

Environmental correlates of adaptive diversification in postglacial freshwater fishes

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Abstract

Determining how environmental conditions contribute to divergence among populations and drive speciation is fundamental to resolving mechanisms and understanding outcomes in evolutionary biology. Postglacial freshwater fish species in the Northern Hemisphere are ideal biological systems to explore the effects of environment on diversification in morphology, ecology, and genetics (ecomorph divergences) within lakes. To date, various environmental factors have been implicated in the presence of multiple ecomorphs within particular lakes or regions. However, concerted evidence for generalizable patterns in environmental variables associated with speciation across geographical regions and across species and genera has been lacking. Here, we aimed to identify key biotic and abiotic factors associated with ecological divergence of postglacial freshwater fish species into multiple sympatric ecomorphs, focusing on species in the well-studied, widespread, and co-distributed genera *Gasterosteus*, *Salvelinus*, and *Coregonus* (stickleback, charr, and whitefish, respectively). We found that the presence of multiple sympatric ecomorphs tended to be associated with increasing lake surface area, maximum depth, and nutrient availability. In addition, predation, competition, and prey availability were suggested to play a role in divergence into multiple ecomorphs, but the effects of biotic factors require further study. Although we identified several environmental factors correlated with the presence of multiple ecomorphs, there were substantial data gaps across species and regions. An improved understanding of these systems may provide insight into both generalizable environmental factors involved in speciation in other systems, and potential ecological and evolutionary responses of species complexes when these variables are altered by environmental change.

KEYWORDS

adaptive divergence, ecomorph, ecotype, lake, salmonid, specialist, speciation, stickleback

1 | INTRODUCTION

The drivers of divergence and speciation are the subject of significant research interest, with evidence for in situ speciation being uncovered

in multiple ecosystems (Nosil, 2012; Schluter, 2009; Seehausen & Wagner, 2014). Environmental factors are often suggested to play a role in generating divergent selection to promote adaptive divergence and the associated ecological and morphological distinctiveness of

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populations or species, from incipient to complete speciation (Langerhans & Riesch, 2013; Nosil, 2012; Nosil et al., 2009; Schluter, 2009; Seehausen & Wagner, 2014). Many of these examples are from freshwater fish species (Seehausen & Wagner, 2014). These include the cichlid fish species of Central American crater lakes (Elmer et al., 2012, 2013; Recknagel et al., 2014), African great lakes (Wagner et al., 2014), and many lines of evidence from temperate fishes inhabiting postglacial lakes of the Northern Hemisphere (Bolnick & Fitzpatrick, 2007; Langerhans & Riesch, 2013; Seehausen & Wagner, 2014). Diversification (or lack thereof) may be dependent on multiple factors, which have recently been considered in the context of the “eco-evo-devo” framework of phenotypic divergence. This model proposes that the appearance of phenotypic divergence depends on the interactions between plasticity and ontogeny (development; devo), heritable divergence (evolution; evo), and environmental factors (ecology; eco) (Abouheif et al., 2014; Skúlason et al., 2019). Environmental factors such as the diversity of habitats present may therefore drive divergence through selection for different traits in different parts of the environment (Seehausen & Wagner, 2014) (Figure 1).

A range of abiotic and biotic environmental aspects have been investigated for their associations with sympatric ecological speciation in different habitats. The effect of ecosystem size and its quantitative components such as lake area and depth have been widely discussed as a potential driving force. This is due to larger habitats potentially allowing for greater opportunity for sympatric species to maintain their distance from one another within the habitat and to utilize different resources (Baillie et al., 2016; Chavarie et al., 2018; Jonsson & Jonsson, 2001; Seehausen & Wagner, 2014). Depth in particular has been implicated for its role in increasing habitat availability and the opportunity for niche exploitation (Chavarie et al., 2018; Gordeeva et al., 2015; Recknagel et al., 2017; Seehausen & Wagner, 2014;

Siwertsson et al., 2010). In addition, significant physiological changes resulting from varying light levels, oxygen levels, and prey types in different areas of a habitat may increase divergent selection (Baillie et al., 2016; Chavarie et al., 2018; Seehausen & Wagner, 2014). Other abiotic factors such as oxygen levels, pH, and nutrient levels may also have an influence by affecting prey availability and physiological viability within a habitat (Klug, 2002; Persson et al., 2008; Straskrabova et al., 2009). Gaining a better understanding of the mechanisms of diversification relies first on identifying generalities about the association between physical environment and speciation.

In addition to abiotic factors that often vary between lakes and populations, biotic factors such as predation and competition level may facilitate and reinforce divergence. For example, the presence of a predator within a particular zone of a lake can differentially select for avoidance strategies and physiologies for the fishes in that zone (Olafsdottir et al., 2007; Vamosi, 2002). High levels of interspecific competition in lakes may reduce the potential for divergence if different ecomorphs are outcompeted in certain lake habitats (Derome & Bernatchez, 2007; Gavrillets et al., 2007; Jorgensen & Klemetsen, 1995; Trudel et al., 2001). Alternatively, the presence of a competitor in a particular habitat may act to alter a niche or increase niche breadth in part of a population, leading to divergence due to competitors and generalists being excluded (Knudsen et al., 2006; Schluter, 1994). The density and size profile of available prey for a focal fish species may also drive divergence, particularly where there is significant intraspecific or interspecific competition for a specific prey type (Knudsen et al., 2006; Schluter, 1994). Thus, biotic factors are clearly closely tied to and may co-vary with abiotic factors within and among lakes.

Following the end of the last Ice Age, the retreating ice in the Northern Hemisphere left behind many isolated freshwater lakes of varying sizes (Fenton et al., 2023; Geirsdottir et al., 2009; Tornqvist &

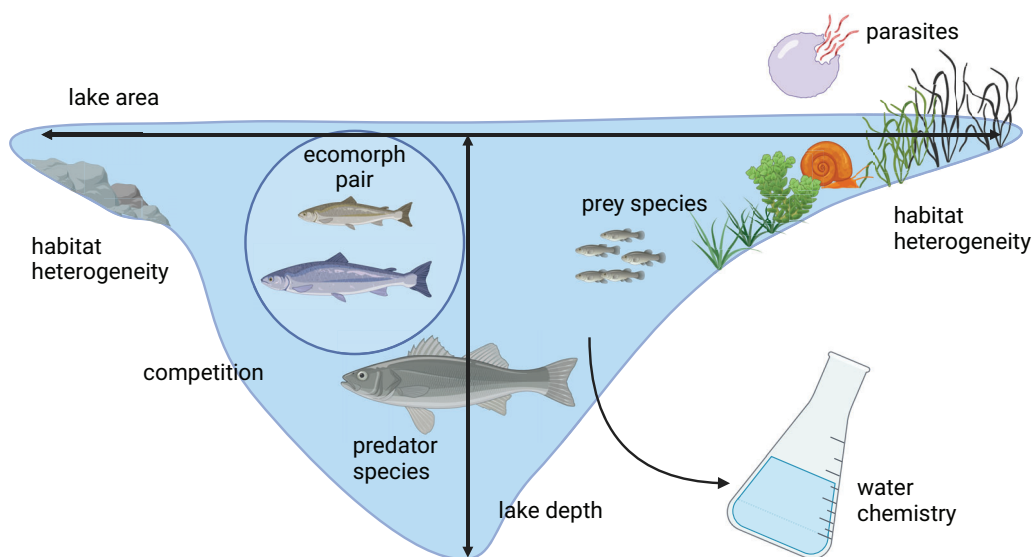


FIGURE 1 Conceptual diagram of the different components examined in this paper and how they may relate to origins and maintenance of sympatric divergent ecomorphs. Created with [BioRender.com](https://www.biorender.com).

Hijma, 2012). Fishes that colonized these lakes came mainly from the marine environment, with limited dispersal and gene flow between lakes following colonization (Wilson et al., 2004). These postglacial lakes were species depauperate and relatively oligotrophic at their origin and remain so in contemporary times (Præbel et al., 2013; Schluter, 1996). Typical extant fish faunas in these regions include perch, salmonids, stickleback, minnow, burbot, and sunfish (Landry et al., 2007; Recknagel et al., 2017; Robinson et al., 1993, 1996; Scharnweber et al., 2016; Siwertsson et al., 2010; Vamosi, 2003). Of these, salmonids and stickleback have been studied particularly in depth.

