Beyond the traditional functional frameworks: novel perspectives on functional structure in fish communities

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Abstract

Beyond the traditional functional frameworks: novel perspectives on functional structure in fish communities

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Functional ecology offers a powerful lens to describe and understand ecological communities and the processes that structure them. Central to this framework is the concept of functional traits, defined as measurable characteristics of individuals or species that approximate their ecological niches. By examining patterns in species traits, functional ecology provides insights into the processes that shape ecological communities and how these processes influence biodiversity and ecosystem functioning. However, common practices in functional ecology often overlook key dimensions of functional structure. In this thesis, I identify several of these blind spots and propose ways forward, using a dataset of more than 700 lake-fish communities from Ontario, Canada, as a case study. First, I revisit the widely used metric of functional dispersion, a measure of trait dissimilarity among co-occurring species, and explore how trait selection influences its patterns. I developed two trait-pooling strategies: one based on prior knowledge of trait function, and another using a novel algorithm that separate traits that maximizes and minimizes variation in functional dispersion. Both approaches strengthen the development of a priori hypotheses about the processes shaping the structure of ecological communities and improve the predictive performance of environmental models for functional dispersion. Second, I introduce the concept of community functional integration, defined as the pattern and strengths of trait correlations within communities, to examine how these relationships vary across communities and influence community structure. Through two empirical analyses, I demonstrate that functional integration captures important, overlooked variation in functional structure and provides novel ecological insights. Finally, I assess temporal and spatial variations across three dimensions of functional structure - functional composition, dispersion, and integration – alongside taxonomic composition. Each dimension of community functional structure had their unique temporal shifts. We also conducted a spatial analysis to understand at which scale these shifts were structured: temporal shifts in functional composition and community functional integration could be explained by broad and fine scale spatial patterns, underscoring the importance of both broadscale and local processes in the temporal changes in the communities' functional structure. Together, these findings call for an expanded view of functional ecology that integrates trait relationships and temporal-spatial dynamics to more fully understand community structure and its drivers. This work broadens the functional ecological framework by highlighting underexplored dimensions of trait structure. In doing so, it contributes new tools and perspectives for uncovering the mechanisms that shape biodiversity across space and time.

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DEDICATIONS

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Research can sometimes feel lonely, especially during lockdowns, but this work was also a teamwork, and I would like to thank my colleagues, and especially my fish comrades, Ali, Tim, Gabriel (honorary fish person) and Paul for their invaluable support and for letting me bother them when I needed to talk in the lab.

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CONTRIBUTION OF AUTHORS

As the primary author for each chapter, I led the conception of the studies, the analysis of the data, the interpretations of the results and the writing of each chapter. Dr. Peres-Neto and Dr. Fraser contributed to each step for all the chapters. The data used in this thesis were collected and curated by the Ontario Ministry of Natural Resources.

For chapter 2, I led the conception, analysis, interpretation of results and writing with critical inputs from Dr. Peres-Neto and Dr. Fraser in each step. Chapter 2 has been submitted and is currently under review at *Ecology*.

For chapter 3, Dr. Khattar and Dr. Savary contributed immensely to the conception of the study. More precisely, the code for the statistical analysis was written by me with critical inputs from Dr. Khattar and Dr. Peres-Neto. I led the writing of the manuscript with feedback from Dr. Khattar, Dr. Savary, Dr. Fraser and Dr. Peres-Neto.

For chapter 4, Dr. Cindy Chu helped with the list of species to be included in the analysis. Dr. Paul Savary assisted with autocorrelation analyses.

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GLOSSARY

Concept	Definition	Accronym and Abbreviation	References
Community	A group of organisms representing multiple species living in a specified place and time.		(Vellend 2010; Stroud et al. 2015)
Community functional integration	Strength and patterns of correlations among traits involved in community assembly and functioning.	CFInt	Coined in Chapter 3
Competitive interactions	Interactions between species when species compete for the same resources. These can either lead to resource partitioning and character displacement when species can limit their similarities enough to stabilise their joint persistence (stabilising niche differences), or lead to competitive exclusion when one competitor led to the local extinction of a lesser competitor.		(HilleRisLambers et al. 2012)
Environmental filtering	Ensemble of abiotic factor preventing the establishment or the persistence of species in particular location		(HilleRisLambers et al. 2012; Kraft et al. 2015)
Functional Composition	Functional role of the different species presents in a community or the average functional identity of species from a community		(Tilman et al. 1997; Ricotta & Moretti 2011)
Functional dispersion/Functional Divergence	Component of the functional diversity representing the average differences among observations	FDis/FDiv	(Pavoine & Bonsall 2011; Mammola et al. 2021)
Functional diversity	The range and values of the species and organismal traits present in a community		(Tilman 2001)
Functional Richness	Component of the functional diversity reflecting the sum of difference among observation	FRic	(Pavoine & Bonsall 2011; Mammola et al. 2021)
Functional trait	Any measurable characteristics that influence directly or indirectly the individual or species' fitness	Trait	(Violle et al. 2007)

Niche	Description of “the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal or superior to its death rate” along with “the set of per capita effects of that species on these environmental conditions”		(Chase & Leibold 2003)
Overdispersion	Pattern of trait dispersion for which species from a same community are more different from one another than what is expected by chance alone. It is often associated with competitive interactions	OD	(Weiher & Keddy 1995; Adler et al. 2013)
Phenotypic integration	Biological relationships among multiple traits of a complex phenotype		(Murren 2012)
Selection filters	A deterministic fitness difference between individuals of different species. It encompasses two mechanisms: environmental filters and biotic interactions		(Vellend 2010)
Standardised Effect Size	Mathematical object describing the comparison of an observation and a null model	SES	
Underdispersion	Pattern of trait dispersion where co-occurring species are more similar to one another than expected by chance. It is often associated with environmental filtering.	UD	(Weiher & Keddy 1995; Kraft et al. 2015)

1 GENERAL INTRODUCTION

Biodiversity encompasses the variation of living forms at multiple spatial scales, from local (e.g. populations or communities) to global, and across organisational levels, from the individual to the species. Numerous concepts and tools have been developed to capture and explain the patterns and processes of biodiversity across these scales (DeLong 1996; Swingland 2001). Ecological communities have many definitions (Stroud et al. 2015); a common one is community as assemblages of species or populations that interact (Stroud et al. 2015). A fundamental premise of community ecology is that these assemblages of species and populations are not entirely random; rather communities is the results of various ecological, evolutionary, and stochastic processes (Drake 1990; Weiher & Keddy 1995; Vellend 2010).

Three prominent frameworks are proposed to understand how biodiversity is organised at the community level: (i) taxonomic diversity, which focuses on species identities, (ii) phylogenetic diversity, which captures the evolutionary history of local biodiversity, and (iii) functional diversity, which examines the morphological, physiological, or ecological traits of the individuals or species (Pavoine & Bonsall 2011). In this thesis, I am focusing on the functional structure of local communities.

Vellend (2010), in his synthesis of community ecology, categorises the potential mechanisms of species coexistence under four main processes: drift, speciation, dispersal and selection. In Vellend's (2010) definition, rift refers to random changes in abundance of species. Speciation is the emergence of new species driven by evolutionary forces operating in the landscape. Dispersal describes the movement of species between communities (Vellend 2010). Finally, Selection encompasses deterministic mechanisms based on the difference of fitness among species (Vellend 2010).

In "Selection", we can find mechanisms such as environmental filtering or inter-specific interactions (Vellend 2010). A very common way to conceptualise selection is with successive filters (Weiher & Keddy 1995; HilleRisLambers et al. 2012). First, an environmental filter will select species that can survive the ecosystem's abiotic conditions (HilleRisLambers et al. 2012). In a second filter, there will be a selection through interspecific interactions, with species excluding (competitive interaction) or maintaining (mutualism) other species within the community (HilleRisLambers et al. 2012). Selection, and specifically competitive interactions, has been the main focus of community ecology since mid-20th century partly due to an overemphasis of niche concepts in explaining local assembly (Chase & Leibold 2003).

While Vellend's categorisation provides a useful structure for community studies, the field of community ecology continues to struggle with the extreme variability observed among communities (Houlahan et al. 2017; Maris et al. 2018). As a result, it often remains challenging to move beyond isolated case studies. Indeed, community patterns can often be explained by multiple, competing hypotheses (Keddy 1992a; Adler et al. 2013). Identifying and quantifying the effects of relevant variables, as well as their joint effects, can be arduous, and the understanding of community functioning is frequently system-specific (Simberloff 2004). Ecologists have long debated the relative immaturity of community ecology and how to advance beyond isolated study cases (e.g. Keddy 1992b; Simberloff 2004); however, achieving generalisations and robust, quantitative predictions remains a challenge (Houlahan et al. 2017). Although case studies provide valuable, in-depth insights (Simberloff 2004), it is crucial for community ecologists to develop models that identify the main drivers of community structure and predict future and independent community dynamics (Mouquet et al. 2015). Such predictive capacity is vital for prioritising conservation efforts and preserving community integrity and functioning in the context of fast biodiversity erosion (Mouquet et al. 2015; Maris et al. 2018).

1.1 Functional ecology: a trait-based framework to study biodiversity patterns and infer assembly mechanisms

Functional ecology has, in the past decades, reframed how scientists study biodiversity at local scales by improving generality and predictability of community ecology (Keddy 1992b; McGill et al. 2006). The strength of functional ecology stems from the concept of "functional traits", which are measurable characteristics of individuals or species that directly or indirectly affect their fitness (Violle et al. 2007).

Because functional traits determine how organisms interact with their environment and one another, they directly link functional ecology with niche theory (see Box 1-1 and citations within) and provide a mechanistic view of biodiversity functioning (McGill et al. 2006; Violle et al. 2007). In the beginning of the 21st century, functional ecology was even described by some as the 'Holy Grail' of ecology (e.g. Lavorel et al. 2007), reflecting hopes for a unifying framework.

Early functional ecology studies produced striking results that highlighted the strong relationship between trait diversity and ecosystem functions. For instance, the Cedar Creek Experiment successfully showed the impact of functional diversity on the biomass production in plant community, underscoring the role of trait complementarity (Tilman et al. 1997). Subsequent research has confirmed the link between functional diversity and a wide range of ecosystem functions and community properties (e.g. resilience: Gerisch 2014; McLean et al. 2019; Biggs et al. 2020, pollination: Gagic et al. 2015, biomass production and biogeochemical cycles: Díaz & Cabido 2001).

A key assumption in applying functional ecology to community assembly is that different ecological mechanisms generate distinct patterns of trait dispersion (e.g., trait divergence or convergence) within communities (Weiher & Keddy 1995; Münkemüller et al. 2012). Distinguishable trait patterns within communities are often associated to two major selection mechanisms: environmental filtering and competitive interactions (MacArthur & Levins 1967; Weiher & Keddy 1995; HilleRisLambers et al. 2012). In the case of environmental filtering, abiotic conditions are expected to permit only species whose traits allow them to survive, leading to communities composed of functionally similar species (Keddy 1992b; Cornwell & Ackerly 2009; Götzenberger et al. 2012). By contrast, competitive interactions favour species that are functionally dissimilar, a pattern often attributed to niche partitioning or complementarity (Weiher & Keddy 1995; Cadotte et al. 2015). Other processes, such as dispersal, predation, or stochastic events, are not expected to result in distinguishable patterns of trait dispersion within communities (Adler et al. 2013).

Although powerful, the functional framework has been criticized. For instance, while competition is typically linked to trait divergence, it can also drive functional similarities, particularly in environments where a single trait value confers competitive advantage. For instance, trees compete for the access to light, and this competition will likely lead to communities of trees of similar canopy height rather than communities with several stores (Cadotte 2017). Environmental filtering is similarly broad, encompassing scenarios where suboptimal abiotic conditions reduce competition by limiting the strongest competitors, thus permitting weaker competitors to persist, or cases of direct habitat selection (Cadotte & Tucker 2017). Understanding how traits are sensitive to different selection filters is a key to address these issues. For example, traits involved in resource exploitation (e.g., trophic levels, mouth size) may respond primarily to competition, while others (e.g., thermal tolerance, locomotion capacity) reflect habitat constraints (e.g. Bower & Winemiller 2019; Jessica Côte et al. 2019). As such, hypotheses about observed trait dispersion patterns within communities should be matched to the specific traits or sets of traits under study, ensuring that inferences about assembly processes are trait-appropriate and mechanistically grounded.

Despite its apparent strengths and the often-striking results, functional ecology faces multiple methodological and conceptual challenges. In the following sections, I focus on two key areas of debate: (1) the selection of traits and (2) the choice of functional metrics

Box 1-1: The long parallel history of niche and traits in community ecology

In today's ecology, the concepts of species' traits and niche are closely entwined: one can hardly discuss the difference of niche of two species without discussing the differences in their requirements and characteristics. If the modern definitions seem well accepted and operational, those are the products of a long history of theoretical and conceptual developments and discussions around their meanings. In this box, I summarise important dates and key developments that led to the modern definitions of the niche and functional trait (Figure 1-1). Creating and discussing a comprehensive chronology of species traits and niche is well beyond the scope of this thesis, and I will be focusing on elements relevant to the discussion of functional ecology.

Niche: one concept, many definitions

A comprehensive history of the niche and controversies associated with it has been done by Chase & Leibold (2003) and completed by Pocheville (2015). The concept of niche is more than a century old, with the first formalisation in 1913 by Grinnell (Chase & Leibold 2003; Pocheville 2015). The first inception of the niche focused on the characteristics of the environment a species can fill. In this sense, the ecological niche is metaphorically close to the architectural definition, as a nook in a wall (an environment) that can be filled by a statue (or species) with appropriate dimensions. Since its first inception, the concept of niche has evolved tremendously and so much so that in 1991, Real and Levin (as reported by Chase and Leibold, 2003) claimed that “no other concept in ecology has been more variously defined and more universally confused than ‘niche’.” Chase and Leibold (2003) pointed that there are two schools of niche: one, born from Grinnell’s definition, focusing on the response of the species to their environment and the other, from Elton’s work on the role of the species in the ecosystems (Chase & Leibold 2003; Pocheville 2015). In the following paragraphs, we will mainly focus on the niche as the response of species to their environment.

Many definitions of the niche have been formalised through the first half of the 20th century, one turning point for the niche was Hutchinson who shifted the definition of the niche from a characteristic of the environment to the characteristics of individuals (Hutchinson 1957). Hutchinson defined the niche as an “hypervolume of n-dimensions”, shifting the analytical framework from a qualitative analysis (a species ability to occupy a vacant or not niche) to a more quantitative point of view (overlapping of niche between two species) (Colwell & Rangel 2009). Even though there has been great development in the definition of the niche afterward, Hutchinson’s definition has laid the foundations of all functional analysis of communities.

After Hutchinson’s paper in 1957, ecologists studying species’ niches started to focus more and more on the competitive interactions between species; by 1975, more than 80% of published papers on the niche were associated with competition (Chase & Leibold 2003). In addition to other criticism on statistical tools and hypothesis, this overemphasis on competitive interactions compared to the other biotic interactions or environmental filters was widely criticked and led to a “downfall” of the niche in the study of species distribution and interactions (Chase & Leibold 2003). It would take up to 2 decades and the early

2000's for the concept of niche to come back in the forefront of ecology studies with a synthetic reframing of the niche by Chase and Leibold (2003) as both an organism's needs from its environment and its activities that will shape said environment.

Functional traits: an old and new concept

Even though the term "functional trait" is rather recent, describing and categorising species according to their observable characteristics is a very old endeavour, with some classifications of plants as early as 300BC (Weiher et al. 1999). Comparisons of species' characteristics were already present in the early conceptualisation of the niche and some of the early concepts find echoes in modern functional ecology.

