stability in gill raker numbers of subarctic European whitefish populations. *Advances in Limnology*, 63, 229–240.
- Siwertsson, A., Knudsen, R., Kahilainen, K. K., Præbel, K., Primicerio, R., & Amundsen, P.-A. (2010). Sympatric diversification as influenced by ecological opportunity and historical contingency in a young species lineage of whitefish. *Evolutionary Ecology Research*, 12, 929–947.
- Siwertsson, A., Knudsen, R., Præbel, K., Adams, C. E., Newton, J., & Amundsen, P.-A. (2013). Discrete foraging niches promote ecological, phenotypic, and genetic divergence in sympatric whitefish (*Coregonus lavaretus*). *Evolutionary Ecology*, 27, 547–564.
- Siwertsson, A., Refsnes, B., Frainer, A., Amundsen, P.-A., & Knudsen, R. (2016). Divergence and parallelism of parasite infections in Arctic charr morphs from deep and shallow lake habitats. *Hydrobiologia*, 783, 131–143.
- Skoglund, S., Siwertsson, A., Amundsen, P.-A., & Knudsen, R. (2015). Morphological divergence between three Arctic charr morphs-the significance of the deep-water environment. *Ecology and Evolution*, 5, 3114–3129.
- Smalås, A., Amundsen, P.-A., & Knudsen, R. (2013). Contrasting life history strategies of sympatric Arctic charr morphs, *Salvelinus alpinus*. *Journal of Ichthyology*, 53, 856–866.
- Snorrason, S. S., Skúlason, S., Jonsson, B., Malmquist, H. J., Jonasson, P. M., Sandlund, O. T., & Lindem, T. (1994). Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): Morphological divergence and ontogenetic niche shifts. *Biological Journal of the Linnean Society*, 52, 1–18.
- Thomas, S. M., Kainz, M. J., Amundsen, P.-A., Hayden, B., Taipale, S. J., & Kahilainen, K. K. (2019). Resource polymorphism in European whitefish: Analysis of fatty acid profiles provides more detailed evidence than traditional methods alone. *PLoS One*, 14, 1–23.
- Turgeon, J., & Bernatchez, L. (2003). Reticulate evolution and phenotypic diversity in north American ciscoes, *Coregonus* ssp. (Teleostei: Salmonidae): Implications for the conservation of an evolutionary legacy. *Conservation Genetics*, 4, 67–81.
- Turgeon, J., Estoup, A., & Bernatchez, L. (1999). Species flock in the north American Great Lakes: Molecular ecology of Lake Nipigon ciscoes (Teleostei: Coregonidae: *Coregonus*). *Evolution*, 53, 1857–1871.
- Vecsei, P., Blackie, C. T., Muir, A. M., Machtans, H. M., & Reist, J. D. (2012). A preliminary assessment of cisco (*Coregonus* spp.) diversity in Yellowknife Bay, Great Slave Lake, Northwest Territories. *Advances in Limnology*, 63, 299–322.
- Walker, A. F., Greer, R. B., & Gardner, A. S. (1988). Two ecologically distinct forms of arctic charr *Salvelinus alpinus* (L.) in loch Rannoch, Scotland. *Biological Conservation*, 43, 43–61.
- Woods, P. J., Skúlason, S., Snorrason, S. S., Kristjánsson, B. K., Malmquist, H. J., & Quinn, T. P. (2012). Intraspecific diversity in arctic charr, *Salvelinus alpinus*, in Iceland: I. Detection using mixture models. *Evolutionary Ecology Research*, 14, 973–992.
- Woods, P. J., Young, D., Skúlason, S., Snorrason, S. S., & Quinn, T. P. (2013). Resource polymorphism and diversity of Arctic charr *Salvelinus alpinus* in a series of isolated lakes. *Journal of Fish Biology*, 82, 569–587.
- Zimmerman, M. S., Krueger, C. C., & Eshenroder, R. L. (2007). Morphological and ecological differences between shallow- and deep-water Lake trout in Lake Mistassini, Quebec. *Journal of Great Lakes Research*, 33, 156–169.
- Zimmerman, M. S., Schmidt, S. N., Krueger, C. C., Vander Zanden, M. J., & Eshenroder, R. L. (2009). Ontogenetic niche shifts and resource partitioning of lake trout morphotypes. *Canadian Journal of Fisheries and Aquatic Sciences*, 66, 1007–1018.
- Zubova, E. M., Kashulin, N. A., Terentjev, P. M., Valkova, S. A., Cherepanov, A. A., & Postnova, S. V. (2018). New data on morphological features of the branchial apparatus of sparsely rakered and medium rakered morphs of whitefish *Coregonus lavaretus* (L.) from the largest subarctic lake. *Inland Water Biology*, 11, 465–476.

## SUPPORTING INFORMATION

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

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