A feature pervasive in many northern postglacial lakes is that some species of fishes within them diverged into multiple “ecomorphs” (or ecotypes) with distinct life histories and ecologies, utilizing different zones within the lakes, feeding on different prey, and being reproductively isolated (Seehausen & Wagner, 2014). Many postglacial lakes that contain multiple ecomorphs of a species are thought to have derived from multiple colonization events (Verspoor et al., 2010) or occasionally from sympatric divergence (Jacobs et al., 2020). Some ecomorphs show signs of reinforcement of historical allopatric differences driven by ecological conditions after populations came into sympatry (Schluter, 2001; Seehausen & Wagner, 2014). The propensity to diverge into ecomorphs appears not to be equally distributed across species; salmonids and stickleback are most abundantly recorded as diversifying while there is no evidence of such diversification in other common fishes such as burbot and minnow (Seehausen & Wagner, 2014). The number of divergent ecomorphs within a lake ranges from two (often called a “species pair” or “ecomorph pair”), as in most lacustrine diverged three-spined stickleback *Gasterosteus aculeatus* populations (Kozak et al., 2013; McGee et al., 2013; Natsopoulou et al., 2012; Olafsdottir et al., 2007) and often benthic-limnetic *Coregonus*, *Salvelinus*, or piscivore *Salmo*, to several in some charr of the genus *Salvelinus* (maximum recorded is 7, found in *Salvelinus malma*) and in whitefishes of the genus *Coregonus* (Bryce et al., 2016; Elmer, 2016; Kahilainen et al., 2019; Markevich et al., 2018; Sibthorpe et al., 2006).

Ecological divergence due to resource competition and character displacement is often considered a likely explanation for the arising of two or more ecomorphs from a single generalist. Factors of the lakes themselves might contribute to the maintenance of and increase in ecological divergence over time in postglacial fish populations (Jonsson & Jonsson, 2001; Schluter, 2001; Seehausen & Wagner, 2014). It has been widely established that postglacial fish populations show high levels of genetic, heritable plastic/epigenetic, and developmental diversity (reviewed in, e.g., Seehausen & Wagner, 2014; Elmer, 2016; Skúlason et al., 2019). This diversity corresponds to niche-related characteristics such as feeding morphology (Ahi et al., 2014; Blain et al., 2023; Guðbrandsson et al., 2018; Lundsgaard-Hansen et al., 2013), body shape and swimming physiology (Laporte et al., 2016; Recknagel et al., 2017), colouration (Boughman, 2001; Boughman et al., 2005), and anti-predator morphology (Smith et al., 2015). It is also widely accepted that selection acting on this variation is likely to be linked to differences in environmental conditions among lakes (Harrod, Mallela & Kahilainen, 2010;

Öhlund et al., 2020; Seehausen & Wagner, 2014; Siwertsson et al., 2010; Skúlason et al., 2019). It is not well understood precisely which conditions are relevant and whether they are consistent drivers of divergence across postglacial fish species and geographical areas, though evidence exists that repeatability of trait divergence may vary among species (Blain et al., 2023). Research to date has investigated biotic and abiotic factors to varying extents and in local or regional contexts and particular species. However, we generally lack a geographical and taxonomically broad synthesis of the state of knowledge and data available for the potential environmental and ecological associates of diversification in postglacial freshwater fishes. Anthropogenic factors such as climate change, dam construction, invasive non-native species, and eutrophication are increasingly affecting freshwater systems, with the collapse of some postglacial fish species complexes already recorded (Taylor et al., 2005; Vonlanthen et al., 2012). Understanding the mechanisms that create and maintain particularly diverse fish species complexes, such as multiple ecomorphs in sympatry, is therefore of significant importance to their conservation and future use as model systems, with potential applications to maintaining species diversity in other systems (Brodersen & Seehausen, 2014; Jacobs et al., 2019; Skúlason et al., 2019).

In the current study, we compile and discuss evidence from a broad base of published literature on the biotic and abiotic factors associated with ecological divergence in postglacial freshwater fish species (see Supplementary Methods). We focused on three well-studied and widely distributed teleost fish genera renowned for frequent divergences and multiple sympatric ecomorphs in freshwater lakes—*Coregonus*, *Salvelinus*, and *Gasterosteus*—to maximize the generality of our results across species and geographical areas. Our aim is not to infer convergent ecomorphs between these three genera, but to focus on the replicated divergence itself; that is, the presence of one v. multiple sympatric ecomorphs. We identified and focused on seven multi-lake geographic regions that had been investigated for biotic and abiotic correlates of ecological divergence in endemic populations of these genera (Figure 2). We explored potential environmental factors associated with the presence of unimodal (single ecomorph) v. multimodal (two or more ecomorphs) populations of the same species in the same area (Table 1), and synthesized background from a range of studies that tested those relationships directly or indirectly. Finally, we highlight key data gaps from biological and environmental perspectives, and suggest the need for further study into some factors, especially with regard to current threats to freshwater ecosystems and their species complexes.

2 | ABIOTIC FACTORS

2.1 | Lake size (area and depth)

2.1.1 | Background

Due to their role in creating and maintaining diverse habitats, lake bathymetric variables have been broadly implicated in the presence of multimodal fish populations. Considering depth and habitat

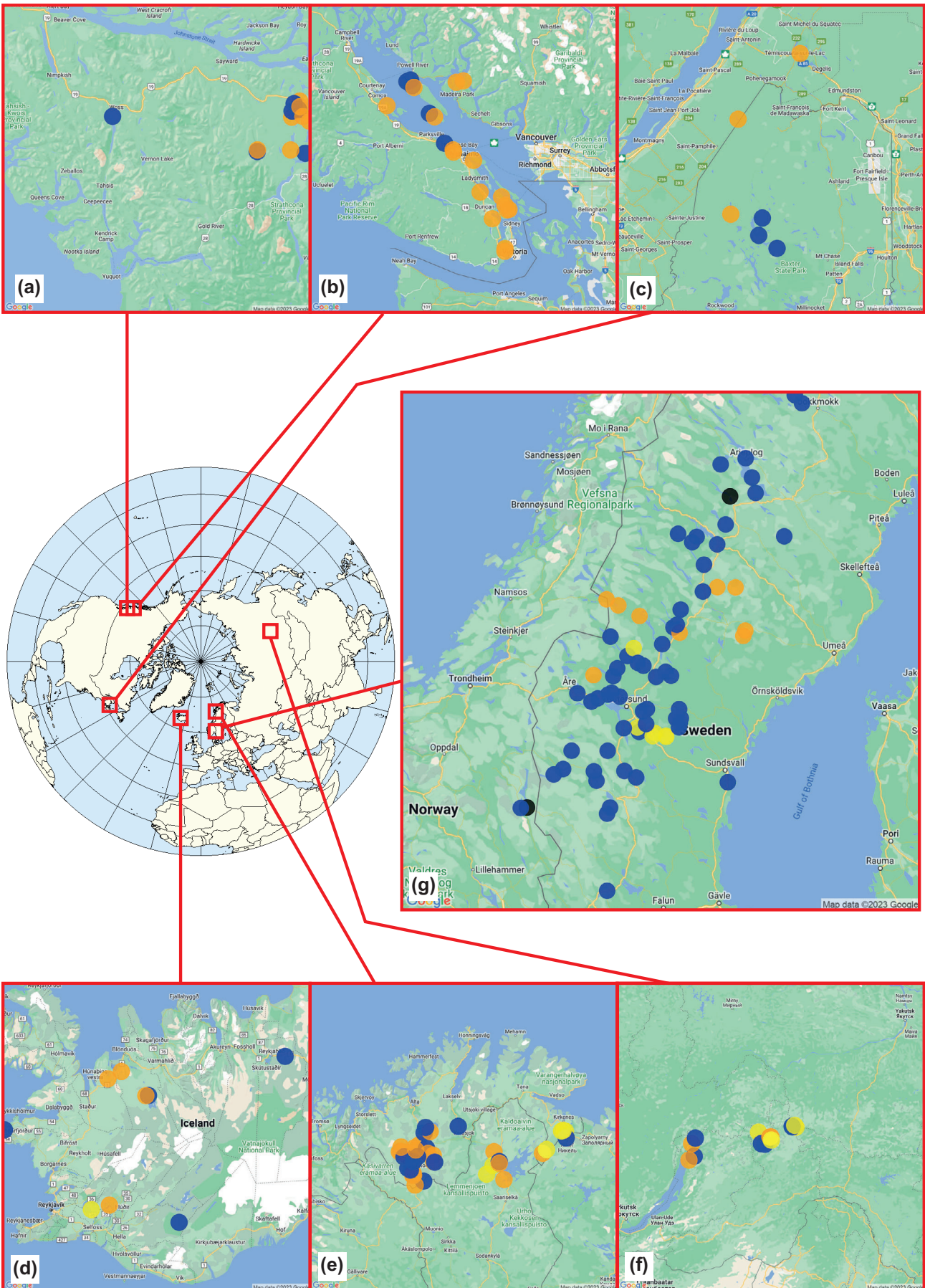


FIGURE 2 Legend on next page.

complexity is key because divergence along continuous habitat gradients (and depth gradients in particular) is one of the most common forms of divergence identified in freshwater fish (Seehausen & Wagner, 2014). Greater lake depth often results in greater habitat complexity, as well as increased overall habitat size, facilitating intra- and interspecific divergence along selection gradients (Bolnick et al., 2015; Recknagel et al., 2017; Schluter & McPhail, 1993; Skoglund et al., 2015). Although it is intuitive and often demonstrated that more area provides greater opportunity for diversification (Kisel et al., 2011; Kisel & Barraclough, 2010; Losos & Schluter, 2000), in lakes the relationship is not simple given that two-dimensional increase in lake surface area does not necessarily link to more complex, volume-dependent habitat.