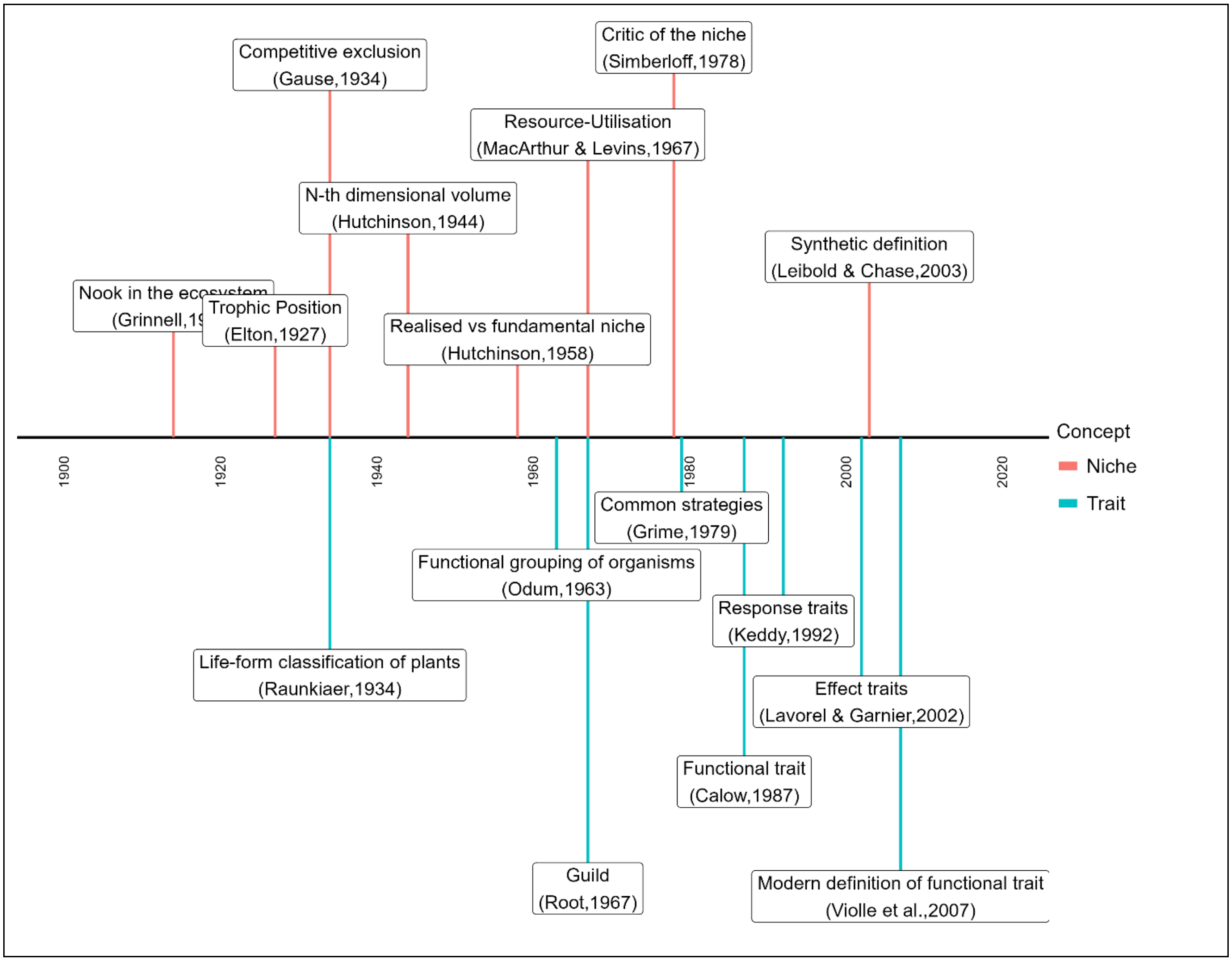
At the very beginning of the niche, Grinnell compared species according to their attributes to assess whether two species could fill the same niche, coining the term of "ecological equivalents" (Chase & Leibold 2003). When discussing interspecific competition, Gause et al. (1934) highlights the similarities between *Paramecium caudatum* and *Paramecium aureli,* noting they "occupy identical ecological niche". The link between species characteristics and niche became even more obvious when the niche became a property of the individual rather than the property of the ecosystem.

In the 20th century, the species comparison was mostly done through categorisation of species, pooling species according to their trophic guilds, plant strategy classification (Figure 1-1). Even though tools to describe community's functional diversity with continuous traits (e.g. Rao's diversity indices, Gower distance) existed, it is not until the end of the 90's and early 2000's that continuous traits will be widely used in the study of community's diversity.

The term "functional traits" itself has been coined by Calow (1987), it described any physiological traits (e.g. efficiency of photosynthesis to convert light and raw materials to biomass, effectiveness of respiratory structure in maximising O_2 intake, etc.) with a particular emphasis on performance and fitness. Similarly to the concept of niche which has deviated from its early definition to become a vague and ambiguous concept through the decades, traits have been defined, re-defined through the 90's and the early 00's, before its modern definition was coined in late 00's.

Following Calow's definition of functional trait, sub-types of traits have been conceptualised, such as response traits (Keddy, 1992), referring to any characteristics that respond to environmental change, and effect traits (Lavorel & Garnier 2002) which refers to characteristics that influence ecosystem functioning (e.g. biogeochemical cycles). Despite these attempts to define more precisely what a trait or functional trait is in the publications, Violle et al. (2007) pointed that the use of such terminology remained ambiguous. In this context, Violle et al. (2007) proposed the modern definition of functional traits: “a trait is any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization”. This modern definition functional traits entails a few properties: 1- a functional trait should be measured at the individual level, without referencing the environmental factors, or characteristics of higher level of organisation (e.g. demographic parameters for population, total biomass for community, etc.), 2- a functional trait should impact directly or indirectly the fitness of an individual.

Figure 1-1 Abridged chronology of the formalisation of different ecological concepts over the last century. Red indicates major advances in niche history (relevant dates and concepts from Chase & Leibold 2003 and Pocheville 2015), and blue indicates milestones in defining functional traits (relevant dates and concept from Weiher et al. 1999, Violle et al. 2007 and Nock et al. 2016)



1.2 Choosing traits: Beyond methodological struggles

The foundation of functional ecology lies in functional traits, defined as any measurable characteristics of an individual or species that directly or indirectly impact the individual's or species' fitness (Violle et al. 2007). The link between trait and fitness is necessary to create a "currency" to compare patterns across species and gradients (McGill et al. 2006).

Overall, the broad definition of trait encompasses a wide range of potential traits (see Box 1-1), influencing both the ecological questions we can address and which traits we ultimately choose to investigate. In the 2000s, researchers distinguishing traits based on how they align with different niche definitions (Nock et al. 2016). Specifically, traits may reflect an organism's ecological requirements or its role in biogeochemical cycles

(McGill et al. 2006; Nock et al. 2016). The first type, termed “response traits”, describes how species respond to biotic and abiotic conditions, aligning with the Hutchinsonian niche concept (Keddy 1992b, and see Box 1-1 for more details). The second, “effect traits”, describes how a species influences its environment via energy and material fluxes, approximating the Eltonian niche (i.e. niche as the effect of the species on the ecosystem’s processes) (Weiher et al. 1999). Both types of traits are functional but capture different processes and mechanisms, and therefore should be used to answer different types of questions (though certain traits can act as both response and effect traits) (Lavorel & Garnier 2002; Nock et al. 2016). In this thesis, I focus specifically on response traits to study assembly mechanisms, drawing on the Hutchinsonian niche concept to infer processes shaping community structure.

Even after distinguishing between response and effect traits, selecting which traits to measure is far from trivial and can significantly alter the ecological inferences drawn. Furthermore, there is no consensus on how many traits should to include in a functional ecology study (Petchey & Gaston 2002; Mouillot et al. 2021). Typically, multiple traits are combined to capture the different biological dimensions of a species’ niche (Villéger et al. 2008; Mouillot et al. 2021). However, indiscriminately pooling traits can be problematic: highly redundant traits inflate the apparent importance of certain functional groups (Petchey & Gaston 2006), while traits more sensitive to different processes may cancel each other out, obscuring real patterns (Côte et al. 2019). One solution for redundant traits involves dimension reduction (by summarising the functional traits into fewer axes), hence controlling for the collinearity between traits, or applying weights that prevent collinear traits from dominating the analysis (Villéger et al. 2008; Laliberte & Legendre 2010). In contrast, if traits respond differently to assembly processes, their combined signals may mask meaningful structure, making trait patterns within communities appear more random than they really are (e.g. Côte et al. 2019). In summary, balancing the use of multiple traits reflecting complex phenotypes with the need to preserve biologically relevant information is crucial for revealing underlying community assembly processes.

1.3 Methods in functional ecology: non-standardisation of the tools and their blind spots

Functional ecology has benefited from progress in quantitative and multivariate analytical tools that facilitate the simultaneous analysis of multiple traits. However, the field’s rapid growth has led to a proliferation of concepts and metrics, without little standardisation in their naming or application(Mouchet et al. 2010; Schleuter et al. 2010; Legras et al. 2018; Mammola et al. 2021).

Similarly to ‘biodiversity’, which can have multiple definitions, ‘functional diversity’ also encompasses various meanings that must be carefully distinguished for meaningful community structure analysis (Scheiner et al. 2017; Schmera et al. 2023). Each of these components captures distinct facets of functional structure within communities: richness reflects trait space occupancy, dispersion reflects trait distances, and evenness reflects distribution across that space (Mason et al. 2005). Another result of the ambiguity in the nomenclature and concepts is the creation of multiple metrics to describe the same phenomenon: many of those indices are redundant and, in fact, summarise similar information (Mouchet et al. 2010; Münkemüller et al. 2012; Mammola et al. 2021). For instance, functional dispersion, often used to infer assembly mechanisms, can be estimated with at least three different metrics, including functional dispersion (Laliberte & Legendre 2010), Rao’s quadratic entropy (Rao 1982) and Hill numbers (Chiu & Chao 2014). Ecologists have put effort into disentangling the confusion and redundancy around the concepts and metrics in functional ecology to separate the different concepts and to highlights the different properties of the functional metrics (Mason et al. 2005; Mouchet et al. 2010; Mammola et al. 2021; Schmera et al. 2023). Yet no clear consensus exists on the best metric for studying assembly mechanisms, leading some author to propose the simultaneous use of multiple metrics (Mammola et al. 2021). This ambiguity around functional diversity and its different metrics hampers cross-study comparisons and complicates efforts to generalise findings, limiting the broader potential of functional ecology to inform theory and practice.

1.4 From phenotypic integration to community functional integration: introducing trait coordination in the study of communities

In classical functional ecology, two main dimensions of the functional structure are frequently examined: functional composition and functional diversity. Functional composition represents the average position of the community in the trait space, often computed as the community weighted-mean (Ricotta & Moretti 2011), and can be used to understand the dominant ecological strategy of the community (Grime 1974; Kleyer et al. 2012; Lepš & de Bello 2023). Functional diversity, as discussed above, reflects the distribution and spread of species within this functional space (Tilman 2001). Although these two concepts and their associated metrics yield numerous insights, they may not fully capture the complexity of community structure, especially in a multi-dimensional trait space. For instance, trait correlations are often dismissed as redundancies (Mouillot et al. 2021), effectively treated as noise rather than a meaningful pattern. Yet these correlations can reveal how traits are distributed, shedding light on the structuring of functional space. Moreover, how these trait correlations vary across scales (from regional to local, for example) or environmental gradients is rarely examined, leaving a critical gap in our understanding of community function.

Trait correlations at the population level are often referred as "phenotypic integration" (Cheverud 1982; Schlichting 1989; Pigliucci 2003, see Box 2 for more examples and details), reflecting how phenotypes respond to local environmental conditions or biotic interactions. However, scaling up observations from populations to communities is not straightforward as different mechanisms shape trait correlation at different organisational levels: for instance, well-known trait correlations in the global leaf economic spectrum may not be found at the local scales (Messier, Lechowicz, et al. 2017; Messier, McGill, et al. 2017). Messier, McGill, et al. (2017) demonstrated that trait correlations observed within populations do not always hold at the community level, reflecting how different assembly mechanisms shape trait relationships at boarder scales.

Box 1-2: Phenotypic integration: the science of trait coordination in individual phenotypes

At the individual and population level

The covariation among traits within an individual or population is extensively studied under the concept of “phenotypic integration”. Originally formulated within evolutionary ecology, phenotypic integration seeks to explain how species’ phenotypes change under selective pressures (Cheverud 1982; Schlichting 1989). The idea is that traits are not isolated within the phenotype. Some coordination among traits will allow the individual to perform some functions more efficiently (Cheverud 1982) and therefore to gain a selective advantage compared to individuals with less coordinated phenotypes (Schlichting 1989; Pigliucci 2003; Klingenberg 2014). For instance, in dragonfly larvae, more coordinated limb morphology and function can improve swimming performance, offering a survival advantage in predator-rich environments by improving escape (Mikolajewski et al. 2015; Mikolajewski et al. 2016). Many studies, especially in plants, have shown greater phenotypic integration in stressful environment (e.g. Schlichting 1989; Dingemanse et al. 2007; Mikolajewski et al. 2015; Michelaki et al. 2019). Other studies in fishes showed a variation of integration patterns depending on water velocity or depth (Peres-Neto & Magnan 2004; Parsons & Robinson 2006; Leavy & Bonner 2009), suggesting that environment shape phenotypes beyond selection of the mean values. Phenotypic integration can also be observed in case of trade-offs among competing functions within organisms (e.g. locomotion and growth in Atlantic silverside, (Ghalambor et al. 2003)). As such, the study of phenotypic integration can uncover different ecological strategies within species.

At the multispecies level

Interspecific comparisons of phenotypic integration often adopt an evolutionary lens, examining to find how species’ phenotypes emerge from their shared evolutionary histories (e.g. Higham et al. 2007; Romanuk et al. 2011; Poorter et al. 2014) . One prominent example at the interspecific level is the Leaf Economic Spectrum (LES, a framework that highlights correlated plants traits such as leaf lifespan, photosynthetic rate, and leaf nitrogen content) at the global scale (Poorter et al. 2014). At broad spatial scales, the LES captures key aspects of plant strategies, allowing researchers to identify trade-offs and synchronisation between traits that shape plant functional performance.

In fishes, some traits such as size and trophic levels are highly integrated across species (Romanuk et al. 2011). Other studies that compared integration of traits among multiple species have shown, for instance, synchronisation among traits involved in locomotion and feeding (e.g. suction feeder and ram feeders (Higham 2007; Higham et al. 2007)). Similarly to the LES, those studies of integration allowed scientists to identify different ecological strategies across different fish species.

1.5 Ontario freshwater fish communities: an ideal case study for community assembly

In my thesis, I focused my investigations on a single study system: lake-fish communities in Ontario, Canada. I selected this region for three reasons: (1) lakes offer discrete boundaries and the potential of clearer assembly patterns, (2) Ontario's freshwater systems are relatively well-studied and of management interest, and (3) there are extensive data bases that facilitate robust analyses of these communities.

1.5.1 Lakes: an ideal playground for studying community assembly mechanisms

In community ecology, a key challenge lies in defining what exactly constitutes a "community" (Palmer & White 1994; Looijen & Van Andel 1999; Ricklefs 2008; Brooker et al. 2009; Stroud et al. 2015). Textbook definitions often characterize communities as ensembles of directly or indirectly interacting species within a shared environment (Stroud et al. 2015). The core idea is that a community represents more than a mere checklist of co-occurring species, encompassing dynamic interactions and functional relationships (Brooker et al. 2009; Stroud et al. 2015). However, this broad definition has sparked debate, as some argue it is too fuzzy for operational use in empirical research (Palmer & White 1994; Ricklefs 2008). A key issue is the lack of boundaries between communities (Looijen & Van Andel 1999), rendering any delineating at least partially arbitrary. Some ecologists have attempted to define communities in more operational ways, by committing to the arbitrariness (Palmer & White 1994), whereas others suggested discarding the concept altogether (Ricklefs 2008).