The extent to which lake depth is required to facilitate divergence is debated (Chavarie et al., 2017). It has been suggested that the role of maximum depth in ecological divergence and ecomorph number is due to the variation in temperature, nutrient, and predation profiles and available prey at different lake strata, an effect that is magnified in deeper lakes and which may promote adaptive divergence between populations at different depths (Helland et al., 2008; Ohlberger et al., 2008; Ohlberger et al., 2013; Schluter and McPhail, 1993). Sexual selection may also play a role due to light levels at depth altering the visibility of signaling colouration (Boughman, 2001; Boughman et al., 2005). In terms of morphology and niche use within a lake, for example, Chavarie et al. (2018) found that for lake charr (also called lake trout) *Salvelinus namaycush* ecomorphs inhabiting Great Bear Lake in Canada, the depth axis could not fully explain divergence between ecomorphs, potentially due to increased environmental complexity at shallower depths and the extremely large lake size (Chavarie et al., 2018). In contrast, division between depth strata explained the greatest degree of molecular divergence and genetic structuring among *S. namaycush* in Lake Superior (Baillie et al., 2016), with similar results found in Lake Neuchâtel (Switzerland) *Coregonus* ecomorphs (Vonlanthen et al., 2009) and in Lake Tinnsjøen (Norway) *Salvelinus alpinus* ecomorphs (Østbye et al., 2020). In a case of extreme diversification, seven divergent ecomorphs of *Salvelinus malma* have been reported in the very large lake Kronotskoye (Russia; 136 m depth, 246 km²) (Markevich et al., 2018). In some cases, lake depth can be seen to play a key role even in small lakes. For example, the relatively small (1.3 km²) Rush Lake near Lake Superior in the USA has a shallow water “lean” ecomorph and a deep water “huronicus” ecomorph (Chavarie et al., 2017). Despite its small area, this lake has a high maximum depth of 86 m, further implicating the importance of lake depth, potentially over lake size, on habitat availability and thus probability of divergence. With depth comes temperature change, and a model-based approach by Ohlberger et al. (2013) attributed divergence

between deep and shallow water *Coregonus* ecomorphs to temperature-associated adaptation to foraging at different depths, effectively linking depth variation to changing selection pressures as well as increased habitat availability.

Habitat availability can be represented roughly by individual size metrics. A more accurate and informative way to describe habitat availability is when it is represented as “ecosystem size,” a descriptor based on the first component of a principal component analysis (PCA) performed on the various available, but often correlated, lake size traits such as volume, surface area, maximum depth, mean (Recknagel et al., 2017) or maximum lake depth, and lake surface area (Jacobs et al., 2020). Other research on the importance of “ecosystem size” has calculated it more simply, for example, from volume (m³) (Post et al., 2000) or lake surface area (Lucek et al., 2016). Research on Scottish *S. alpinus*, which considered ecologically relevant morphological variation within 30 lakes (but not sympatric ecomorph number), found that head depth variation increased positively with ecosystem size (Hooker et al., 2016; Recknagel et al., 2017). A study including Scottish and Transbaikalian *S. alpinus* found that genome-wide genetic diversity and ecomorphological variation (mean trait variance) within ecomorphs, including from unimodal populations through to multimodal populations, increased positively with ecosystem size (Jacobs et al., 2020). Further, difference in ecosystem size among lakes correlated with the direction of allele frequency differentiation in putatively adaptive loci and genome wide, suggesting gene flow reduction and selection operating with lake size and depth (Jacobs et al., 2020).

Background evidence is, therefore, present in concept reviews and single-lake/single-species studies for the role of lake size in ecomorph diversification.

2.1.2 | Synthesis of focal studies

Evidence for the role of lake size in our focal genera and regions (Table 1) was mixed. The majority of studies identified a positive correlation between the presence of ecomorphs and at least one measure of habitat size (Figure 3), yet the significance of different bathymetric characteristics varies among systems. In Fennoscandian *C. lavaretus* populations, the number of distinct ecomorphs was found to be positively associated with lake bathymetric characteristics, including surface area, perimeter, and maximum depth (Öhlund et al., 2020; Siwertsson et al., 2010). Research on Transbaikalian *S. alpinus* found no effect of lake surface area but increased ecomorph divergence in deeper lakes (depth range 17–80 m) (Gordeeva et al., 2015). In contrast, a study of Icelandic *G. aculeatus* found greater divergence in larger (by surface area) but not deeper lakes

FIGURE 2 Map showing locations of lake regions included in focal multi-lake comparison studies explored in our review, constructed using the ggmaps package in R (Kahle & Wickham, 2013; RStudio Team, 2021). Orange dots indicate lakes containing one ecomorph, blue indicates two ecomorphs, yellow indicates three ecomorphs, and black indicates four ecomorphs. (a) Lakes in British Columbia, Canada; (b) lakes on and near Vancouver Island, British Columbia, Canada; (c) lakes in Maine, USA, and Quebec, Canada; (d) lakes in Iceland; (e) lakes in Fennoscandia; (f) lakes in Siberia; (g) lakes in Scandinavia (a subset from Öhlund et al., 2020). Northern Hemisphere map from Wikipedia (2021).

TABLE 1 Summary of focal papers studying ecomorph divergence of *Gasterosteus*, *Salvelinus*, or *Coregonus* in multiple lakes.

References	Location	Species	Factors differing between ecomorphs	Number of lakes	Variables investigated	Effects identified
Bolnick and Lau (2008)	British Columbia	<i>Gasterosteus aculeatus</i>	Gill raker length and number	14	Surface area Perimeter Littoral/pelagic ratio	Greater divergence in gill raker number (not length) in lakes with intermediate surface area and perimeter Greater divergence in gill raker number (not length) in lakes with intermediate littoral/pelagic ratio
Gordeeva et al. (2015)	Trans-baikalia	<i>Salvelinus alpinus</i>	Body size, gill raker length and number, number of lateral line scales, genetic divergence	14	Surface area Maximum depth	No effect of surface area Greater divergence in lakes with greater maximum depth
Landry et al. (2007)	Northeast USA	<i>Coregonus clupeaformis</i>	Body shape, gill raker number, genetic divergence	6	Mean depth Dissolved oxygen gradient Dissolved Organic Matter (DOM) Dissolved Inorganic Carbon (DIC) Phosphorus pH Chlorophyll- α concentration Zooplankton biomass and density Zooplankton length	Reduced divergence in lakes with greater mean depth Greater divergence in lakes with a steeper dissolved oxygen gradient Greater divergence in lakes with more DOM No effect of DIC Greater divergence in lakes with higher phosphorus No effect of pH No effect of chlorophyll- α No effect of zooplankton biomass or density Greater divergence in lakes containing smaller zooplankton and narrower size distributions
Landry and Bernatchez (2010)	Northeast USA	<i>C. clupeaformis</i>	Body shape, gill raker number, genetic divergence	6	Benthic prey density Benthic prey length	No effect of benthic prey density Greater divergence in lakes containing longer benthic prey
Lucek et al. (2016)	Iceland	<i>G. aculeatus</i>	Spine length, pelvic girdle length, head and upper jaw length, snout length and width, eye diameter, body shape	9	Surface area Maximum depth	Greater morphological divergence in lakes with greater surface area but no effect on number of ecomorphs No effect of maximum depth

TABLE 1 (Continued)

References	Location	Species	Factors differing between ecomorphs	Number of lakes	Variables investigated	Effects identified
Öhlund et al. (2020)	Scandinavia	<i>Coregonus lavaretus</i>	Gill raker number, Fst, body size	358 (73 sampled for gill raker number and Fst)	Surface area Maximum depth Number of non-focal species Presence of predator (pike <i>Esox Lucius</i>)	Greater divergence in lakes with greater surface area and maximum depth Greater divergence in lakes with greater non-focal species diversity Greater divergence in lakes with pike
Stiwertsson et al. (2010)	Fenno-scandia	<i>C. lavaretus</i>	Gill raker number	39	Surface area Perimeter Maximum depth Phosphorus Nitrogen Number of non-focal species	Greater divergence with increasing surface area, perimeter, and maximum depth (summarized as PC1) Greater divergence with increasing phosphorus No effect of nitrogen Greater divergence in lakes with greater non-focal species diversity
Vamosi (2003)	British Columbia	<i>G. aculeatus</i>	Body shape, spine length, pelvic girdle length	22	Surface area Perimeter Mean depth Littoral zone area (%) pH Secchi depth Number of non-focal species	No effect of surface area, perimeter, or mean depth on level of divergence No effect of littoral zone area on level of divergence No effect of pH or Secchi depth on level of divergence Multiple ecomorphs only found in lakes with no other species, except cutthroat trout <i>Oncorhynchus clarkii</i>

Note: All were multi-lake comparisons that distinguished between single and multi-ecomorph populations.

(Lucek et al., 2016). It was speculated that this may be due to the relatively shallow depth of many Icelandic lakes containing multimodal *G. aculeatus* populations (Lucek et al., 2016). In addition, European *G. aculeatus* populations tend to diverge between benthic habitats rather than along a steep depth axis (in contrast to the divergences seen in *Coregonus* and *Salvelinus*) (Lucek et al., 2016; Olafsdottir et al., 2007). Alternatively, this may be due to biological differences between salmonids and stickleback. Lake surface area and its relationship to area of benthic habitat may therefore be of greater importance in these shallow lakes.

In contrast, deep lakes found in Russia and Scandinavia show greater effects of depth compared with surface area. The correlation of bathymetric variables with the number of ecomorphs, which differ in gill raker numbers, indicates that increased habitat size may allow greater dietary divergence among ecomorphs, possibly by providing more diverse or abundant prey types. Interactions between predation regime and prey availability with lake size in determining selection regime have been suggested (Bolnick & Ballare, 2020; Öhlund et al., 2020). However, further studies of the relationships between lake size and biotic agents of selection would be beneficial to determine the mechanisms by which lake size may affect divergence.

Although some studies found positive correlations between ecomorph number and lake size, other studies found negative or non-linear relationships. Western North American *G. aculeatus* studied by Bolnick and Lau (2008) were found to be more diverged in gill raker number (but not length) in intermediate-sized (c. 0.5 km²) compared to large or small lakes, reflecting response to disruptive selection by limnetic and benthic ecomorphs with different foraging morphology. This divergence corresponds to dietary divergence, with a later study of the same lakes finding that interindividual dietary dissimilarity was greatest in lakes of intermediate size (Bolnick & Ballare, 2020). Intermediate-sized lakes may therefore provide greater prey diversity. Greater consumption of pelagic prey was found in large lakes (Bolnick & Ballare, 2020). This may indicate a greater availability of pelagic prey in large lakes; however, it may also indicate a reduced availability of benthic prey. If availability of benthic prey is low but pelagic prey is readily available, a single pelagic-foraging ecomorph may be favored over divergence into benthic and pelagic foragers (Bolnick & Ballare, 2020). In contrast, also in western North American lakes, Vamosi (2003) found that the occurrence of multimodal *G. aculeatus* populations was not associated with lake surface area, perimeter, or mean depth.

A negative association between lake size and divergence was found only in lakes containing distinct “dwarf” and “normal” *C. clupearformis* ecomorphs, which were shallower (lower mean depth) compared with those containing monomorphic populations (Landry et al., 2007). Although the mean depth of the lake is expected to be positively correlated with maximum depth (Recknagel et al., 2017), this may not be straightforward in lakes with large areas of shallow topography. Mean depth is also often negatively related to factors such as the area of littoral zone (i.e., shallow, vegetated area) (Recknagel et al., 2017). Littoral zone area increases the potential for divergence due to increased habitat divergence and availability

(Verspoor et al., 2010). The relationship between lake depth and ecomorph divergence is indirect and driven also by other environmental factors.

There are too few comprehensive studies available to make definite conclusions about how lake size relates to ecomorph number, considering factors such as lake location and species studied. However, it is interesting to note that all North American studies produced negative, non-significant, or non-linear results, whereas Eurasian studies mainly found positive associations. The positive associations between degree of phenotypic divergence and lake size in Icelandic, Scandinavian, Fennoscandian, and Siberian lakes (Gordeeva et al., 2015; Lucek et al., 2016; Öhlund et al., 2020; Siwertsson et al., 2010) support the idea that increasing lake size increases ecological opportunity for divergence, particularly in terms of feeding ecology, and may therefore be key in allowing multiple ecomorphs to coexist. However, the lack of a relationship found in British Columbian lakes (Vamosi, 2003), the non-linear relationship identified in western Canadian lakes (Bolnick & Lau, 2008), and the negative correlation by Landry et al. (2007) show that the relationship between divergence and lake size is complex and may depend on other characteristics of the lake and the species (Blain et al., 2023). Importantly, although lake size is relatively frequently studied and reported, the studies we evaluated used different statistical and descriptive approaches of bathymetric and biological diversity. This makes it challenging to draw comparisons across studies. Overall, our synthesis suggests that lake size is often but not always associated with ecological divergence in postglacial freshwater fish populations, tending to a linear positive relationship (Figure 3). Nonetheless, the role of lake size likely depends also on other factors.

2.2 | Habitat heterogeneity

2.2.1 | Background

The degree of habitat heterogeneity within a lake is a likely candidate for driving or maintaining ecological divergence into multiple ecomorphs due to its contribution to the availability of different niches and thus opportunities for divergent adaptation (Verspoor et al., 2010). A review by Seehausen and Wagner (2014) identified various (mainly single-lake) examples in postglacial and other fish species of habitat gradients being correlated with ecological opportunity for divergence in freshwater fish populations. However, heterogeneity is a challenging underwater characteristic to measure and compare, and often simplified as “littoral zone area” or as the “ratio of littoral to pelagic habitat” within a lake. Research on Scottish and Irish lakes suggests that proportion of littoral zone is negatively correlated with lake depth (Recknagel et al., 2017), meaning that important aspects of its role might be more easily summarized in other bathymetric characteristics. Larger and deeper lakes often contain a relatively lower proportion of littoral zone area and vice versa, and metrics such as the ratio of littoral to pelagic zone (Bolnick & Lau, 2008) or ecosystem size (Nosil & Reimchen, 2005; Recknagel et al., 2017) (also see “lake size”