In certain ways, lakes offer an avenue that simplifies this problem: similarly to islands, lakes have discrete boundaries and clear geographical identities (Olden et al. 2001; Hortal et al. 2014). Defining communities as the ensemble of species and their interactions present in a lake adheres closely to the operational definition. This perspective is also supported by empirical evidence of limited dispersal among lakes (Olden et al. 2001; Shurin et al. 2009; Heino et al. 2015). We can assume that all habitats necessary for the present species exist within the boundary of the lake. Hence, while not every species in a lake interacts with each other, all interactions should be accounted for if we take the lake as a boundary.

Beyond resolving definition ambiguities, lakes also serve as an ideal model for investigating community assembly mechanisms. A central challenge in assembly ecology is disentangling the multitude of ecological and evolutionary processes structuring communities. Because dispersal among lakes is typically limited (Shurin et al. 2009; Heino et al. 2015), one can reasonably assume that dispersal plays minor influence on the formation and persistence of lake-fish communities (Hortal et al. 2014). Referring back to the Vellend's (2010) synthetic model of community assembly, removing dispersal leaves three main processes: Selection, Drift and Speciation. In this low-dispersal and contemporary context, functional traits can primarily reveal the influences of selection (environmental and biotic filters) and drift (stochastic processes), each potentially generating recognisable trait dispersion patterns.

1.5.2 Drivers of local fish diversity in Ontario: Past, contemporary and future changes in local assembly stressors.

Ontario harbours more than 100 freshwater fish species, which began colonizing Ontario’s waterbodies following the retreat of the last ice sheet between approximately 10,000 and 8,000 years ago (Jackson & Harvey 1989; Mandrak & Crossman 1992). Glacial processes formed numerous lakes via moraines, which were then colonized by fishes dispersing from Missouri and Atlantic refugia (Mandrak & Crossman 1992). These historical factors, particularly lake age, remain influential in shaping local community composition (Ordonez & Svenning 2015). However, the dispersal of numerous species was (and continues to be) constrained by their thermal tolerance limits (Alofs et al. 2014;

Van Zuiden et al. 2016; Loewen et al. 2022). Indeed, the range expansions of certain warm-water fishes (e.g., smallmouth bass, walleye) are determined by their northern range, by their thermal tolerance (Minns & Moore 1995; Alofs & Jackson 2015a; Van Zuiden et al. 2016). Beyond climatic factors, biotic interactions also shape species distributions in lakes. For example, in Ontario, brook trout are limited not just by temperature regimes but also by competition with predators, such as smallmouth bass (Alofs & Jackson 2015b; Van Zuiden et al. 2016). While these studies examined only a few species, their findings underscore how both environmental filtering and biotic interactions jointly govern species occurrences.

Contemporary freshwater ecosystems face many and various pressures, with several studies indicating greater extinction rates in these systems than in marine and terrestrial ecosystems (Burkhead 2012; Ceballos et al. 2015; Albert et al. 2021). They contend with broad-scale threats such as global warming, species invasions and overexploitation, as well as localised pressure such as civil constructions (such as dams) or pollution due to land use (Geist 2011; Reid et al. 2019; Albert et al. 2021). Such stressors frequently alter local and regional biodiversity, leading to biotic homogenization. Biotic homogenization refers to the tendency of communities to become increasingly similar over time (Olden 2006; Olden et al. 2016), driven largely by the extirpation of taxonomically and functionally rare species and the expansion of widespread or functionally redundant taxa (Olden et al. 2004; Clavel et al. 2011; Buisson et al. 2013; Campbell & Mandrak 2020). Environmental changes alter filtering processes, often causing the extirpation of vulnerable species lacking suitable traits to persist in the community, while facilitating the colonization and dominance of more generalist or tolerant species (Olden et al. 2004; Clavel et al. 2011; Woods et al. 2023). Moreover, species introductions disrupt biotic interactions, affecting predator-prey or competitive relationships (Alexander et al. 2015; Van Zuiden et al. 2016; Hansen et al. 2018).

In Ontario, where thermal tolerance critically constrains fish dispersal, climate warming is expected to favour large warm-water predators (e.g., smallmouth bass), enabling them to expand northward and colonise additional lakes (Alofs et al. 2014; Van

Zuiden et al. 2016). On the other hand, cool- and cold-water species will see their viable thermal ranges contract toward higher latitudes northern territories, common cool-water species such as brook trout may become rare, and endangered (Van Zuiden et al. 2016). It is also worth noting that climate change affects polar areas much faster than temperate regions, hence northern lakes may be the ones witnessing the greatest change in their composition by the extirpation of the most vulnerable cold-water fishes.

1.5.3 Extensive data on Ontario's lake-fish communities

Because the Ontario Ministry of Natural Resources actively manages these fisheries, Ontario's lakes are exceptionally well surveyed and studied. Consequently, extensive datasets are readily accessible for scientific research. Two datasets are particularly relevant to this thesis: the Broadscale Monitoring Program (BMP; Lester et al. (2020)) and the Aquatic Habitat Inventory (AHI; Dodge et al. (1985)). The BMP represents the Ontario Ministry of Natural Resources' latest, ongoing sampling initiative, offering publicly available data on fish species and environmental parameters across more than 700 lakes sampled between 2008 and 2012 (Lester et al. 2020). These sampled lakes span over ten latitudinal degrees, encompassing diverse environmental conditions and climate regimes, from southern temperate lakes to northern boreal lakes. The AHI was conducted between 1960 and 1980,compiling data for over 10,000 lakes throughout Ontario (Dodge et al. 1985). Although their sampling protocols differ to some extent, these resources collectively enable a comprehensive investigation of freshwater ecosystems across large-scale environmental gradients and extended temporal scales.

1.6 Going beyond the traditional functional ecology framework for community studies: Overview of the thesis chapters

In this thesis, I explored some of the limitations of the classical analytical framework of functional ecology challenges described in the Section 1.2, 1.3 and 1.4. The thesis starts with a classical analysis of functional dispersion across communities with a particular emphasis on the choice of traits and our ability to predict variation in functional dispersion across large-scale gradients. The third chapter builds on this chapter by introducing the concept of community functional integration into the analysis of communities: we demonstrated that including community functional integration improved our capacity to predict patterns of species richness. Finally, the third chapter is a thorough analysis of temporal shifts multiple dimensions of community functional structure and how those temporal shifts are structured in space.

1.6.1 Chapter 2: Optimizing functional trait selection: a quantitative framework to enhance predictions of ecological community assembly

Inferring assembly mechanisms through patterns of trait dispersion is a long endeavour of functional ecologists. Two patterns are of interest and can be interpreted through the lens of community assembly: underdispersion and overdispersion. Underdispersion describes communities whose species are more similar to one each other than by chance and is commonly associated with environmental filtering. On the other hand, over-dispersion, where species are more dissimilar to one each other than by chance alone, is traditionally associated with competitive interactions.

As discussed in the sub-section *1.2*, the choice of traits is crucial to the functional analysis and the interpretation of the patterns in functional dispersion, for instance. Pooling traits together is a common practice in functional analysis (Strauß et al. 2010; Toussaint et al. 2016); however, it may not be the most optimal one. In this Chapter, we explore the benefits of two analytical frameworks to chose traits and compare them with the traditional way of pooling traits together. The first method, that we called *a priori* categorisation, is based on previous knowledge of traits and their supposed functions in the organisms. This method allows for more precise hypotheses but relies on the assumptions about how traits are combined and how they may respond to different mechanisms. The second method, that we called *a posteriori* categorisation, relies on an algorithm that will find the best combination of traits to optimise the dispersion patterns. The strength of this method is that it does not rely on *a priori* knowledge of how traits respond to assembly mechanisms. With this method, the trait combination is also a pattern to be analysed and interpreted. In this sense, making hypotheses on which traits combination will be selected can be a bit less straightforward than the previous method.

Our results showed the importance of carefully grouping traits into meaningfully categories to be able to interpret their functional dispersion patterns. Indeed, pooling all traits together prevented us from observing signals of competitive interactions and reduced our capacity to predict the variations of functional dispersion with environmental variables. Separating traits by either their functions or their patterns revealed stronger patterns, where communities could be at the same time under and over-dispersed, while the analysis with all traits simultaneously only showed patterns of weak underdispersion. Our results also demonstrated that the traits important to assembly mechanisms varied greatly across the landscape.

1.6.2 Chapter 3: Community functional integration: an underexplored dimension of functional structure and its role in community assembly

As stated in *Section 1.4*, there are only few studies that explore the variations of trait correlations across environmental gradients, all of them in plant communities. Those studies have shown some very promising results, that mirror some phenomenon found at the intraspecific level. For instance, Delhaye et al. (2020) showed that plants community tend to be more integrated when environmental stress is high (in this case, heavy metal concentration). Other studies showed little change in the degree of phenotypic integration but great changes in the trait network structures between communities in dry and moist forests (Flores-Moreno et al. 2019; He et al. 2020; Sanaphre-Villanueva et al. 2022). Those results suggest that trait correlations can be selected to respond to varying environmental conditions.

In this Chapter, our goal is to develop the concept of community functional integration. First, to echo the concept of phenotypic integration at the population level, we define Community Functional Integration as the strength and patterns of correlations among traits involved in community assembly and functioning. Second, we demonstrated the usefulness of such concept in the analysis of community’s functional structure through two empirical examples. The first one focuses on the variation of the trait correlations networks across fish communities in Ontario. The second example aims to show that including community functional integration in the study of communities can improve our understanding of those communities.

The first notable result of this Chapter is that pairwise trait correlations vary from one community to another, that there are patterns of community functional integration that can be observed and therefore analysed. We also showed that the variations of trait correlations networks were not geographically random, with Northern and Southern communities showing distinct trait correlation networks, suggesting that trait correlations responded to environmental variables. In the second empirical study, we focused on the average absolute trait correlation within a community. We showed that the correlation strength was partly determined by thermal gradients (i.e. water temperature, number of ice-free days, etc.) but more importantly that the average absolute trait correlation improved the prediction of local taxonomic diversity. By including community functional integration in the functional analysis of communities, we could improve our understanding and predicting abilities of local biodiversity.

1.6.3 Chapter 4: Quantifying and predicting temporal shifts in lake-fish communities' functional structure in Ontario

Despite covering about 0.1% of Earth's surface, freshwater ecosystems are home to almost 10% of the world's animal species (Balian et al. 2008). Freshwater species are extremely vulnerable, with higher extinction rates than their terrestrial and marine counterparts (Olden et al. 2007; Reid et al. 2019). This vulnerability is the result of multiple threats that varies in nature and spatial scales (Olden et al. 2007; Strayer & Dudgeon 2010; Reid et al. 2019): from local disturbance such as overexploitation, to global changes.

Biodiversity is a multi-facet concept, whose components (taxonomic, phylogenetic, functional) do not respond similarly to changing environmental conditions (Devictor et al. 2010; Doxa et al. 2020): studying only one component will fail to capture all the variation that a community goes through (e.g. Campbell & Mandrak 2020). Similarly, functional structure of a community is composed of different elements: functional composition, functional dispersion and community functional integration. Each of these concepts can respond differently to stressors and give different insights on how the communities are structured. It is therefore essential to take into consideration the different components of the communities' functional structure to fully understand how they changed over time.

Our goal is also to predict those potential temporal shifts. To achieve this, we decomposed the spatial data with a Moran's Eigenvector Maps or MEM (Legendre &

Legendre 2012; Dray et al. 2012). The MEM can be used as explanatory variables to understand at which spatial scales, biodiversity patterns are structured and therefore infer potential processes determining those patterns (Diniz-Filho & Bini 2005; Dray et al. 2012; Biswas et al. 2016). For instance, broadscale MEM can represent broadscale processes (Legendre & Fortin 1989; Diniz-Filho et al. 2003): in Ontario, climatic gradients and migration patterns are broadscale processes influencing local diversity (Mandrak & Crossman 1992; Minns & Moore 1995). While fine scale MEMs can represents fine scale environmental gradients or other processes as biotic interactions (Legendre & Fortin 1989; Biswas et al. 2016).

In this Chapter, we used historical and contemporary data on Ontario's fish communities and spatial analysis, to identify the main scales of temporal variations of the functional structure. Specifically, we quantified temporal shifts across multiple functional metrics and ran a decomposition of spatial data to identify and quantify at which scale the variation in temporal shifts is structured.

Our results showed that the different dimensions of community functional structure had different temporal shifts with little to no correlation. This first tells us that no dimension can be used as a proxy for another. Additionally, functional composition, functional dispersion and CFInt showed average temporal shifts different from 0, indicating changes in functional structure across all communities. Furthermore, we showed that temporal shifts in functional structure were poorly correlated with changes in taxonomic changes. The second part of the analysis was to understand where most changes occurred, and at which scale temporal shifts were structured. The spatial analysis with the decomposition of spatial structures showed that functional composition and functional integration were mostly explained by large-scale structures and partly by fine-scale structures, while functional dispersion could not be explained by broadscale or fine scale spatial structures. Overall, our results underscore the importance of a multidimensional approach when quantifying and monitoring changes in biodiversity.

2 CHAPTER 2: Optimizing functional trait selection: a quantitative framework to enhance predictions of ecological community assembly

2.1 Abstract

Functional trait analyses provide crucial insights into the drivers and predictive factors underlying community structure. The study of trait dispersion (random, over- and underdispersion) as the means to understand the mechanisms underlying community assembly is an extremely common approach. However, striking a balance between quantifying complex community trait patterns using comprehensive trait sets and ensuring their accurate detection and prediction remains a significant challenge. This study underscores the importance of strategic trait selection in community ecology and introduces a framework designed to optimize patterns of functional trait variation across communities. Building on this framework, we explored the responses of three trait groups across substantial environmental gradients in approximately 700 lake-fish communities in Ontario, Canada. We began by applying the traditional approach of integrating all traits while also leveraging fish biology knowledge to categorize traits into functional groups (Diet, Locomotion, Temperature Preference). We then contrasted this approach with a novel computational strategy to select trait combinations that maximize overdispersion and minimize underdispersion. Our findings demonstrate that separating traits based on function or dispersion patterns revealed signals that appeared random or weak when all the traits were collectively analyzed. Furthermore, we showed that the same community can exhibit combinations of traits that are both underdispersed and overdispersed, a phenomenon not commonly acknowledged in community ecology. By integrating our computational approach with environmental modeling, we demonstrate that environmental features can reliably predict variation in communities that exhibit both underdispersion and overdispersion across different traits

2.2 Introduction

Functional ecology provides a robust foundation for understanding and predicting species occurrence patterns and ecological community assembly (Götzenberger et al. 2012; Münkemüller et al. 2012; Adler et al. 2013; Munoz et al. 2023). Functional traits capture many of the ecological requirements of individuals, populations, and species, providing a valuable approximation of their niches (Violle et al. 2007). Unlike species composition, functional traits often transcend individual ecosystems, serving as versatile predictive “currencies” that enable comparisons among communities, even in the absence of shared species (McGill et al. 2006). Moreover, trait variation can be quantified by metrics (e.g., diversity) that capture ecological patterns such as trait under- or overdispersion of traits within species assemblages. Contrasting communities based on trait patterns is feasible across taxa lacking common traits, as these patterns reflect standardized effects of trait variation across communities. As such, this approach enables robust comparisons across extensive geographic regions, including at a global scale.

Functional traits are particularly informative for understanding the mechanisms that shape community assembly (HilleRisLambers et al. 2012; Adler et al. 2013). For instance, associations between environmental features and variation in trait patterns offer valuable insights into how environmental conditions shape the composition of local communities (Cadotte & Tucker 2017). In functional ecology, two key mechanisms are often highlighted: environmental filtering and biotic interactions. These mechanisms produce contrasting predictions related about trait patterns within communities. Environmental filtering is expected to decrease functional diversity by favoring species with trait that traits that enhance survival and persistence under specific environmental conditions (Mouillot et al. 2007; Adler et al. 2013; Mason et al. 2013). Conversely, density-dependent interactions (e.g., competition) are predicted to increase functional dispersion, as similar species with similar traits are more likely to exclude one another (Adler et al. 2013; Mason et al. 2013).