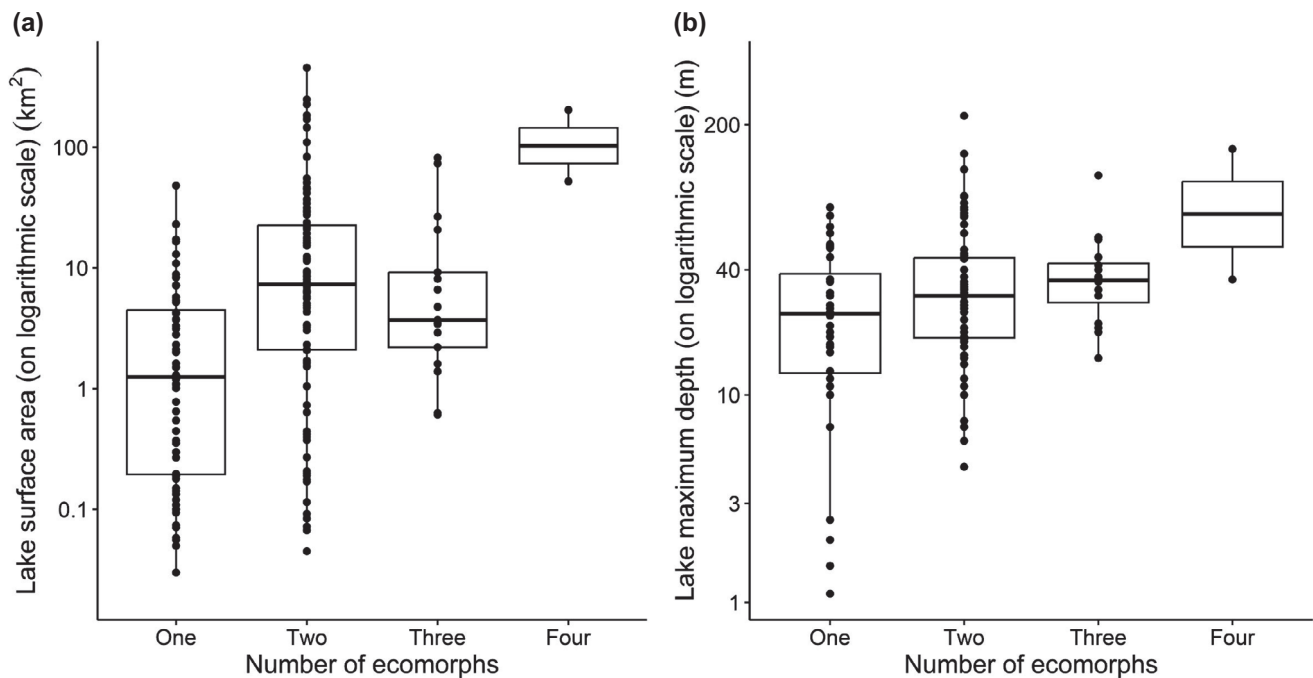


FIGURE 3 Visual representation of trends in ecomorph number based on bathymetric traits. (a) Lake surface area (km²). Data from Bolnick and Lau (2008), Gordeeva et al. (2015), Lucek et al. (2016), Öhlund et al. (2020), Siwertsson et al. (2010), and Vamosi (2003). (b) Lake maximum depth (m). Data from Gordeeva et al. (2015), Landry et al. (2007), Öhlund et al. (2020), and Siwertsson et al. (2010). Box plots indicate median and interquartile range. Note that the y-axes in graphs consist of untransformed data but are plotted on logarithmic scales due to the large range in reported values for these variables. Graphs plotted in R using the ggplot2 package (Wickham, 2016).

earlier) can seek to unite this information on the relationship of size and ecological opportunity that is meaningful for fishes.

2.2.2 | Synthesis of focal studies

The effects of habitat heterogeneity as a separate variable appear mainly to have been investigated in multi-lake studies focusing on British Columbian *G. aculeatus*. Intermediate ratios of littoral to pelagic habitat were found to be associated with greater divergence in gill raker number between *G. aculeatus* ecomorphs (Bolnick & Lau, 2008), indicating that dietary divergence may therefore be facilitated by areas of both littoral and pelagic habitat, allowing space for a diversity of fish and prey in each (Table 1). However, Vamosi (2003) found no effect of percentage littoral zone on ecomorph number. Evidence for Icelandic *G. aculeatus* populations found that ecomorphs were strongly associated with different benthic habitats, with morphs differing in antipredator defenses and diet associated with rocky substrate (“lava” morph), muddy substrate (“mud” morph), and algae of the genus *Nitella* (“nitella” morph) (Lucek et al., 2016).

Overall few studies examine the relationship between habitat heterogeneity and increasing ecomorph number. More examples are needed from more species and geographical areas in replicate across lakes and taxa. This variability in reporting and rarity of measurement means we could not draw concerted conclusions in the case of post-glacial fish populations.

2.3 | Nutrient levels and environmental chemistry

2.3.1 | Background

Although lake bathymetric variables have received relatively more attention as drivers of ecological divergence, other abiotic factors such as aspects of water chemistry may also play a role. Nutrients such as phosphorus and nitrogen, as well as water qualities such as pH, may alter prey availability and level of vegetated habitat (Klug, 2002; Persson et al., 2008; Straskrabova et al., 2009), as well as water clarity and color. Opportunity for divergence and specialization to different diets, habitats, and light regimes depends on these factors to varying extents (Blain et al., 2023). Selection on traits such as sexual signaling depend on light regime at different depths or levels of vegetation, and thus visibility of signals such as red coloring in *G. aculeatus*, leading to sexual isolation (Boughman, 2001; Boughman et al., 2005). Water color may also contribute to loss or maintenance of sexual coloration, particularly if loss of visibility at key wavelengths (e.g., 400 nm for red coloration) occurs (Boughman, 2001; Reimchen, 1989). Greater availability of a range of prey types may increase the probability of niche specialization and thus divergence between ecomorphs, whereas high availability of a single prey type (or a lack of prey diversity) may facilitate generalist feeding by reducing competition (Garduño-Paz & Adams, 2010; Huss et al., 2008; Landry & Bernatchez, 2010). Evidence for diversifying selection has been found in European perch *Perca fluviatilis* inhabiting low pH lakes

with very low visibility (“humic” lakes) v. clear lakes (Ozerov et al., 2022). Fish in humic conditions show high levels of genetic adaptation to these conditions, mainly associated with neural development and ion exchange. Although these parameters may be consistent across nearby lakes, they can also vary at short temporal scales, by seasons, and can be strongly influenced by the regional geology (Hamilton et al., 2001; Moss, 2011). It may therefore be challenging to draw conclusions about the long-term selective effects of chemical and nutrient-related parameters, and it has been proposed that in systems with high nutrient flux, plasticity may be favored over divergence (Skúlason et al., 2019).

Although limnological factors are well characterized in some regions, their correlations with fish diversity and ecomorphs are less well explored from the perspective of diversification and ecological speciation. The effects of nutrient levels are possibly due to correlations between these and increased vegetation and prey availability in some instances (Rijal et al., 2021; Wang et al., 2020). At the extreme, excessive nutrient loading resulting in eutrophication has been implicated in the collapse of species flocks of postglacial fishes in some Alpine lakes (Vonlanthen et al., 2012) and its reduction with a return to ecomorph diversity with re-oligotrophication (Hirsch et al., 2013; Jacobs et al., 2019). The environmental gradients that come with lake depth and other aspects of habitat size may therefore be as—if not more—important than the simple presence of larger habitats in allowing multiple ecotype populations to persist.

2.3.2 | Synthesis of focal studies

Across our regionally replicated studies, significant positive correlations were found between phosphorous, nitrogen, and dissolved organic matter levels and the number of morphologically and/or genetically distinct ecomorphs in European and North American *Coregonus* species (Figure 4) though no effect of dissolved inorganic carbon was found (Landry et al., 2007; Siwertsson et al., 2010) (Table 1). These studies demonstrate that increased nutrient levels may increase productivity and therefore divergence through increased diversity or abundance of prey items.

No effect of pH, chlorophyll α levels, or water clarity was found on probability of divergence in well-studied populations of western North American *G. aculeatus* and eastern North American *C. clupeaformis* (Landry et al., 2007; Vamosi, 2003) (Table 1). But with little data, an effect of these parameters cannot be ruled out until more systems are analysed both across depths and annual cycles. Chlorophyll α levels and water clarity may be used as indicators of productivity and therefore food availability and diversity within lakes, and therefore be associated with divergence (Hamilton et al., 2001). It could therefore be theorized that increased chlorophyll α and reduced water clarity may be associated with increased diversification; however, these were not found to be correlated with degree of divergence in *C. clupeaformis* (Landry et al., 2007).

These results indicate potential positive effects of nitrogen, phosphorus and dissolved organic matter. Further analysis of ecological

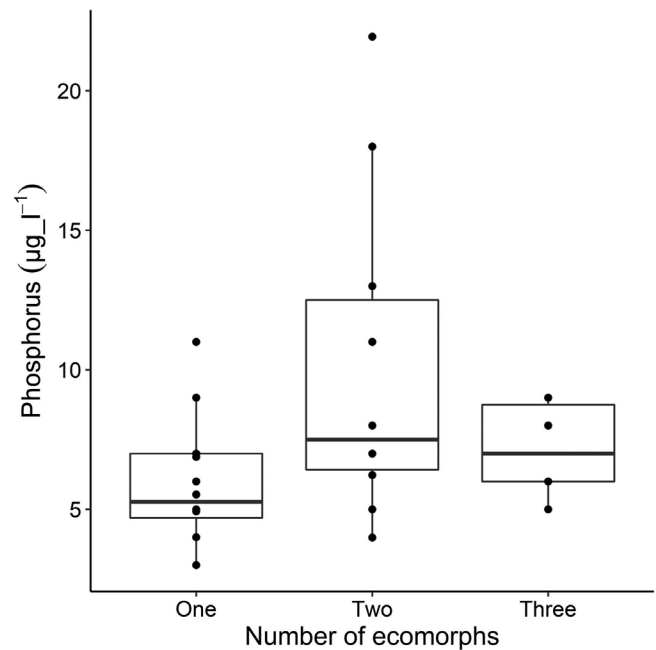


FIGURE 4 Visual representation of trends in ecomorph number based on phosphorus concentration ($\mu\text{g L}^{-1}$). Data from Landry et al. (2007) and Siwertsson et al. (2010). Graph plotted in R using the ggplot2 package (Wickham, 2016).

gradients associated with increasing habitat size would be highly beneficial for the research field to unravel the effects of bathymetric and limnological variables on ecological speciation.