Numerous metrics exist to assess trait dispersion within communities (Mammola et al. 2021; Mouchet et al. 2010; Schleuter et al. 2010; Mason et al. 2013), all of which are used in a similar analytical framework. The framework typically involves constructing a functional space using multivariate tools, followed by quantifying community properties through a reduced set of multivariate axes for subsequent analyzes and interpretation (Villéger et al. 2008). A key step in this process is summarising multiples traits into fewer axes – a strategy designed to capture complexity of phenotypes composed of various trait combinations while addressing potential redundancies among correlated traits. Using a single trait risks oversimplifying the multifaceted nature of species phenotypes, whereas incorporating too many traits may introduce redundancy, skew results, and lead to inferences and predictions being dominated by a few highly correlated traits (Zhu et al. 2017; Mouillot et al. 2021). Therefore, the careful selection and/or aggregation of traits is essential for developing robust predictions and inferences, such as distinguishing between environmental filtering versus biotic interactions.

A frequently overlooked source of quantification and inferential biases is the failure to select traits based on their functions and sensitivities to different trait community patterns. This oversight can obscure community structure, weaken predictive capacity, and hinder the accurate inference of the mechanisms driving these patterns. For example, environmental selection and biotic interactions are frequently treated as mutually exclusive, with communities assumed to be shaped predominantly by one mechanism or the other (e.g.Mouillot et al. 2013; Lamothe et al. 2018; Cooke, Bates, and Eigenbrod 2019) . However, it is critical to consider that multiple mechanisms can operate simultaneously within single local communities (Mason et al. 2013; Trisos et al. 2014). As a result, certain trait combinations may falsely suggest random community assembly when, in fact, this pattern may result from combining traits with opposing dispersion patterns, where some traits are overdispersed and others underdispersed within the same community. This highlights two critical points. First, different mechanisms may select for different sets of traits within the same community. For instance, some traits may respond more strongly to competitive interactions, resulting in high functional dispersion or overdispersion, while others may be more sensitive to environmental filtering, leading to underdispersion.

Second, aggregating diverse traits can obscure the detection of distinct trait patterns within communities (Cornwell & Ackerly 2009; Côte et al. 2019), particularly in highly heterogeneous environments such as lakes, streams, or ecotones. This is a critical consideration, as most studies calculate single metrics of functional dispersion using multiple traits without fully accounting for how different trait combinations can lead to vastly different inferences or how environmental variation may influence their predictive ability. We propose that categorizing traits based on their sensitivity to specific ecological mechanisms can substantially enhance the accuracy of functional pattern detection.

In this study, we present and validate a robust quantitative framework designed to optimize functional trait selection, significantly improving environment-based predictions of ecological communities. To showcase the empirical strength of our framework, we analyzed an extensive dataset comprising approximately 700 lake-fish communities distributed across a broad latitudinal gradient, paired with a detailed environmental dataset featuring nearly 90 different variables (predictors). Our framework for aggregating trait sets demonstrate that these communities often exhibit signals of both under- and overdispersion. Furthermore, we demonstrate that environmental factors reliably predict variation in communities displaying these contrasting dispersion patterns across different traits, indicating that these patterns are not random but emerge from underlying ecological processes that structure these communities to be both under- and overdispersed.

2.3 Methods

While the analytical frameworks proposed here are applicable to any ecological system, lake-fish communities present a valuable case for study. Similar to island ecosystems, these communities are isolated by boundaries that significantly limit species dispersal (Magnuson et al. 1998), more so than in continuous terrestrial ecosystems, streams, or marine environments. This isolation heightens environmental pressures and intensifies biotic interactions, such as competition and predation, as local fish populations have limited ability to escape these pressures due to restricted movement between lakes

(Olden et al. 2001). Consequently, lake-fish communities are well-suited systems for investigating how different trait combinations affect the detection of overdispersion and underdispersion patterns, and for predicting community dispersion responses to environmental variability.

2.3.1 Data and sampling design

The Ontario Ministry of Natural Resources have sampled 707 lakes across Ontario (Canada) for their Broadscale Monitoring Program (OBMP, Lester et al. 2020). Lakes were sampled in summers (June to September) from 2008 to 2012 along a large latitudinal and longitudinal gradient (Figure 2-1). The OBMP uses stratified sampling; lakes were chosen randomly among lakes of similar sizes within the same region. They spread over three primary watersheds and 26 secondary watersheds (22 were kept in the analysis as more than 3 lakes were sampled within their boundaries).

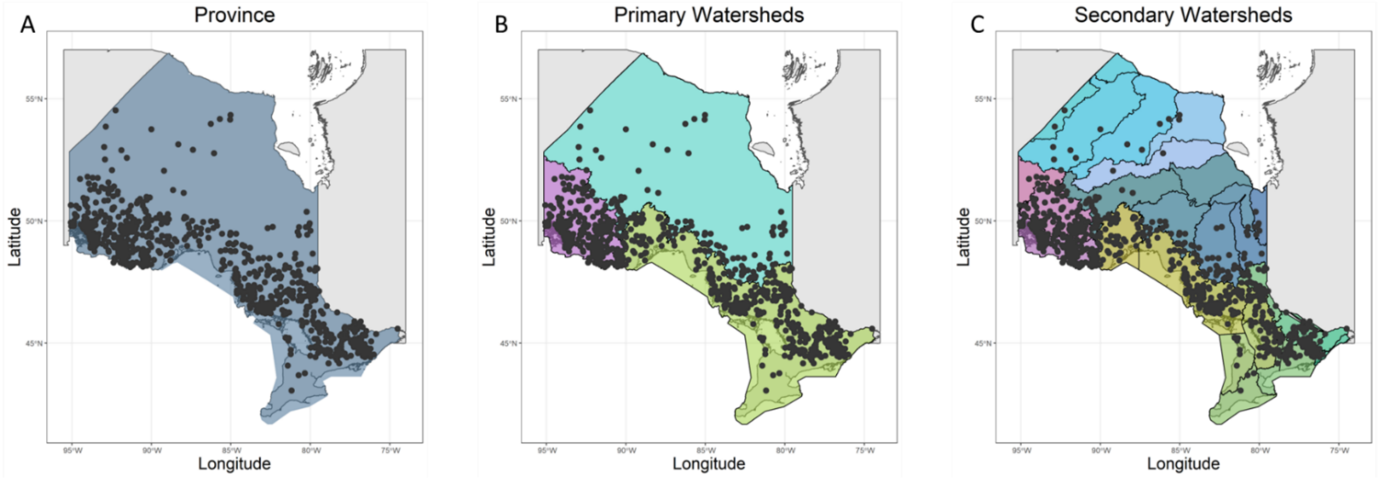


Figure 2-1: Maps of the spatial definition of the different species pools for lake-fish communities of Ontario, Canada. The polygons represent the geographical boundaries within which the species pools were defined. The points are the sampled lakes.

Each lake was sampled using a standardized design. Fish were caught at different depths with two multi-mesh gill nets; one small mesh net, which stretched from 13 to 38 mm, and one large mesh net that stretched from 38 to 107 mm. The number of nets per lake was set based on lake size and average depth. Nets were set overnight, following the standards for freshwater community sampling (Appleberg 2000 for the general sampling guidelines and Lester et al. 2020 for details on the sampling in Ontario). For each lake, every fish was identified at the species level. The number of species ranged from two to 25 per lake. We kept lakes with assigned watersheds (696 out of 707).

Lake environment was characterized by 86 variables recorded for each lake, which we then divided into six environmental categories (details in Supplementary Materials: Table S2-2): Climate (e.g., minimum monthly air temperature (MnMonTP), cumulative temperature below or above 0°C), Water quality (e.g., Nitrate or Potassium concentration), Hydro-morphology (lake area, littoral perimeter), Watershed and spatial characteristics (e.g. altitude, lake age, Tertiary Watershed elevation), and Fishing Activities (e.g., angling pressure, number of boats during summer). Before linking trait dispersion patterns to environmental variation via regression models, we normalized the variables with the function BestNormalize (package BestNormalize, Peterson 2021) and standardized (mean=0, variance=1) them. Given the large number of environmental variables, some of which were highly correlated we used principal component analysis (PCA) to summarize their variation within each environmental category. We retained enough axes to capture at least 80% of the variance in each category. Because our interest was in predicting trait patterns as a function of environmental variability rather than assessing the roles of specific environmental variables, using a PCA to reduce the dimensionality of environmental data allowed us to capture major gradients of variability while minimizing the number of predictors (PC axes).

2.3.2 Species traits and selection of trait sets

We selected 15 traits (Table 2-1, details in Supplementary Materials: Table S2-1) representing different aspects of species ecology: diet, locomotion (related to habitat use, Schleuter et al. (2012)) and temperature preference. A fourth set of traits combined all traits (Table 2-1). All traits data except temperature preference were sourced from FishBase (Froese & Pauly 2025).

Temperature preferences were mainly sourced from Ontario Freshwater Fish Life History Trait Base (Eakins 2025), and completed with data from FishBase and existing literature (details in the supplementary materials Table S2-3). Including an estimation of the upper and lower limit of a fish's thermal preference is important as climatic conditions, and specifically temperature, is an important limiting factor for numerous species in Ontario (Minns & Moore 1995).

As is common in trait-based studies, these traits were summarized at the species level. Before analysis, traits were standardized to zero mean and unit variance to ensure that no trait was given disproportionate weight over others. Since we used different sets of traits, we only kept species that had full trait coverage. The total number of species used in the analysis was 68 (78% of the species present in our species dataset).

Table 2-1 List of fish traits by function based on Villéger et al. (2017) and Schleuter et al. (2012) and their expected patterns. The "*" signals that the trait is a ratio (details in Supplementary Materials Table S1- 2).

Function	Traits	Expectations
All traits pooled together (15 traits)	All traits	Random patterns
Diet (5 traits)	Length, Eye diameter, Trophic level, Preorbital length*, Head Length *	Mainly over-dispersion: competitive interactions
Locomotion (7 traits)	Standard length*, Fork length*, Preanal length*, Predorsal length*, Prepelvic length*, Body depth *, Aspect Ratio	Mainly under-dispersion: environmental filtering
Temperature tolerance (3 traits)	Minimum temperature, maximum temperature, interval between minimum and maximum temperature	Mainly under-dispersion: environmental filtering

In this study, we explored two approaches to assess how trait combinations influence our ability to detect and predict variation in functional dispersion among communities. First, we defined *a priori* categories based on the functional roles commonly associated with traits, drawing on established knowledge of fish biology. Following Villéger et al. (2017) and Schleuter et al. (2012), traits were grouped into three categories: diet, locomotion, and temperature preference (Table 2-2).

To ensure equal influence of each category when combining all trait sets, we applied Gower's standardization of matrices (Gower 1975) on each category separately. This approach, which to our knowledge has not been previously applied in trait studies, standardizes the total sum of squares of each set to one (see Peres-Neto & Jackson, 2001) so that each category has equal weight in the calculation of functional dispersion.

The second approach for generating trait combinations used a novel exploratory framework designed to optimize for under- or overdispersion patterns. Here, we aggregated all traits and implemented a novel forward selection process: 1) Select the trait T_1 that, on average across lakes, has the smallest standardized community trait dispersion (i.e., the most underdispersed; see metric and null models below); 2) Quantify community trait dispersion combining T_1 with each remaining trait, and identify the trait T_{12} that, when combined with T_1, most reduces dispersion; 3) Repeat this process (i.e., T_{123}, T_{1234}, and so on) until no further reduction is possible. The algorithm stops at this point, and the selected traits are retained for further analyses. The same procedure is employed for optimizing overdispersion.

2.3.3 Characterization of functional trait associations

While our selection procedure is designed to enhance the detection of trait patterns in an exploratory manner, it also allows to uncover the complex interconnections among different functions in the assembly process. To accomplish this, for each species pool (province, secondary watersheds, and tertiary watersheds, we determined which pairs of traits were selected together. This analysis clarifies if, and how, trait associations arise emerge during the community assembly process. This analysis uncovered complex relationships among traits typically regarded as functionally distinct, such as temperature and locomotion traits, revealing that they can be positively or negatively correlated but contribute to similar trait patterns (e.g., under- or overdispersed).

Statistical analyses

2.3.4 Quantifying multivariate trait patterns within local communities

The starting point of community-trait analyses is to calculate pairwise distances among species based on individual or combinations (sets) of traits as outlined earlier. We used the Gower distance (Gower 1971) given its ability to handle missing trait values for a few species. The resultant pairwise matrix was then used to estimate functional dispersion for each community (lake). We calculated functional dispersion (diversity) based on Hill numbers (Chiu & Chao 2014), as these indices are among the most robust for detecting under- and/or overdispersion (Mammola et al. 2021):

$$ {}^{2}FD(Q)_k = \left[\sum_i^S \sum_j^S d_{ij} \times \left(\frac{p_i p_j}{Q}\right)^2\right]^{-1} \text{ (Eq. 2-1)} $$

where $Q = \sum_i^S \sum_j^S d_{ij} p_i p_j$ (i.e., Rao's quadratic entropy; sum of the weighted pairwise distance in the community), *S* is the total number of species, d_{ij} is the pairwise (Gower) distance between species *i* and *j*, p_i and p_j are weights for species *i* and *j*, respectively (here p is either 1 or 0 if the species is present or absence in a particularly lake, respectively) and k is an index to indicate the k^{th} lake (i.e., each lake has its own dispersion metric).

As Hill number measures the absolute functional dispersion of communities, FD_Q increases with the number of species in local communities (lakes), challenging direct comparisons between lakes. For example, FD_Q could be higher in a lake with many randomly selected species than in a lake with fewer, non-randomly selected species. To enable meaningful comparisons of FD_Q across local communities, we used its Standardized Effect Size (SES):

$$SES_k = \frac{{}^{2}FD(Q)_{k_{observed}} - \overline{{}^{2}FD(Q)}_{k_{simulated}}}{sd\left({}^{2}FD(Q)_{k_{simulated}}\right)} \quad \text{(Eq. 2-2)}$$

where SES_k is the standardized effect size for the *k*th lake and ${}^{2}FD(Q)_{k_{observed}}$ is the observed functional dispersion for that lake, $\overline{{}^{2}FD(Q)}_{k_{simulated}}$ and $sd\left({}^{2}FD(Q)_{k_{simulated}}\right)$ are the average and the standard deviation, respectively, expected for randomly assembled communities (simulated under a particular null model; see below). Negative *SESs* for a given lake indicate that its species exhibit higher trait similarity than expected by chance (underdispersed), while positive SES values suggests that its species are more functionally distinct than expected by chance (overdispersion). We also calculated the p-value for each SES value using Eq.2-3:

$$p - value = \frac{\left(numberof\ \overline{{}^{2}FD(Q)}_{k_{simulated}} \geq \left| {}^{2}FD(Q)_{k_{observed}} \right|\right) * 2}{numberofsimulations} \quad \text{(Eq. 2-3)}$$

2.3.5 Null models for simulating randomly assembled communities

SES values were calculated by simulating null communities through the random sampling of the same number of species present in each lake from a species pool, representing potential colonizers and thus mimicking random species assembly. For each lake, 999 such communities were generated. Additionally, the selection of species pools in null model analyses enables determining the spatial scales at which communities are more or less structured (Lessard et al. 2012). We considered species pools across three spatial scales: 1) the provincial scale, encompassing all species across the entire data set; 2) primary watersheds; and 3) secondary watersheds, where species pools were defined distinctly at each watershed level (Figure 2-1).

2.3.6 Environmental models for predicting variability in functional trait patterns across communities

In our study system Ontario, the strongest variation in environmental features follow a south-north gradient (e.g., Henriques-Silva et al. 2019). Therefore, we began by evaluating latitudinal trends in SES values across the three different spatial scales (species pools) by fitting a Generalized Additive Model (GAM) for each trait combinations using the two methods outlined earlier and spatial scale, with latitude as a predictor. The maximum number of splines in GAMs was set to 20. Smoothing parameters were extracted using restricted maximum likelihood (REML).

The next step was to understand how SES varies as a function of environmental gradients. To fit the environmental models, we used two methods: one with simple GAMs on different environmental summarised variables and one selecting for the best combination of environmental variables. In the first method, we fitted a GAM model for the different SES (spatial scale and trait combinations) against the PCA for axes (see section *Data and sampling design*) for each environmental category. The number of splines for each estimator was set in the same way as described above.

The second method to fit the environmental model consisted in variable selection applied on the GAM (package plsmselect, Ghosal & Kormaksson (2019)) to identify parameters that best fitted the SES values. In GAM, variable selection can be done by shrinkage penalization which filter out the smoothing coefficients that are too similar to a null space (Marra & Wood 2011). Contrary to the previous environmental models, the variables used in this variable selection procedure, were the 86 scaled variables described in *Data and sampling design*. As such, we kept all the variation present in the initial dataset. We then extracted the adjusted R^2 to assess how different set of predictors were able to explain patterns of community trait variation (SES).

All analyses were performed in R (R Core Team 2020). The Gower's distance and trait metrics were calculated with the package 'FD' (Laliberté et al. 2014) and 'mFD' (Magneville et al. 2022). Null models and trait combinations that maximized or minimized SES were computed using a custom-built function. GAMs were fitted with 'mgcv' package (Wood et al. 2016), while the GAM-lasso models were fitted with the 'plsmselect' package (Ghosal & Kormaksson 2019).

2.4 Results

2.4.1 Trait combinations and functional dispersion patterns

Traits were combined either *a priori*, by grouping them into function types (here diet, temperature preference, and locomotion), or *a posteriori*, by using our computation strategy selection (see Methods) to uncover trait combinations that either maximized or minimized functional dispersion patterns (SES). Figure 2-2 presents the distribution of SES across all lakes, comparing the two trait grouping strategies with a scenario where all traits were combined into a single set. Our selection approach, which combines traits independently of their *a priori* functional types, greatly improved the detection of functional dispersion patterns compared to aggregating traits *a priori* or combining all traits together, especially for overdispersion (Figure 2-2). This indicates that traits traditionally considered distinct in function – such as diet, temperature preference, and locomotion – are interrelated, thereby affecting patterns of functional dispersion and subsequent potential inferences about their roles in community assembly. As expected, combining all traits reduced dispersion, confirming that trait under- or overdispersed trait combinations can produce seemingly random species assemblages. Independent of the method used for trait selection, the strength and direction of SES values across lakes were influenced by the species pool (i.e., spatial scale) employed for their calculation (Figure 2-2). Across all scenarios, whether analysing traits in combinations (all traits together, or a priori or posteriori trait selection) or individually, there were pronounced patterns of under- and overdispersion among lakes. Some trait combinations and individual traits typically exhibited more underdispersion, while others were more overdispersed (on average; see Figure 2-2), yet all showed considerable variation across lake-fish communities. This indicates a high degree of variability in how traits influence their community assembly. Given the substantial variation in environmental characteristics across the lakes in our study system, it is likely that these differences in trait dispersion are driven more so by environmental variation than biotic factors. Specific environmental conditions may lead to either under- or overdispersion of the same traits or trait combinations, as explored in the next results section.

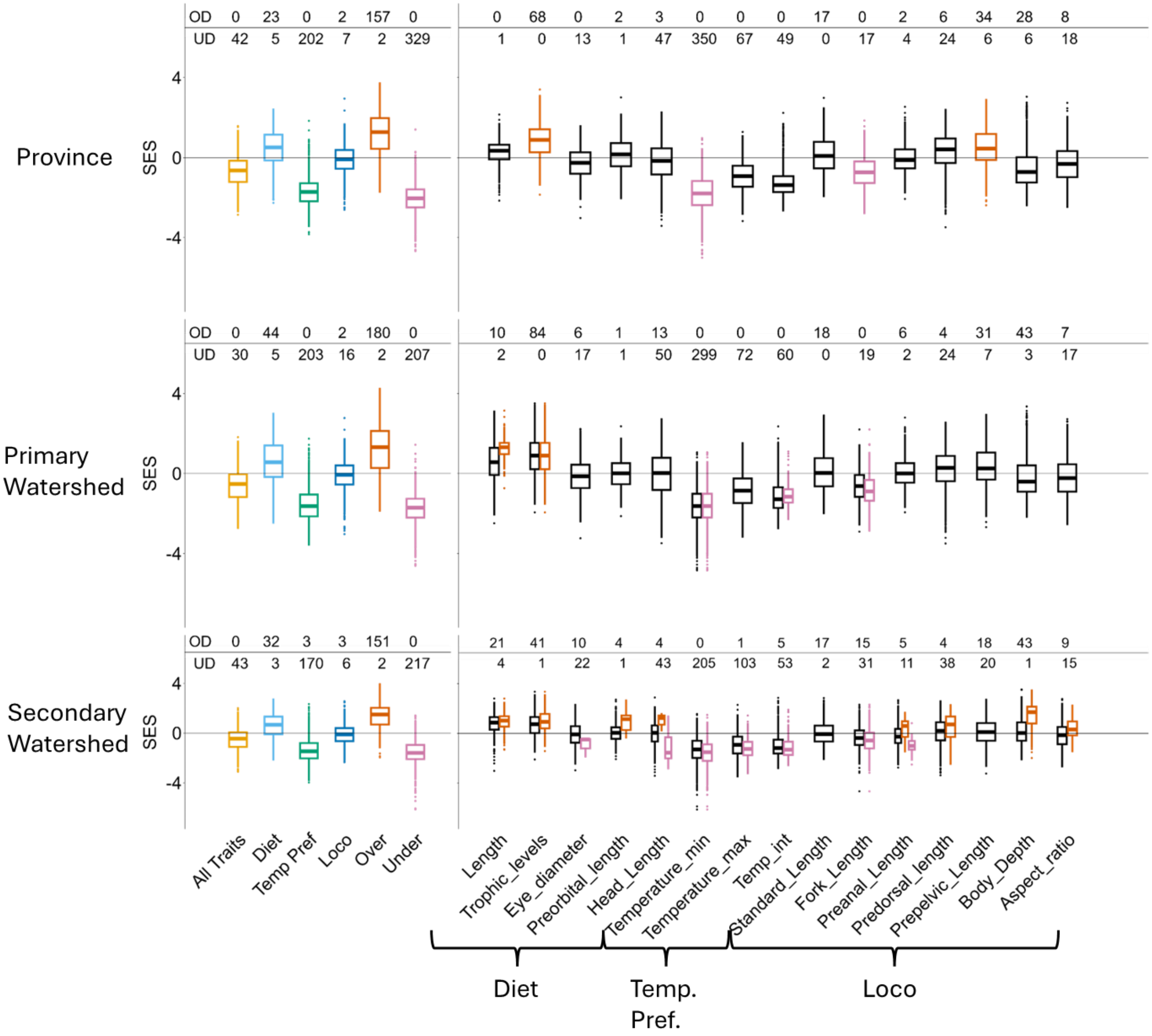


Figure 2-2: Distributions of standardized effect sizes (SES) across different trait sets and spatial scales. Trait sets include All Traits (all three sets pooled), Diet (diet-related

traits), Loco (Locomotion traits), Temp Pref (temperature preference), Under (traits optimizing under-dispersion), Over (traits optimizing over-dispersion), and individual traits. SESs values were calculated for species pools defined within distinct spatial units based on hydrographic boundaries (one Provincial pool, three Primary Watersheds, and 22 Secondary Watersheds). Text boxes indicate the number of communities that were significantly overdispersed (OD) and underdispersed (UD) (significance threshold = 0.05). Total number of communities in this analysis is 696. For individual traits, the boxplot colors reflect the dispersion patterns they were selected to optimise orange for traits selected for overdispersion, pink for underdispersion, and black for the overall SES distribution across all lakes. For example, at the Secondary Watershed scale, Aspect Ratio was selected at least once to optimize underdispersion, with its pink boxplot representing SES values when selected for underdispersion, while the black boxplot shows its SES distribution across all lakes.

It is important to highlight that the *a posteriori* selection of trait combinations that minimized (underdispersion) or maximized (overdispersion) SES values differed across watersheds (Figure 2-3). As the spatial scale of species pools decreased - from province level to primary and then to secondary watersheds – the variety (number) of traits combinations associated with the selection process increased (Figure 2-3). This suggests that smaller spatial scales foster a richer diversity of trait combinations, highlighting that local environmental conditions and species interactions exert a more complex influence on community structure at smaller scales compared to larger ones.

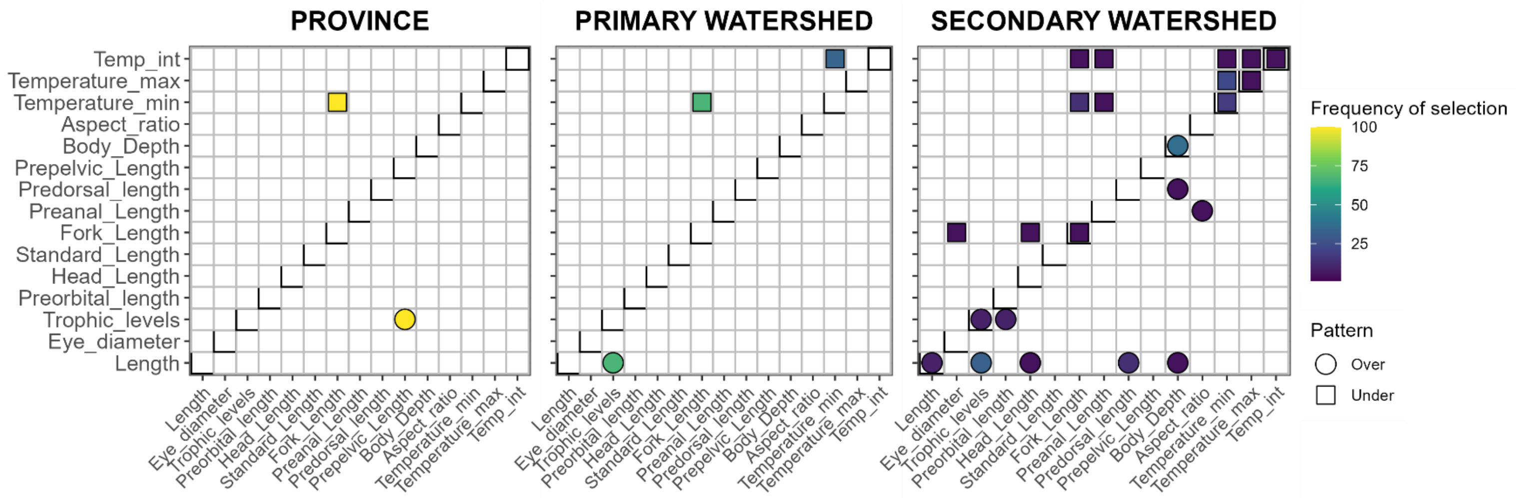


Figure 2-3: Frequency of trait combinations selected to optimize either overdispersion or underdispersion. A computational selection method was used to identify traits that maximize under- and overdispersion at different spatial scales (species pools; 1 Province, 3 Primary Watersheds, 22 Secondary Watersheds). Trait selection frequency was calculated as the number of times a trait was selected, divided by the number of species pools at a given scale. Pairs selected for underdispersion are represented in the upper triangle (squares), while pairs selected for overdispersion are shown in the lower triangle (circles). Color intensity represents selection frequency across species pools: yellow indicates high selection frequency, dark blue indicates low selection frequency, and unselected are not displayed. Some traits were selected individually (singletons) and are shown on the diagonal with darker cell outlines. For example, at the Secondary Watershed scale, Temperature_min was selected as a singleton for underdispersion in one instance across all primary watersheds, represented as a dark blue square on the diagonal.

2.4.2 Functional dispersion patterns: minimal deviation from null community expectations

Based on significant tests alone (i.e., thresholded p-values), most lake-fish communities resembled what might be expected from random species assemblages in their respective species pools (Figure 2-2). These findings yield two key insights. First, while the *a posteriori* method did produce some stronger SES values showing under- and overdispersion, the overall improvement in generating significantly stronger values and corresponding p-values was modest. This outcome may be specific to our system and should not be regarded as a general limitation of our *a posteriori* selection procedure. Notably, this approach significantly enhanced the ability of some environmental models to predict variations in trait patterns (Table 2-2). Second, SES values may still be highly predictable by environmental features, even when statistical significance is low, suggesting that commonly used null models might not be sufficiently powerful for studying trait dispersion patterns. Indeed, if environmental models better predict SES values obtained through our *a posteriori* method compared to the *a priori* approach, it implies that null models for both trait selection methods have low statistical power, and that our *a posteriori* method provides a more robust framework for analyzing trait patterns across environmental gradients (see next section).

2.4.3 Latitudinal and environmental trends in predicting functional dispersion

Although it is commonly observed in the literature the SES of functional dispersion often has limited statistical power for detecting over- and underdispersion, it is also observed that its variation among local communities strongly correlates with variation in environmental features in geographical space (e.g. Ordonez and Svenning 2015; Lamothe et al. 2018; Mouillot, Dumay, and Tomasini 2007). In our study, despite the weak signals of community structure based solely on the functional statistical significance of dispersion patterns (SES; Figures 2-2), we observed pronounced latitudinal (Figure 2-4) and environmental variation (Table 2-2). The latitudinal trends were more influenced by the specific trait combinations used to calculate functional dispersion rather than by the species pools used to generate null communities (Figure 2-4). Despite their non-linearity, variations in the SES for each trait combination and species pool displayed directional latitudinal trends—either positive or negative (Figure 2-4).

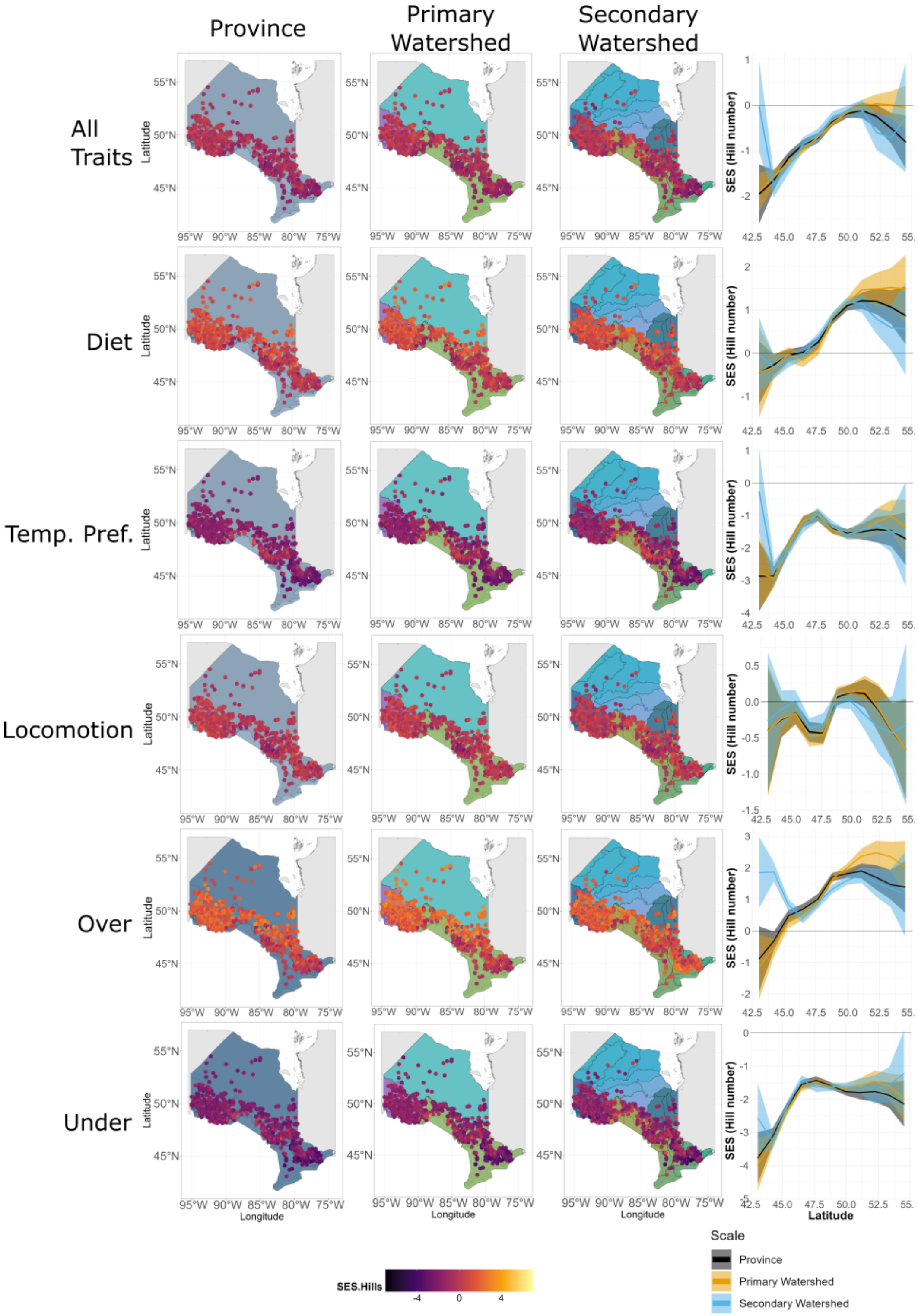


Figure 2-4: Latitudinal gradients of Standardized Effect Size (SES) for the different trait sets (All traits, Diet, Locomotion, Temperature Preference (Temp. Pref.),

Overdispersion, and Underdispersion) and geographically defined species pools (one Province, three Primary Watersheds, 22 Secondary Watersheds) across 696 lake-fish communities in Ontario, Canada. Each point on the maps represents a community (lake), with colors indicating SES values of functional dispersion: dark purple denotes underdispersion, while bright yellow represents overdispersion. Latitudinal trends were modeled using Generalized Additive Models (GAMs), with line colors representing the species pool used to calculate SES: black for the provincial species pool, yellow for species pools defined at the Primary Watershed scale, and blue for species pools at the Secondary Watershed scale.