2.4 | Dissolved oxygen

2.4.1 | Background

Access to dissolved oxygen is essential for fish, which rely on aqueous gas exchange for their respiratory needs. However, adaptation to low oxygen levels is well documented among fishes, in some cases leading to significant changes in morphology, behavior, or physiology to cope with hypoxic conditions (Domenici et al., 2017; Pineda et al., 2020). Adaptation to low oxygen through increased ventricle thickness (associated with higher cardiac output) has been recorded in *S. alpinus* (Anttila et al., 2015), though changes in morphology or physiology in postglacial species have not yet been linked to divergence. Evidence for divergence based on oxygen level has also been found in cichlid fishes, where plastic increases in gill length and associated increases in head depth have been found to result from exposure to low oxygen (Crispo & Chapman, 2011). Such adaptations may be costly, however, and therefore reduce the fitness of fishes not exposed to hypoxia. Changes in oxygen availability, which are frequently found along depth gradients (Seehausen & Wagner, 2014), therefore have the potential to produce significant adaptive divergence between populations living under different conditions.

2.4.2 | Synthesis of focal studies

Despite evidence for behavioral, physiological, and morphological changes resulting from exposure to low oxygen, we found only one study on postglacial fish related to number of ecomorphs (Table 1). Landry et al. (2007) found that lakes containing two ecomorphs also contained the lowest levels of dissolved oxygen at the bottom of the lake, indicating a high oxygen depletion gradient compared to the lakes containing single ecomorphs (Table 1). As ecomorphs are divergent in both feeding ecology (gill raker number) and body shape (Bernatchez et al., 1999), the authors (Landry et al., 2007) suggested that the oxygen depletion gradient corresponds to greater divergence between benthic and limnetic feeding types. Adaptation to low oxygen concentrations in benthic feeders may increase adaptive divergence by reducing the potential for habitat crossover and mating between ecomorphs, particularly if the limnetic ecomorphs are more sensitive to hypoxia (Landry et al., 2007; Landry & Bernatchez, 2010). Tests of hypoxia tolerance among ecomorphs in this system may therefore be a good starting point to identify any physiological adaptations associated with this gradient.

3 | BIOTIC FACTORS

In addition to the abiotic factors, biotic factors are potential driving elements of ecological speciation in postglacial freshwater fishes. Primarily these revolve around the deeply interrelated aspects of predation upon the diverging ecotypes, competition with other species in the lake (outside the diversifying species pairs), and prey availability (Knudsen et al., 2016; Landry et al., 2007; Landry & Bernatchez, 2010; Öhlund et al., 2020; Siwertsson et al., 2010, 2016; Vamosi, 2003). Diet is a key component of divergence in freshwater fish populations (Seehausen & Wagner, 2014), with many indicators of divergence, for example, gill raker length, being primarily driven by changes in diet. Competitors and predators also play a key role, by both creating and filling niches within the environment (Skúlason et al., 2019). Intraspecific competition may be dampened by predation and interspecific competition, such that it is not strong enough to drive further specialization of diversifying taxa due to reduced density of individuals and shifting selective landscapes during ontogeny (Schluter, 2000; Vamosi, 2003). Because other fish species can be both competitors and predators of the diversifying ecomorphs depending on life stage, these categories tend to be challenging or impossible to disentangle in studies of natural populations. Therefore, most studies have considered overall species diversity within lakes rather than competitors and/or predators.

3.1 | Prey density

3.1.1 | Background

Prey density itself is not commonly studied but clearly relates to prey availability and is reflected in diet, which is extensively studied with

regard to ecomorph specialization and ecomorph number (Jonsson & Skúlason, 2000; Sandlund et al., 1992). Stomach contents analysis shows a common trend of specialization into benthic sources v. pelagic open water plankton sources (Jonsson & Skúlason, 2000; Roesti et al., 2023; Sandlund et al., 1992). These closely associate with trophic morphology and feeding behavior, including characteristics such as gill raker length and number, which are frequently used to indicate the presence of divergent ecomorphs, and specialization to different prey items has been linked to sympatric ecomorph divergence in many species (Bolnick & Ballare, 2020; Bryce et al., 2016; Gordeeva et al., 2015; Jacobs et al., 2019; Öhlund et al., 2020; Siwertsson et al., 2010). It has also been shown that divergence may reinforce itself. For example, diversification in *C. lavaretus* has been found to reduce the size and diversity of zooplankton communities, which in turn may lead to reduced feeding opportunity for morphs not specialized to feed on zooplankton due to intraspecific competition (Kahilainen et al., 2019). Further divergence via specialization on other prey types may therefore be more likely.

Presence of dietary variation and associated morphology such as gill raker length and number may also reinforce diversification through sexual selection (Snowberg & Bolnick, 2008), as intermediate phenotypes are likely to have reduced feeding success and therefore fitness (Hatfield & Schluter, 1999; Vamosi, Hatfield & Schluter, 2000). Although such specialization is a well-recognized feature, the dynamics of its relationship with prey density and availability are less well understood; however, these may explain some trends regarding which lakes do or do not support ecomorph divergence.

3.1.2 | Synthesis of focal studies

Research on eastern North America *C. clupeaformis* found no correlation between the presence of genetic and morphologically differentiated ecomorphs and overall zooplankton prey density, a food source favored by the limnetic “dwarf” ecomorph (Landry et al., 2007). However, a significant correlation with zooplankton prey size distribution was found. The lakes utilized in this study containing more divergent populations also contained a lower density and biomass of large zooplankton prey items, as well as a narrower zooplankton prey size distribution than that of the less diverse lakes. The smaller size and narrower distribution of prey in these lakes may result in increased intraspecific (inter-ecomorph) competition, leading to greater levels of adaptive divergence in feeding ecology and morphology between ecomorphs (Schluter, 1994). A related study by Landry and Bernatchez (2010) using the same *C. clupeaformis* populations found that benthic invertebrates, a major food source for the epibenthic “normal” ecomorph, tended to be longer in lakes containing more divergent populations. Taken together, these papers imply that reduced prey availability in the limnetic habitat and increased availability of larger benthic prey may have facilitated divergence between limnetic and epibenthic *C. clupeaformis* ecomorphs in these lakes. This may stem from greater competition for food in the limnetic zone and greater opportunity for specialization in the benthic zone. It is important to note, however, that direct multi-lake comparisons have only been

carried out on one group of six lakes in the same river basin containing *C. clupearformis*, and further study of the effects of diet more broadly within multi-lake systems would be an important area for further research.

Despite the frequent occurrence of large piscivorous morphs in species such as *S. alpinus*, studies of specialization on piscine prey items are lacking. Although it may be challenging to disentangle precise relationships among fish species at different life stages, identifying whether diversity of piscine food sources may contribute to selective pressures would be an interesting avenue for future research. It would be beneficial to combine studies of prey density and diversity with stomach analyses in lakes of single and multiple ecomorphs, while accounting for seasonal fluctuations in prey availability (Jonsson & Skulason, 1999, 2000).

3.2 | Predation

3.2.1 | Background

Most research has focused on how fish species acting as predators might be driving divergence in ecomorph pairs. Predator species that are not fish but prey upon those fish in diverging ecomorphs likely also play a role. Predator avoidance has been suggested as a driver of adaptation in freshwater *G. aculeatus* populations and their divergence from the defensive phenotypes of their marine ancestors and from phenotypes in other lakes. For example, *G. aculeatus* ecomorphs in Icelandic lakes have been found to differ in predation-related traits such as spine length and size of the pelvic girdle, indicating adaptation to different predation regimes in lakes (Lucek et al., 2016). In British Columbian *G. aculeatus*, significantly improved survival of limnetic compared to benthic stickleback ecotypes has been found in the face of predation by birds that feed on limnetic fish (Vamosi, 2002). However, when predation was incurred by insects feeding on benthic fish, benthic ecotypes showed higher survival rates (Vamosi, 2002). Insects that prey upon fishes have also been implicated in increased juvenile growth rate and reduction in extent of armor and spine development in freshwater stickleback (Marchinko, 2009). Using mathematical modeling based on *C. clupearformis*, Thibert-Plante et al. (2020) found that the model predicted the presence of three ecomorphs in lakes with strong predation pressure from some fish species (pike and perch) but weak predation pressure from other fish species (trout and burbot). The type and size of predators present in a lake may therefore alter selection pressure, due to factors such as varying gape and habitat use (Thibert-Plante et al., 2020).