The performance of generalized additive models (GAMs) linking trait dispersion patterns (SES) and environmental variation varied between trait combinations and environmental categories (Table 2-2). Although climate conditions explained the highest proportion of variation in SES, especially for the Province's species pool (Table 2-2), a model selection procedure (GAM select) selecting among all predictors led to a very strong predictive power, with several R^2 values higher than 60%. Some R^2 values tended to decrease as the spatial scale of species pools decreased (Table 2-2). Note that this is the scale where many traits were retained by our forward selection procedure, indicating more complex trait relationships in lake-fish community assembly. The performance of these models demonstrate that environmental factors reliably predict variation in communities displaying contrasting dispersion patterns across different traits. This suggests that these patterns are not random but emerge from underlying ecological processes that structure these communities to be both under- and overdispersed.

Table 2-2: Performance of different environmental models predicting the Standardized Effect Size (SES) for different combination of traits (Temperature Preference is noted Temp. Pref). We fitted Generalized Additive Models (GAMs) model to assess the predictive power of various environmental variables. Models included: (1) a full model incorporating all environmental categories (Complete), (2) separate models for each environmental category, (3) a model with variable selection using GAM with lasso regularization (GAM select), and (4) a model including only latitude. Each model was run separately for each trait set and at each spatial scale. Model performance is reported as the adjusted R^2 value (ranging from 0 to 1). Except for the GAM lasso model, environmental variables were summarized using Principal Component Analyses (PCAs); for example, the Climate model was based on the first three PCA axes summarizing all climatic variables.

		Model performances (R^2)								
Scale	Trait set	Latitude	Climate	Hydro-morphology	Conductivity	Productivity	Watershed characteristics	Fishing activities	Complete	GAM select
Province	All	0.31	0.44	0.20	0.17	0.13	0.26	0.20	0.51	0. 63
	Diet	0.29	0.31	0.09	0.22	0.22	0.24	0.17	0.47	0.62
	Temp. Pref.	0.29	0.31	0.13	0.38	0.20	0.30	0.28	0.58	0.68
	Locomotion	0.11	0.19	0.13	0.13	0.05	0.14	0.11	0.35	0.50
	Underdispersion	0.29	0.35	0.10	0.30	0.16	0.29	0.25	0.51	0.65
	Overdispersion	0.34	0.41	0.10	0.18	0.12	0.30	0.20	0.50	0.63
Primary Watershed	All	0.32	0. 43	0. 21	0.17	0.13	0. 27	0.22	0.52	0.64
	Diet	0. 34	0. 36	0. 16	0.24	0.20	0. 30	0.20	0.51	0.65
	Temp. Pref.	0.27	0. 28	0. 12	0. 35	0.19	0. 28	0. 27	0. 56	0.66
	Locomotion	0.12	0. 19	0. 12	0. 14	0. 06	0. 14	0.11	0.34	0.51
	Underdispersion	0.31	0. 36	0.08	0. 30	0. 15	0. 29	0.27	0. 50	0.62
	Overdispersion	0. 44	0. 48	0. 12	0. 25	0. 17	0.38	0. 25	0.57	0.69
Secondary Watershed	All	0.37	0.44	0.15	0.15	0.12	0.31	0.22	0.53	0.65
	Diet	0.33	0.36	0.10	0.20	0.20	0.28	0.17	0.48	0.62
	Temp. Pref.	0.27	0.23	0.11	0.31	0.18	0.24	0.20	0.26	0.67
	Locomotion	0.06	0.11	0.06	0.12	0.05	0.08	0.10	0.52	0.41
	Underdispersion	0.25	0.25	0.10	0.19	0.09	0.23	0.19	0.41	0.60
	Overdispersion	0.22	0.22	0.10	0.17	0.14	0.16	0.10	0.30	0.48

2.5 Discussion

This study aimed to explore different methods for combining traits to describe patterns of species associations (here under-, random, and overdispersed). Additionally, we introduced an innovative trait selection framework that provides strong evidence that 1) ecological communities often exhibit signals of both under- and overdispersion; 2) environmental factors reliably predict variation in communities displaying contrasting dispersion patterns across different traits, indicating that these patterns are not random but emerge from underlying ecological processes that structure these communities to be both under- and overdispersed; 3) detecting and predicting patterns in functional trait dispersion can heavily depend on the prior and often arbitrary selection of traits included in community trait analyses.

To establish guidelines for functional trait selection, we contrasted two methods: one grounded in biological knowledge (here fish biology) and another that optimizes trait combinations to detect over- and underdispersion. The biology-based method considers *a priori* hypotheses about trait functions but may dilute community trait patterns by including traits that respond inconsistently across environmental gradients. In contrast, our approach highlights that community structure can arise also from complex relationships among traits, such as the influence of temperature on locomotion traits that shape the diversity patterns of lake-fish communities. By contrast, as commonly observed in traits empirical studies, indiscriminately pooling all traits in our study system obscured patterns in trait variation among lakes. In our case, pooling traits together completely blurred signals of overdispersion, and underestimated underdispersion. Defining trait sets based on specific biological characteristics or patterns revealed clearer signals for both patterns. This aligns with findings from previous studies (Trisos et al. 2014; Lopez et al. 2016; Côte et al. 2019), which suggest that haphazardly pooling of traits can mask signals of both to under- and overdispersion.

2.5.1 Defining trait selection enhances the detection of functional dispersion patterns

For each set of traits, we anticipated distinct patterns of functional distribution for our specific system: for the *a priori* sets, we expected that diet would primarily exhibit overdispersion, while locomotion and temperature preference would show underdispersion (see Table 2-1 for the predictions). Diet and temperature preference conformed closely to this expectation. However, locomotion traits approximated a random pattern at the Secondary Watershed scale. This pattern may result from either pooling trait with different functional dispersion that cancel each other out, or from homogenous habitats that support communities with diverse locomotion strategies.

We anticipated diet traits to generally enhance trait overdispersion and locomotion and temperature preferences to increase underdispersion. This was only partly confirmed. For example, trophic levels were selected for overdispersion primarily at the Provincial level and in most Watersheds. Minimum temperature was also consistently selected to optimise underdispersion. Locomotion traits like fork length and aspect ratio, typically underdispersed, highlight environmental filtering's impact. Interestingly, traits such as predorsal and prepelvic length were often chosen for overdispersion. In some cases, traits like head length and preanal length were selected for both over- and underdispersion at the Secondary Watersheds level, underscoring the local context's role in shaping functional diversity across Ontario’s lake-fish communities. As spatial scale narrows, the diversity of trait combinations affecting functional dispersion increases, illustrating that local processes more complexly influence species selection within lake communities.

Our selection procedure also clarified the patterns in the *a priori* trait sets. The locomotion includes traits with varying distribution patterns, effectively canceling each other’s tendencies toward over- or underdispersion. This indiscriminate trait pooling can obscure signals of environmental filtering and abiotic interactions, suggesting that such combinations may be less informative than initially expected. Our findings indicate that some *a priori* (predefined) trait combinations still yielded patterns nearing randomness.

Conversely, our *a posteriori* selected trait sets revealed more conspicuous trait signals (i.e., overdispersion or underdispersion). Our environmental models indicate that organizing trait sets may improve predictive performance in many cases and reveal associations with environmental variables not captured when all traits are pooled together (i.e. models with productivity variables). More importantly, these models reliably predict variation in communities exhibiting both under- and overdispersion across different traits, indicating that these patterns are not random but arise from ecological processes that shape community structure. Collectively, this approach of trait combinations, guided by either *a priori* knowledge or by our selection framework, reveals patterns that would be otherwise hidden.

2.5.2 Integrating trait combinations to improve understanding of functional dispersion patterns

Environmental filtering and abiotic interactions both play significant roles in structuring ecological communities. Although elucidating abiotic (environmental filtering) versus biotic (density-dependent interactions) roles based solely on patterns of trait diversity is challenging, the combination of traits significantly influences the strength of under- and overdispersion signals. To effectively discern the contexts in which various mechanisms underlying functional diversity operate, it is essential to distinguish traits according to their function or to how they maximize different patterns of functional diversity. This consideration is particularly critical in scenarios where different processes simultaneously influence the same local community. Asserting that one process predominantly governs community assembly is overly simplistic; an assumption prevalent in numerous contemporary empirical trait studies (e.g. Mouillot et al. 2007; Lamothe et al. 2018; Poveda-Cuellar et al. 2022), yet it may oversimplify the complex interplay of factors shaping community dynamics.

Although the trait combinations in most of our communities appeared random purely based on null model significance tests, the strong predictive performance of our environmental models for Standardized Effect Sizes (SES) suggests that the trait-driven assembly processes in these lakes are complex and far from random. For temperature preference traits, communities exhibited strong underdispersion in southern lakes and weaker underdispersion in Northern lakes. The weaker underdispersion of thermal traits in the North may indicate that cold winters, even though limiting for warmer-water fishes (such as the smallmouth bass (Alofs & Jackson 2015a)), may not be as limiting for a number of Ontario fishes.. For diet traits, a clear positive latitudinal pattern emerged, consistent with our predictions. Northern communities displayed greater signal of biotic interactions due to limited resource availability. We observed similar patterns in the a *posteriori* selected trait sets, where overdispersion was more pronounced and underdispersion weaker in the northern communities.

Additionally, the predictive performance of models that related climate variables to functional patterns were high. For Ontario fishes, climate is one of the strongest constraints for successfully colonizing lakes (Mandrak & Crossman 1992; Jackson et al. 2001; Alofs & Jackson 2015a). The pronounced latitudinal trends observed are strongly influenced by the significant climatic gradient across Ontario. Fishing activities also contribute to the variation in dispersion patterns among communities, as they can alter functional diversity by preferentially targeting species with similar functional traits (Olden et al. 2007). Additionally, watershed characteristics account for some of the variance in the functional dispersion patterns of lake-fish communities in Ontario. The historical context further shapes community assembly, reflecting both post-glaciation colonization and the contemporary and historical connectivity of habitats (Layeghifard et al. 2015; Loewen et al. 2022).

2.5.3 Advantages and limitations of trait selection processes

One of the foremost challenges in ecology is transitioning from merely describing patterns to generating robust hypotheses (Houlahan et al. 2017; Green et al. 2022). Our analyses suggest that abiotic and biotic interactions may, together, shape trait distributions (HilleRisLambers et al. 2012), creating distinct and analyzable patterns of under and over-dispersion. However, in current analytical frameworks, which pools multiple traits together, often result in patterns that are often not distinguishable from randomness (e.g., Lamothe et al. 2018 in the same study system as ours). These analyses not only obscure true ecological patterns but may also constrain ecologists to a false dichotomy between abiotic and biotic interactions (Cadotte & Tucker 2017).

Both of our proposed frameworks for trait selection aim to achieve four main objectives: 1) uncover functional dispersion patterns that would otherwise remain obscured; 2) uncover more complex processes underlying community assembly by demonstrating that the same community may be over- and underdispersed depending on the combination of traits; 3) determine the combination of traits within a community that may appear random, over- or underdispersed; 4) increase the ability of environmental models to predict patterns in function trait diversity. It also has the potential to formulate more precise hypotheses about the function of specific sets of traits and how they result from community assembly processes. In this sense, our *a posteriori* selection framework enhances our understanding of community assembly by recognizing that both abiotic and biotic interactions can significantly influence community dynamics, albeit affecting different types of traits in varying ways. The *a priori* combination process focuses on how different traits or functions respond to assembly mechanisms. Conversely, *a posteriori* selection framework allows one to hypothesize which traits are selected to optimize certain observed patterns within and across communities.

As in any selection framework, inconsistency may be an issue in our procedure. We define inconsistency as the phenomenon where multiple variables or traits can be selected interchangeably due to small sampling perturbations (Whittingham et al. 2006). This issue becomes particularly acute when the traits involved are highly correlated, which can influence the robustness of the conclusions drawn from our analysis in terms of which traits are important. It is also possible that traits that have many but weak relationships with multiple traits to be not selected by our procedure. These challenges are not unique to our framework but are inherent to many model selection processes widely employed across various disciplines. Despite these challenges, model selection remains a critical tool in ecological research. Acknowledging these limitations opens an avenue for further research, potentially leading to the development of more robust selection methodologies that mitigate these issues.

Finally, while our study underscores the importance of trait selection in optimizing patterns of functional diversity—and, in turn, how functional diversity is shaped by environmental variation—other studies focus on how individual traits contribute to functional diversity and how these contributions shift along environmental gradients (e.g.,Kaarlejärvi et al. (2024)). Notably, the approach used by Kaarlejärvi et al. (2024) suggests that some traits may increase functional diversity while others reduce it along the same environmental gradient. This aligns with our environmental models, which identify the types of environments that promote or constrain local functional diversity. However, their model may not capture fine-scale variation at the community level, potentially limiting its ability to distinguish traits that increase from those that decrease functional diversity within single communities. A more localized approach might provide a stronger test of whether the same community can exhibit both overdispersion and underdispersion, depending on the trait combination. As a result, in our selection procedure, each local community may assemble different sets of trait combinations that either minimize or maximize functional diversity. These differences highlight two key approaches to modeling traits across environmental gradients: one, like ours, that selects traits before environmental modeling, and another that selects traits based on environmental modeling. Comparing these two strategies, along with their respective methodological and conceptual frameworks, should be a priority for future research.

Our study underscores the critical role of trait selection in unveiling and interpreting patterns of functional dispersion in ecological communities. Aggregating traits tend to mask the distinct responses of individual traits to environmental gradients, thus complicating our understanding of community assembly. One key finding is that traits with distinct functional biological expectations exhibit complex relationships that influence the assembly process. Finally, future studies should invest in building more robust selection procedures. Two such avenues are: 1) build algorithms that select trait combinations based on how environmental models improve their predictive ability rather than just selecting on patterns of over- and underdispersion as in this study; and 2) build algorithms that select trait combinations based on their complex correlation structure. Despite the potential limitations of our selection procedure, ecologists are heavily invested in assessing and interpreting patterns of trait over- and underdispersion. We expect that our study will contribute to refining these assessment techniques and offer a more robust framework for understanding how traits influence community assembly and ecological dynamics.

2.6 Supplementary materials for Chapter 2

Table S 2-1: Detailed descriptions of the traits and their units (extracted from FishBase (Froese & Pauly 2025)) and from the Ontario Freshwater Fishes Life History Trait Base (Eakins 2025) for the thermal traits.

Trait	Unit	Meaning
Aspect Ratio	NA	Caudal height/Caudal fin area
Body Depth	Percentage of Total Length	Height of the body/Length
Eye Diameter	Percentage of Head Length	Eye diameter/Length of the head
Fork Length	Percentage of Total Length	Proportion of length to the fork over total length
Head Length	Percentage of Total Length	
Length	cm	Common total length
Maximum Temperature	Celsius	Maximum preferred Temperature
Minimum Temperature	Celsius	Minimum preferred Temperature
Preanal Length	Percentage of Total Length	Length between the mouth to pre-anal fin/Length
Predorsal Length	Percentage of Total Length	Length between the mouth to the pre-dorsal fin /Length
Preorbital Length	Percentage of Head Length	Length between the mouth to eye /Length
Prepelvic Length	Percentage of Total Length	Length between the mouth to pre-pelvic fin/Length
Standard Length	Percentage of Total Length	Length to the tail
Temperature Interval	Celsius	Minimum Temperature – Maximum Temperature

Table S 2-2 Description of environmental variables, their units and the transformation method used to normalise the data

. Name	Description	Category	Unit	Transformation
AirTemp_8110	Mean Annual Air Temperature for 1981-2010	Climate	Celsius	Ordered quantiles normalization (orderNorm)

Alkalinity.mg.L.CaCO3	concentration of CaCO3 in the lake	Conductivity	mg/L	Log10(x)
Alkalinity.mg.L.CaCO3_pctl	Percentile of concentration of CaCO3 in the lake class (Lake size)	Conductivity		Ordered quantiles normalization (orderNorm)
Altitude_m	Altitude above the sea level of the lake	Watershed characteristic	m	Ordered quantiles normalization (orderNorm)
Amonia_Amonium.mg.L	Concentration of Amonia and Amonium	Productivity	mg/L	Ordered quantiles normalization (orderNorm)
Amonia_Amonium.mg.L._pctl	Percentiles of the concentration of Amonia and amonium within lake class	Productivity		Ordered quantiles normalization (orderNorm)
Angling Pressure	Annual angling pressure (angler-hours/ha-year) - based on aerial survey counts	Fishing activities	angler-hours/ha-year	Ordered quantiles normalization (orderNorm)
Area_km2	Surface Area of the lake	Hydromorphology	km^2	Ordered quantiles normalization (orderNorm)
Aut0	Average date of the last day above 0 from 1981-2010	Climate	Days	Ordered quantiles normalization (orderNorm)
Calcium.mg.L	Concentration of Calcium	Conductivity	mg/L	Ordered quantiles normalization (orderNorm)

Calcium.mg.L_pctl	Percentile of Concentration of Calcium	Conductivity		Ordered quantiles normalization (orderNorm)
Chloride.mg.L.	Concentration of Chloride	Conductivity	mg/L	Ordered quantiles normalization (orderNorm)
Chloride.mg.L._pctl	Percentile of the concentration of Chloride within lake size class	Conductivity		Ordered quantiles normalization (orderNorm)
Conductivity.uS.cm.s.	Conductivity	Conductivity	uS/cm/s	Ordered quantiles normalization (orderNorm)
Conductivity.uS.cm.s._pctl	Percentiles of the conductivity within lake size class	Conductivity		Box Cox Transformation
Conservation_Land	Conservation status (1 implies some form of conservation status)	Fishing activities		Arcsin transformation
DD5_8110	Degree Days above 5C for 1981-2010	Climate		Ordered quantiles normalization (orderNorm)
Depth_Max	Maximum Depth	Hydromorphology	m	Box Cox Transformation
Depth_Mn	Mean Depth	Hydromorpholgy	m	Log10(x)
DIC..mg.L.	Dissolved Inorganic Carbon	Productivity	mg/L	Box Cox Transformation
DIC..mg.L._pctl	Percentiles of the concentration of DIC within lake class	Productivity		Ordered quantiles normalization (orderNorm)

DOC..mg.L_pctl	Percentiles of the concentration of DOC within lake class	Productivity		Ordered quantiles normalization (orderNorm)
DOC..mg.L	Dissolved Organic Carbon	Productivity	mg/L	Box Cox Transformation
FreezDD	Cumulative Degree Days with a temperature <0C	Climate		Ordered quantiles normalization (orderNorm)
Hypo.Space.Area.obs	Observed Hypolimnetic Area: Area of the layer of water below the thermocline	Hydromorphology	km^2	Ordered quantiles normalization (orderNorm)
Hypo.Space.Area.pred	Predicted Hypolimnetic Area: Area of the layer of water below the thermocline	Hydromorphology	km^2	Ordered quantiles normalization (orderNorm)
Hypo.Space.Vol.pred	Predicted hypolimnetic Volume	Hydromorphology	m^3	Ordered quantiles normalization (orderNorm)
Hypo.Space.Vol.obs	Observed Hypolimnetic volume	Hydromorphology	m^3	Ordered quantiles normalization (orderNorm)
Iron	Concentration of Iron	Conductivity	mg/L	Yeo-Johnson Transformation
Iron_pctl	Percentiles of the concentration of iron within lake class	Conductivity		Ordered quantiles normalization (orderNorm)

Lak_age	Estimated age of the lake	Spatial	Kyr	Box Cox Transformation
Magnesium.mg.L.	Concentration of Magnesium	Conductivity	mg/L	Ordered quantiles normalization (orderNorm)
Magnesium.mg.L._pctl	Percentiles of the concentration of Magnesium within lake class	Conductivity		Ordered quantiles normalization (orderNorm)
MAT_8110	Mean Annual Air Temperature for 1981-2010	Climate	Celsius	Ordered quantiles normalization (orderNorm)
Max.surface.T	Maximum Surface Temperature	Climate	Celsius	Arcsin transformation
MxMonTP	Maximum Monthly surface Temperature	Climate	Celsius	Ordered quantiles normalization (orderNorm)
MxWatTP	Boosted estimation of the maximum summer water temperature	Climate	Celsius	Ordered quantiles normalization (orderNorm)
Nitrate.Nitrite.ug.L	Concentration of Nitrate and Nitrite	Productivity	µg/L	Ordered quantiles normalization (orderNorm)
Nitrate.Nitrite.ug.L._pctl	Percentiles of the concentration of Nitrate and Nitrite within lake class	Productivity		Ordered quantiles normalization (orderNorm)
No..ice.free.days	Estimated umber of icefree days	Climate	Days	Ordered quantiles normalizatio

				n (orderNorm)
pArea_LE20	Proportion of Lake area < 20 m in depth	Hydromorphology		Ordered quantiles normalization (orderNorm)
pDays.Cold	Proportion of days Cold (between 8-12C) during icefree period	Climate		Ordered quantiles normalization (orderNorm)
pDays.Cool	Proportion of days Cool (12 and 22 C) during icefree period	Climate		Ordered quantiles normalization (orderNorm)
pDays.Warm	Proportion of warm days (22-26C) during icefree period	Climate		Ordered quantiles normalization (orderNorm)
pH	pH	Conductivity		Arcsin transformation
pH_pctl	Percentiles of pH within lake class	Conductivity		Ordered quantiles normalization (orderNorm)
Perim_km	Perimeter of the lake	Hydromorphology	km^2	Ordered quantiles normalization (orderNorm)
pLittoral	Proportion of littoral	Hydromorphology		Box Cox Transformation
PodDD	Cumulative Degree Days with a temperature >0C	Climate		Yeo-Johnson Transformation
PosDays	Number of day > 0C	Climate		Ordered quantiles normalizatio

				n (orderNorm)
PosPrecip	Average rainfall from 1981-2010	Climate		Ordered quantiles normalization (orderNorm)
Potassium.mg.L.	Concentration of Potassium	Conductivity	mg/L	Ordered quantiles normalization (orderNorm)
Potassium.mg.L._pctl	Percentiles of the concentration of Potatium within lake class	Conductivity		Ordered quantiles normalization (orderNorm)
Secchi_Su	Secchi depth of the lake in summer	Productivity	m	Ordered quantiles normalization (orderNorm)
Secchi_Sp	Secchi depth of the lake in spring	Productivity	m	Box Cox Transformation
Shoreline_Development_Factor	Shoreline Development Factor	Hydromorphology		Box Cox Transformation
Shoreline_km	Total shoreline of lake (include islands and perimter)	Hydromorphology	km	Box Cox transformation
Silicate..mg.L.	Concentration of silicate	Productivity	mg/L	Box Cox transformation
Silicate..mg.L._pctl	Percentiles of the concentration of silicate within lake class	Productivity		Ordered quantiles normalization (orderNorm)
Sodium.mg.L	Concentration of Sodium	Conductivity	mg/L	Ordered quantiles normalization (orderNorm)

Sodium.mg.L._pctl	Percentiles of the concentration of sodium within lake class	Conductivity		Ordered quantiles normalization (orderNorm)
Spr0	Average date of the first day above 0 from 1981 - 2010	Climate		Center + Scale
Sulphate.mg.L.	Concentration of sulphate	Conductivity	mg/L	Standardised arcsin
Sulphate.mg.L._pctl	Percentiles of the concentration of sulphate within lake class	Conductivity		Ordered quantiles normalization (orderNorm)
Summer.Shore.Count	Mean Count of shore fishers in summer	Fishing activities		Square-root Transformation
Summer.Vessel.Count	Mean count of fishing boats in summer	Fishing activities		Ordered quantiles normalization (orderNorm)
TDS	Total Dissolved Solids	Productivity	mg/L	Yeo-Johnson Transformation
Thermo.Obs	Observed Thermocline Depth	Climate	m	Square-root transformation
Thermo.Pred	Predicted Thermocline Depth	Climate	m	Ordered quantiles normalization (orderNorm)
TKN.ug.L	Total Kjeldahl Nitrogen	Productivity	µg/L	Square-root transformation
TKN.ug.L_pctl	Percentile of Total Kjeldahl Nitrogen	Productivity		Ordered quantiles normalization (orderNorm)

Total.Phosphorus.ug.L	Concentration of Phosphorus+	Productivity	µg/L	Box Cox Transformation
Total.Phosphorus.ug.L_pctl	Percentile of the concentration of Phosphorus within lake size class	Productivity		Ordered quantiles normalization (orderNorm)
TP	Total Phosphorus	Productivity		Standardised arcsin
True.Colour..TCU.	True Color	Productivity	TCU	Box Cox Transformation
True.Colour..TCU._pctl	Percentile of True Colour within lake class	Productivity		Ordered quantiles normalization (orderNorm)
TSI…Avg	Mean of Trophic Status Index (from Phosphorus and Secchi)	Productivity		Arcsin transformation
TSI…Phosphorus	Trophic Status Index based on Phosphorus	Productivity		Yeo-Johnson Transformation
TSI…Secchi	Trophic Status Index based on Secchi	Productivity		Square-root transformation
TWS_age	Age of the Tertiary Watershed	Watershed Characteristics		Ordered quantiles normalization (orderNorm)
TWS_area	Tertiary watershed area	Watershed Characteristics	km^2	Ordered quantiles normalization (orderNorm)
TWS_eleva	Tertiary watershed elevation (m a.s.l.)	Watershed Characteristics	m	Ordered quantiles normalization (orderNorm)

TWS_elevd	Difference between the lowest and highest point in the tertiary watershed	Watershed Characteristics	m	Ordered quantiles normalization (orderNorm)
Volume	area*max depth	Hydromorphology	m^3	Ordered quantiles normalization (orderNorm)
Waterbody_LID	Lake Identifier			NA
Winter.huts.Counts	Mean count of ice huts in winter	Fishing activities		Square-root transformation
Winter.Open.Ice.Counts	Mean Count of open-ice fishers in winter	Fishing activities		Square-root transformation

Table S 2-3: List of species considered in the study with the source from which thermal data were extracted. Ontario Freshwater Fishes Life History Trait Base (Eakins 2025) is noted with the anagram OFFLHTB. We also report the source from which FishBase extracted their data.

Species (scientific name)	Species (common name)	Source for the Temperature traits
Alosa pseudoharengus	Alewife	Ontario Freshwater Fish Life History Trait Base (OFFLHTB)
Amblopites rupestris	Rock bass	OFFLHTB
Ameiurus melas	Black Bullhead	Fishbase (Baensch & Riehl 1991)
Ameiurus natalis	Yellow Bullhead	OFFLHTB
Amia calva	Bowfin	Fishbase (Baensch & Riehl 1991)
Aplodinotus grunniens	Freshwater Drum	OFFLHTB
Carpiodes cyprinus	Quillback	OFFLHTB
Catostomus catostomus	Longnose Sucker	OFFLHTB
Catostomus commersonii	White Sucker	OFFLHTB
Chrosomus eos	Northern Redbelly Dace	(Stauffer et al. 1980)
Coregonus artedi	Cisco (lake herring)	OFFLHTB
Coregonus clupeaformis	Lake Whitefish	OFFLHTB
Cottus bairdii	Mottled Sculpin	OFFLHTB
Cottus cognatus	Slimy Sculpin	OFFLHTB
Cottus ricei	Spoonhead Sculpin	OFFLHTB

Couesius plumbeus	Lake Chub	Fishbase (Baensch & Riehl 1991)
Culaea inconstans	Brook Stickleback	Fishbase (Baensch & Riehl 1991)
Cyprinella spiloptera	Cyprinella_spiloptera	(Mathur et al. 1983)
Cyprinus carpio	Common Carp	(Wismer & Christie 1987)
Dorosoma cepedianum	Gizzard Shad	OFFLHTB
Esox lucius	Northern Pike	OFFLHTB
Esox masquinongy	Muskellunge (muskie)	OFFLHTB
Etheostoma exile	Iowa Darter	OFFLHTB
Etheostoma nigrum	Johnny Darter	Fishbase (Baensch & Riehl 1991)
Fundulus diaphanus	Banded Killifish	Fishbase (Baensch & Riehl 1991)
Gasterosteus aculeatus	Threespine Stickleback	OFFLHTB
Hiodon alosoides	Goldeye	OFFLHTB
Hiodon tergisus	Mooneye	OFFLHTB
Ictalurus punctatus	Channel Catfish	OFFLHTB
Labidesthes sicculus	Brook Silverside	Fishbase (Baensch & Riehl 1997)
Lepisosteus osseus	Longnose Gar	OFFLHTB
Lepomis cyanellus	Green Sunfish	OFFLHTB
Lepomis gibbosus	Pumpkinseed	OFFLHTB
Lepomis macrochirus	Bluegill	OFFLHTB
Lepomis megalotis	Longear Sunsfish	(Wismer & Christie 1987)
Lota lota	Burbot (ling)	OFFLHTB
Luxilus cornutus	Common Shiner	(Ulvestad & Zar 1977)
Micropterus dolomieu	Smallmouth Bass	OFFLHTB
Micropterus salmoides	Largemouth Bass	OFFLHTB
Morone chrysops	White Bass	OFFLHTB
Moxostoma erythrurum	Golden Redhorse	OFFLHTB
Moxostoma acrolepidotum	Shorthead Redhorse	OFFLHTB
Neogobius melanostomus	Round Goby	OFFLHTB
Notemigonus crysoleucas	Golden Shiner	OFFLHTB
Notropis atherinoides	Emerald Shiner	OFFLHTB
Notropis bifrenatus	Bridle Shiner	Fishbase (Baensch & Riehl 1985)
Notropis hudsonius	Spottail Shiner	OFFLHTB
Oncorhynchus mykiss	Rainbow Trout	OFFLHTB
Oncorhynchus tshawytscha	Chinook Salmon	OFFLHTB
Osmerus mordax	Rainbow Smelt	OFFLHTB
Perca flavescens	Yellow Perch	OFFLHTB
Percina caprodes	Logperch	(Singkran 2007)
Percopsis omiscomaycus	Trout-perch	OFFLHTB
Pimephales notatus	Bluntnose Minnow	OFFLHTB
Pimephales promelas	Fathead Minnow	OFFLHTB
Pomoxis nigromaculatus	Black Crappie	OFFLHTB
Prosopium coulterii	Pygmy Whitefish	OFFLHTB
Prosopium cylindraceum	Round Whitefish	Fishbase (Scott & Crossman, 1973)