Significant variation in spine length has been identified between *G. aculeatus* ecomorphs occupying different benthic habitats in Lake Thingvallavatn (Iceland) (Olafsdottir et al., 2007). This may indicate adaptation to different predation regimes, as spines are suggested to provide defense against predation. Significant differences in predation avoidance behavior have also been recorded between *G. aculeatus* ecomorphs inhabiting different benthic habitats in Lakes Thingvallavatn and Frostastadvavatn (Doucette et al., 2003). Behavioral response to predation and other stimuli in *G. aculeatus* has been found to

contain interindividual variation, with predator avoidance behavior and feeding in the presence of a predator showing a high degree of individuality (Bell, 2005, 2009; Bell & Stamps, 2004). Degree of heritability may also vary between populations, implying variation in degree of plasticity (Bell, 2005, 2009). Trait variation, therefore, exists on which selection may act depending on predation regime, and the presence of such variation and adaptation in other species is worth investigating. Trait expression may also vary with ontogeny, meaning that the life stage at which selection pressures are experienced may also play a role (Bell, 2009; Bell & Stamps, 2004).

3.2.2 | Synthesis of focal studies

We found little evidence for geographical or species-specific patterns in the effects of predation or competition. Presence of northern pike *Esox lucius* was found to be a strong predictor variable for presence of multiple *C. lavaretus* ecomorphs in Scandinavian lakes, but only in lakes that were large (>0.88 km²) and deep (>9.6 m) enough to support these ecomorphs (Öhlund et al., 2020). Environmental factors such as lake size may therefore also impact fish anti-predator behaviors and refuges (Reimchen, 1994). Further studies of both intra- and interspecific predation are recommended, as few studies of either specific predator species (Öhlund et al., 2020) or cannibalism by large piscivorous morphs have been carried out, and without these it is challenging to draw conclusions on the mechanisms whereby predation may drive divergence in different systems, particularly in salmonid species.

3.3 | Competition

3.3.1 | Background

Competition, both intra- and interspecific, may force diversification by limiting use of a specific niche for less well-adapted individuals. Alternatively, presence of competitors may limit divergence by reducing the number of available niches that species may utilize. Several studies have identified competition between *C. clupearformis* and the lake cisco *Coregonus artedii*, which occupies a very similar ecological niche to the limnetic dwarf *C. clupearformis* ecomorph (Derome & Bernatchez, 2007; Landry et al., 2007; Landry & Bernatchez, 2010; Trudel et al., 2001). *C. clupearformis* populations with sympatric diversified ecomorphs are thought to occur only in lakes lacking *C. artedii*, implying a significant effect of interspecific competition on the origins or maintenance of diversification of the dwarf ecomorph (Derome & Bernatchez, 2007; Landry et al., 2007; Landry & Bernatchez, 2010; Trudel et al., 2001). Recent work indicates that the competition between *C. artedii* and *C. clupearformis* may not be as extreme as previously considered (Rook et al., 2021); however, evidence is so far correlational and limited by the number of diversified lake replicates.

Competition between very divergent fish species such as prickly sculpin *Cottus asper* and *G. aculeatus* has also been found to shift trait values in both species (Roesti et al., 2023); however, it has not been

directly linked to ecomorph divergence. It was found that *G. aculeatus* in lakes with *Co. asper* displayed increased antipredator traits and greater gill raker numbers, whereas the opposite pattern was observed for *Co. asper*. Stickleback also showed a reduction in benthic diet items consumed, with both species becoming more divergent in diet in sympatry, though this trend was greater for *G. aculeatus* (Roesti et al., 2023). Knudsen et al. (2016) observed almost identical niche use in allopatric profundal benthivorous *S. alpinus* ecomorphs and similar niche use in littoral omnivorous ecomorphs in two Norwegian lakes, suggesting parallel evolution of the profundal specialist despite differing fish communities between the lakes. However, the lake with the more diverse fish community contained an additional piscivorous *S. alpinus* ecomorph, indicating potential effects of increased competition and/or prey availability (Knudsen et al., 2016). Evidence of competition influencing morph divergence is therefore present; however, few multi-lake studies of postglacial populations have been carried out.

3.3.2 | Synthesis of focal studies

In a case where diversifying ecotypes are found in lakes near non-diversifying populations, Vamosi (2003) identified a notable correlation with fish community in the British Columbian *G. aculeatus* system. All lakes studied contained the predatory cutthroat trout *Oncorhynchus clarkii*, but those lakes housing multiple *G. aculeatus* ecomorphs (species pairs) had no other species besides the stickleback and trout. Lakes containing a single *G. aculeatus* ecotype and no sympatric species pair contained on average three other fish species besides *O. clarkii*, indicating that competition reduced opportunity for divergence in these systems. In contrast, research on *C. lavaretus* in Scandinavia (Siwertsson et al., 2010) identified a positive association between the number of divergent ecomorphs and overall species diversity (total number of species) within lakes (Figure 5). Another study on *C. lavaretus* also found a positive correlation between bimodal populations and overall non-focal species richness when richness was standardized for lake size, though this effect was not as strong as *E. lucius* presence (Öhlund et al., 2020). Although species diversity may indicate increased competition, it is also possible that lakes containing greater resource diversity may be able to support both more species and greater numbers of ecomorphs.

Although these studies provide evidence for an effect of lake biota on divergence, they did not separate species into potential competitors and predators (with the exception of *E. lucius* in Öhlund et al., 2020), focusing only on species number. Although identifying competitor species may be challenging, identifying candidate species for competition will depend on future studies identifying the role of species in relation to focal species, and comparing systems with and without these species. In addition, identification of specific species as competitors may provide further links to abiotic factors, depending on the conditions under which different competitors may be present in lakes.

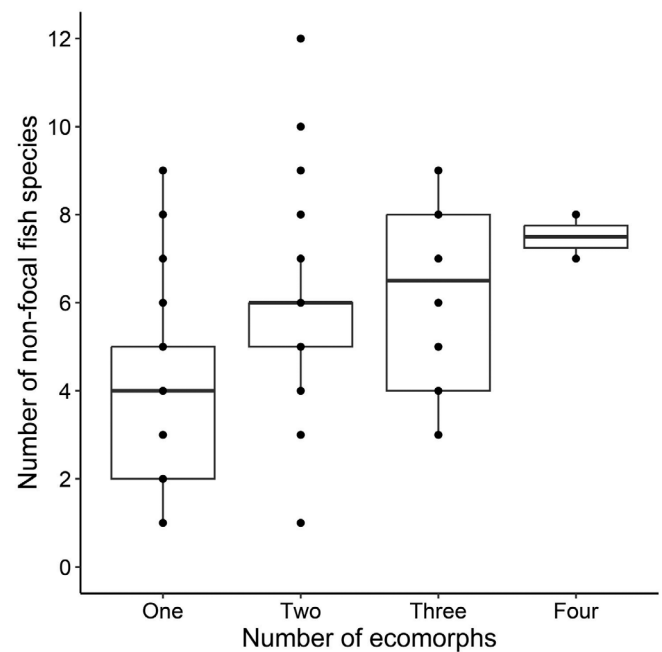


FIGURE 5 Visual representation of trends in ecomorph number based on the number of fish species present in a lake, other than the diversifying species pairs/groups. Data from Siwertsson et al. (2010), Vamosi (2003), and Öhlund et al. (2020). Graph plotted in R using the ggplot2 package (Wickham, 2016).

3.4 | Parasite burden

3.4.1 | Background

In addition to the effects of predation, other interspecies interactions such as parasite burdens may reflect and reinforce isolation between ecomorphs in multimodal populations. Parasite burdens often reflect that fishes consume different diets, which in itself may reinforce isolation through different niche adaptations. Consumption of different prey items may expose fishes to different parasites, as prey items may act as intermediate hosts for different parasites. For example, degree of variation in parasite burden has been linked to degree of variation in diet in *G. aculeatus* (Bolnick & Ballare, 2020). Parasites may also be unrelated to diet but may still vary between ecomorphs based on association with other species. Trematode parasites of the genus *Diplostomum* are thought to be passed to *G. aculeatus* from the freshwater snail species *Radix peregra* (Natsopoulou et al., 2012). These snails are more commonly found in the shallow stony littoral zone and are therefore more likely to affect the ecomorph that inhabits such areas.

Different immune and defensive responses to these parasites may contribute to diversifying selection and canalisation of immune genes. Benthic *G. aculeatus* ecomorphs inhabiting lava habitats in Icelandic lakes (Lakes Thingvallavatn and Hredavatn) hosted significantly more parasites and a different parasite community compared with mud-dwelling ecomorphs from the same lakes (Natsopoulou et al., 2012). The allelic diversity present in each ecomorph at the MHCII β immune locus differed significantly, and this was positively correlated with

parasite diversity and abundance of some parasite species in Lake Thingvallavatn. Arctic charr in Lake Thingvallavatn were also found to exhibit significant intermorph variation in allele frequency at the MHCII α and Cath2 immune genes; however, this was not found to be linked to parasite burden (Kapralova et al., 2013). Significant divergence in allele frequency was found at the MHCII α and β loci between *S. alpinus* ecomorphs in Gander Lake (Canada) and at the MHCII β locus in the Kiryalta Lake system (Russia), though parasite data putatively associated with these immune responses was not included (Conejeros et al., 2014). In addition, significant differences in MHCII β allele frequencies were found between dwarf and normal *C. clupeaformis* ecomorphs in the St John's River basin (USA/Canada) (Pavey et al., 2013). However, this study did not identify parallelism in ecomorph parasite community or allele frequency among lakes, nor did it compare pathogen communities between lakes with distinct multimodal populations and those with indistinct divergence between potential ecomorphs. Research on two Fennoscandian lakes (Fjellfrøsvatn and Skogsfjordvatn) identified greater parasite abundance and diversity in omnivorous littoral zone *C. lavaretus* ecomorphs compared to in profundal benthivorous ecomorphs in the same lake (Siwertsson et al., 2016). In addition, the piscivorous ecomorph present in one lake (Skogsfjordvatn) displayed a parasite burden significantly higher than either of the other ecomorphs inhabiting this lake, suggesting potentially greater parasite risk associated with the piscivorous diet. In *G. aculeatus*, limnetic ecomorphs from Priest and Paxton lakes in British Columbia were found to harbor greater parasite burdens and different parasite communities compared to their benthic counterparts (Maccoll, 2008). However, neither Siwertsson et al. (2016) nor Maccoll (2008) linked their findings to evolutionary responses (or specific parasites) in multimodal populations. Thus, although there is extensive evidence about parasites, host responses, and associations with ecomorphs, it is usually site specific.

3.4.2 | Synthesis of focal studies

Although some studies indicate parasitism-induced selective pressure on immune genes, potentially leading to selection against hybrids and thus increased divergence, comparisons between unimodal and multimodal populations have yet to be carried out. This would be a valuable area for future research, potentially linking limnological and other abiotic factors to parasite burden and associated divergence. It is possible that dietary or habitat changes between diverging ecomorphs lead to differences in burdens of parasites (Siwertsson et al., 2016), which then provide reinforcing selection on immune genes. Further study of dietary habits and habitat use and divergence in allele frequency in immune-associated genes in the early stages of diversification would be needed to confirm this, however.

4 | CONCLUSIONS

Based on the status of the research conducted to date, with emphasis on *Coregonus*, *Salvelinus*, and *G. aculeatus*, we identified two

abiotic environmental factors with a high likelihood of being involved in the origin and maintenance of postglacial freshwater fish ecological divergence into multimodal populations. These were lake size (surface area/perimeter) and lake maximum depth, which several studies found to be positively associated with divergence into multiple ecomorphs. Evidence of positive effects of habitat diversity in the littoral zone was also found (Bolnick & Lau, 2008; Kahilainen et al., 2019). Our synthesis suggests that the bathymetric conditions most conducive to allowing divergence into two or more distinct ecomorphs are likely to be large lakes containing both deep pelagic areas and significant shallow, littoral areas, thus providing diverse benthic and limnetic habitats (Baillie et al., 2016; Chavarie et al., 2018; Ohlberger et al., 2013).

We encourage studies to include a range of bathymetric characteristics, including maximum depth and proportion of littoral zone to describe their study habitats. We suggest that mean depth, being a result of arithmetic rather than a real physical feature of the environment, may be a poor summary of the biologically relevant habitat diversity in a lake. Analysis of environmental variables is further limited by their changes over time with topography and climate. For example, it is possible that some features of depth and complexity observed today may not be representative of the conditions under which multimodal populations arose in the past. Thus, the relationships between contemporary and historical environmental variables and ecological divergence would also benefit from further study.

Nutrient levels may also play a significant role. Phosphorous, nitrogen, and dissolved organic matter levels were identified as being positively correlated with the presence of multimodal populations, though evidence also exists that eutrophication due to excessive nutrient levels may lead to the collapse of species complexes (Vonlanthen et al., 2012), and nutrient reduction to emergences (Jacobs et al., 2019). Both competition and predation have been theoretically implicated in ecological divergence by relationships with overall species number (Öhlund et al., 2020; Siwertsson et al., 2010; Vamosi, 2003); however, only one study (Öhlund et al., 2020) found an effect of a specific predatory species (*E. lucius*). Prey availability was identified as an important and also somewhat understudied variable (Landry et al., 2007; Landry & Bernatchez, 2010). Changes in ecomorph diet may also have indirect effects, including alterations to parasite load, potentially leading to disruptive selection on immune gene complexes (e.g., Siwertsson et al., 2016) and further reducing hybrid fitness.

Although the papers analysed in this study highlight several potentially key factors associated with ecological divergence in postglacial freshwater fish species, the small number of studies that analysed multiple lakes with the aim to identify consistent, putatively causative factors is a significant limiting factor in drawing conclusions. The literature focuses heavily on several well-known species and populations of postglacial fishes such as British Columbian *G. aculeatus*, Scandinavian *C. lavaretus*, and Lake Thingvallavatn *S. alpinus*, though evidence exists of ecological speciation in less well-documented species such as perch *Perca fluviatilis* L. 1758 and sunfish *Lepomis* spp. (Robinson et al., 1993, 1996; Scharnweber et al., 2016). Research effort spanning other multimodal populations would be very

valuable for supporting generalities and overcoming local variation and would facilitate comparing divergence patterns across species and geographical areas. A further difficulty arises in that many papers do not present or make available untransformed data, making it more difficult for reviews and meta-analyses to draw meaningful conclusions. We recommend that future publications consider making untransformed data associated with the paper available for this purpose.

The focus for studies of speciation in postglacial fishes has often been the morphological and genetic features of the ecomorphs themselves, rather than the ecological conditions under which these ecomorphs persist or reasons for divergence (Blain et al., 2023; Østbye et al., 2006; Scharnweber et al., 2016; Verspoor et al., 2010). A large number of lakes therefore remain unstudied or understudied, with presence of multimodal ecomorphs frequently not being linked to ecological data. Lake environments, especially ecosystem size or lake depth, are clearly important drivers of variability especially in salmonids, and this is reflected both within and between species, in natural (Recknagel et al., 2017) and constructed (such as reservoirs) environments (Koene et al., 2020). Rapid environmental changes in some populations have led to species collapse in certain lakes in recent years (e.g., *G. aculeatus* in Enos lake, British Columbia; *C. lavaretus* complex spp. in various Alpine lakes) demonstrating the high value of environmental information in ecological and evolutionary model systems for understanding those changes (Brodersen & Seehausen, 2014; Huuskonen et al., 2017; Vonlanthen et al., 2012). Additionally understudied are the wider ecological consequences of the divergence and collapse of species flocks. This is significant as many of these species play key roles in postglacial ecosystems (Skúlason et al., 2019). Presence or absence of species and associated divergent ecomorphs affect food chain lengths, density and diversity of prey, competitors, and predators (Brodersen et al., 2015; Thomas et al., 2017), and the contribution of other species to food web dynamics (Kahilainen et al., 2019). Terrestrial organisms may also be affected, for example, through changes in prey availability associated with diversification. While availability of piscine prey may increase with diversification, other prey sources may be less available to amphibious and terrestrial predators (Finlay & Vredenburg, 2007). Knowledge of the interactions between environmental conditions and species complexes is therefore vital to management of these systems, which often also provide nutritional and recreational resources to human communities.

The impact of environmental variables on speciation is becoming increasingly appreciated (Jacobs et al., 2020; Knudsen et al., 2016; Seehausen & Wagner, 2014; Siwertsson et al., 2010), and postglacial fish populations provide an excellent opportunity for study due to their isolation and the large number of populations present. Improved knowledge of the reasons behind the persistence or collapse of multimodal fish populations within postglacial freshwater lakes may provide an early indication of what we can expect to see in other diverging species pairs and groups as habitats become altered, and allow us to identify key conservation targets in the coming years.

AUTHOR CONTRIBUTIONS

Kathryn R. Elmer and Kevin Schneider conceived the study and planned the study design. Isabelle C. Tiddy conducted the literature review. Isabelle C. Tiddy analysed data with support from Kevin Schneider. Isabelle C. Tiddy wrote the paper with contributions from Kathryn R. Elmer. All authors read and approved the final version of the manuscript.

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DATA AVAILABILITY STATEMENT


The paper is based on published data, and raw entries are archived as a datasheet in Univ. Glasgow Enlighten repository: <https://doi.org/10.5525/gla.researchdata.1526>.

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SUPPORTING INFORMATION

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

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