Pungitius pungitius	Ninespine Stickleback	OFFLHTB
Rhinichthys atratulus	Eastern Blacknose Dace	OFFLHTB
Rhinichthys cataractae	Longnose Dace	OFFLHTB
Salvelinus fontinalis	Brook (speckled) Trout	(Wismer & Christie 1987)
Salvelinus namaycush	Lake Trout	OFFLHTB
Sander canadensis	Sauger	OFFLHTB
Sander vitreus	Walleye	OFFLHTB
Semotilus atromaculatus	Creek Chub	(McMahon 1982)
Umbra_limi	Central Mudminnow	(Wismer & Christie 1987)

3 CHAPTER 3: Community functional integration: an unexplored dimension of functional structure and its role in community assembly

3.1 Abstract

Functional ecology provides a powerful framework for understanding biodiversity patterns and the processes that structure ecological communities. Traditionally, community ecologists have focused on functional composition and diversity metric to infer assembly processes. While informative, these approaches overlook an important dimension of functional structure: the correlations among traits. Here, we formalize the concept of community functional integration (CFInt), which captures variation in the strength and structure of trait correlations within and between ecological communities. Using a comprehensive empirical data from lake-fish communities across Ontario, we show that trait correlation dataset on lake-fish communities across Ontario, Canada, we Demonstrate that CFInt varies geographically, with distinct patterns emerging across latitudinal and environmental gradients. We further show that CFInt provides explanatory power for species richness beyond climate and conventional functional diversity metrics, highlighting its potential as a key predictor of biodiversity. Together, these findings position CFInt as both a sensitive indicator of environmental filtering and community assembly processes, and as a valuable complement to traditional trait-based approaches. We advocate for the routine inclusion of trait correlations in functional ecology to more fully capture the complexity of community structure and biodiversity dynamics.

3.2 Introduction

Over the past few decades, researchers have increasingly embraced the functional framework to describe biodiversity patterns and to uncover the mechanisms behind them. Functional ecology has revolutionized our understanding of community structure and functioning (McGill et al. 2006) by establishing robust mechanistic links between biodiversity and emergent community properties (e.g., biomass productivity, Tilman et al. 1997; resilience, Biggs et al. 2020 pollination, Gagic et al. 2015). Today, it serves as a central paradigm for studying community assembly, providing both an analytical (Villéger et al. 2008; Laliberte & Legendre 2010) and conceptual frameworks (Weiher & Keddy 1995; HilleRisLambers et al. 2012) to assess biodiversity patterns and infer assembly mechanisms (i.e., pattern to process inference). The strength of functional ecology lies in the concept of functional traits - measurable characteristics of an individual or species that directly or indirectly impact fitness (*sensu* Violle et al. 2007). These traits bridge functional frameworks with the longstanding theory of the niche, particularly the Hutchinsonian niche (Chase & Leibold 2003), offering a basis to infer assembly mechanisms from community functional structure.

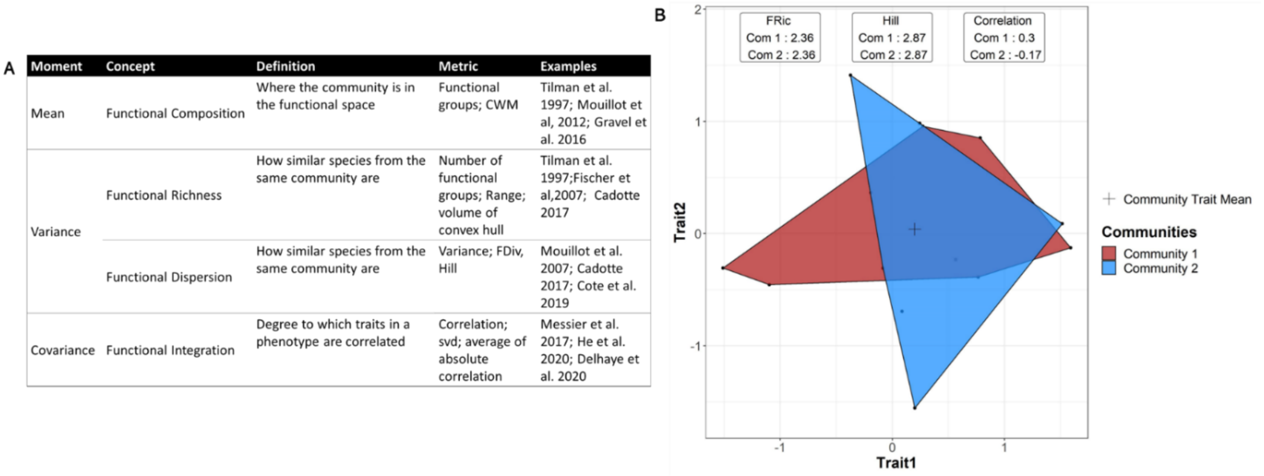
Traditionally, the functional structure of a community is described through multiple statistical multivariate moments, such as functional composition and functional diversity – each encompassing a range of related diversity concepts (Figure 3-1A). Extensive efforts have been made to break down functional structure into meaningful concepts and measurable metrics (Mason et al. 2005; Mouchet et al. 2010; Münkemüller et al. 2012). For instance, functional diversity can be partitioned into components like functional richness and functional dispersion, which can then be analysed and interpreted within the framework of established community assembly concepts and theories (Mason et al. 2005, Figure 3-1A). Given the complexity inherent in community functional structure, ecologists employ a variety of concepts and metrics to capture its variation along environmental gradients (e.g. Mouillot et al. 2007; Gagic et al. 2015; Klais et al. 2017).

However, some statistical moments (aspects) of functional structure remain underexplored. In community functional ecology, trait correlations are typically overlooked. Traits are often assumed uncorrelated or their correlations are reduced to common variation space via multivariate analysis such as principal component analysis (PCA) or principal coordinate analysis (PCoA) (see analytical frameworks in Villéger et al. 2008). When using conventional metrics such as functional richness and diversity, traits correlations are implicitly assumed to be invariant across spatial scales - from regional to local - and across local communities. Yet, this assumption is rarely scrutinized, and two communities may exhibit identical functional richness and dispersion while differing in their trait correlations (Figure 3-1B). While metrics like functional richness and dispersion quantify the volume occupied by a community in trait space - reflecting the impact of selection filters (Cornwell et al. 2006; Mason et al. 2013; Mammola et al. 2021) - trait correlations reveal the shape of that space and whether species are organized around particular axes of correlated variation. Analysing trait correlations would allow researchers to detect hidden patterns of trait integration and potential trade-offs between functions, providing insights into niche differentiation, trait complementarity, and the processes by which local communities select species based on their position within a correlated multivariate trait space. This approach highlights that the interplay among traits - not just their individual values and variation among species and communities - can be essential for understanding how species are selected to compose local communities and species coexistence.

Although some researchers have highlighted the potential insights from investigating these correlations and their variation across communities (Nock et al. 2016; Messier, Lechowicz, et al. 2017), this statistical multivariate moment of functional structure has been largely neglected. Our study underscores that trait correlations are not static but vary meaningfully across communities, highlighting the need to incorporate this dimension routinely into functional ecological frameworks to better capture the complexity of community assembly and biodiversity patterns. To address this gap, we propose to adapt the concept of phenotypic integration to community functional ecology – a framework we term community functional integration (CFInt). In evolutionary biology, phenotypic integration describes the correlation among traits within a complex phenotype (Schlichting 1989; Murren 2012), capturing how trait canalization, plasticity, trade-offs, and the structure of trait correlation networks vary across environments. Similarly, we define CFInt as the strength and patterns of correlations among traits that underpin community assembly and functioning. This approach should allow researchers to build upon current frameworks - which already assess the individual roles of traits - by further investigating how the interdependencies among traits, and the roles individual traits play within these correlation networks, shape species coexistence and ecosystem processes in response to environmental pressures.

Several studies have examined how phenotypic integration responds to environmental gradients at the community level, particularly in plant communities. These studies have focused on either the degree of integration within local communities or the structure of community traits across landscapes, through frameworks such as the Leaf Economic Spectrum (e.g., Messier, Lechowicz, et al. 2017; Candeias & Fraterrigo 2020; Delhaye et al. 2020; Sanaphre-Villanueva et al. 2022). Although these studies are not explicitly framed in the context of community assembly, they suggest that strong environmental and biotic filters (e.g., pollution - Delhaye et al. 2020; competition, Sanaphre-Villanueva et al. 2022) can intensify the differentiation of species' strategies, resulting in stronger community phenotypic integration. This is likely because strong environmental and biotic filters create selective pressures that favor specific combinations of traits (Messier, McGill, et al. 2017). In such environments, only species possessing the optimal trait syndromes can persist, which leads to an increased alignment - or integration—of those traits within the community. Essentially, as these filters eliminate species with suboptimal trait combinations, the remaining species display more pronounced correlations among their traits, reflecting a more tightly constrained and differentiated set of strategies. This heightened correlation is what we refer to as stronger CFInt.

This paper aims to formalize CFInt to improve our understanding of the links between functional ecology and community assembly. We demonstrate its utility through two empirical analyses of lake-fish communities as a proof of concept. First, we examine how trait correlation networks vary across a large latitudinal gradient and respond to variation in environmental conditions across local communities (lakes). Second, we investigate the role of CFInt in explaining variation in species richness across communities, showing that incorporating CFInt can improve our understanding of biodiversity patterns. Ultimately, our findings underscore the potential of CFInt to enrich our understanding of community dynamics and reveal the intricate links between environmental filters, species traits, and biodiversity patterns.



A

Moment	Concept	Definition	Metric	Examples
Mean	Functional Composition	Where the community is in the functional space	Functional groups; CWM	Tilman et al. 1997; Mouillot et al, 2012; Gravel et al. 2016
Variance	Functional Richness	How similar species from the same community are	Number of functional groups; Range; volume of convex hull	Tilman et al. 1997;Fischer et al,2007; Cadotte 2017
	Functional Dispersion	How similar species from the same community are	Variance; FDiv, Hill	Mouillot et al. 2007; Cadotte 2017; Cote et al. 2019
Covariance	Functional Integration	Degree to which traits in a phenotype are correlated	Correlation; svd; average of absolute correlation	Messier et al. 2017; He et al. 2020; Delhaye et al. 2020

Figure 3-1: (A) Conceptual illustration of different statistical moments used to describe communities in functional trait space, along with examples of how these moments used are applied in community ecology. **(B)** Two simulated communities occupying the same functional space, each with identical Community Trait Mean (represented as "+"), Functional Richness (FRic), and Functional Dispersion (FDis), but differing in the correlations between Trait 1 and Trait 2.

Empirical applications and insights from community functional integration

3.2.1 Exploring variations in pairwise trait correlations along latitudinal and environmental gradients

In our first empirical example, we aim to demonstrate that CFInt varies among communities in a spatially structured predictive manner. Recognizing that climate is one of the strongest environmental constraints on fishes (Loewen et al. 2022) and is inherently structured along a latitudinal gradient, this analysis focuses on how variation in trait correlation networks can pinpoints pairs of traits that exhibit the strongest and weakest responses to latitudinal and environmental variation.

In their discussion of the variation of the leaf economic spectrum across scales, Messier, McGill, et al. (2017) argue that variation in trait correlations both across and within spatial scales is governed by mechanisms that most strongly constrain trait pairs. For example, pairs of traits constrained by biophysical laws such as biochemical constraints linking nitrogen content and photosynthesis rate in plants tend to remain across scales (Messier, McGill, et al. 2017). In contrast, when trait pairs are less constrained, each trait may respond differently to environmental conditions, leading to variation in their correlation. Consequently, specific environmental conditions can select not only for particular trait values but also for distinct associations among traits across species. Within this framework, community functional integration (CFInt) can reveal the underlying connections and dependencies between traits, offering deeper insights into the functional organization of ecological communities.

In fishes, variation in trait integration has been documented for morphological traits: traits, such as position, shape and size of fins, varied both in their degree of integration and the trait correlation patterns, between populations of different fish species from different habitats (e.g. with water velocity: Peres-Neto & Magnan (2004); Fischer-Rousseau et al. (2009), with depth: Parsons & Robinson (2006)). Even though, those studies were at the population levels, this indicates that integration of morphological traits can vary as a response to environmental gradients. Other pairs of traits may vary less in their correlations, due to physical or biological constraints: in fish - as in many other taxa - body size is strongly correlated with trophic levels, a relationship observed across diverse taxonomic groups (Romanuk et al. 2011). While this correlation has been documented for fishes on a global scale, we can expect only minor variation in the relationship (correlation) between these two traits at the community level along environmental gradients

As we further explore patterns of CFInt along a latitudinal gradient, we anticipate identifying which trait pairs are strongly and weakly correlated and how these associations relate to spatial variations. By analysing and determining which trait correlations are most labile in response to environmental variation, we aim to enhance our understanding of how these correlations influence community assembly through environmental selection. Conversely, traits that consistently exhibit weak or strong correlations across environments likely indicate that their inter-relationships may play a less critical role in community assembly, even though they may still affect overall functional composition and diversity.

3.2.2 Community functional integration: implications for alpha diversity

For the second empirical analysis, we propose an inferential model linking CFInt, functional diversity, and variation in species richness across lakes (Figure 3-2). Local species richness is the simplest way to characterise a community and explaining its variation across landscapes has long been a central question in ecology. In this study, we focus specifically on the climate-diversity gradient to illustrate how CFInt can be foster new insights into well-studied ecological patterns. In Ontario, the main determinant of biodiversity patterns is climate (Minns & Moore 1995; Loewen et al. 2022); more specifically, water temperature is a strong limiting factor of dispersal for many warm and cool-water species in Ontario (Alofs et al. 2014; Van Zuiden et al. 2016). In general, greater species richness and functional richness are associated with warmer climate (Minns & Moore 1995; Lamothe et al. 2018).

Harsh climates and resource availability can drive the intensity of CFint. He et al. (2020) demonstrated that climate in forest was associated with changes in the structure of the trait correlations network. Other studies have shown that plant communities display greater CFInt when water is scarce (Zeballos et al. 2017; Michelaki et al. 2019). Michelaki et al. (2019) explained that coexisting species would employ different strategies to avoid competitive exclusion. Similarly, we hypothesize that greater competition among fish species will lead to a greater differentiation of strategies among species, with species needed to invest their energy to develop one function or another, resulting in trade-offs and canalisation of traits. In fish, food limitation can increase competition among species (Hayden et al. 2015; Borcherding et al. 2019). More generally, limited available energy in the system will reduce the number of species in the community (Storch et al. 2005), by decreasing the diversity of available resources or increasing the overlap between species (and thus competitive exclusion) (Evans et al. 2005). In Ontario, greater competition is expected in northern and colder communities due to shorter growth period for fishes and more limited primary productivity due to reduced energy availability in the system. Therefore, we hypothesise that CFInt should have a positive relationship with temperature (Figure 3-2).

CFInt can be also used here to describe the shape of the niche partitioning volume among species. In our model (Figure 3-2), we hypothesise that strong pairwise correlations among traits will act as an additional selection filter CFInt constrains the local functional space in which species must fit to coexist in any given community. In this sense, strong CFInt should mediate the number of potential species that can be selected, resulting in a negative relationship between CFInt and local species richness.

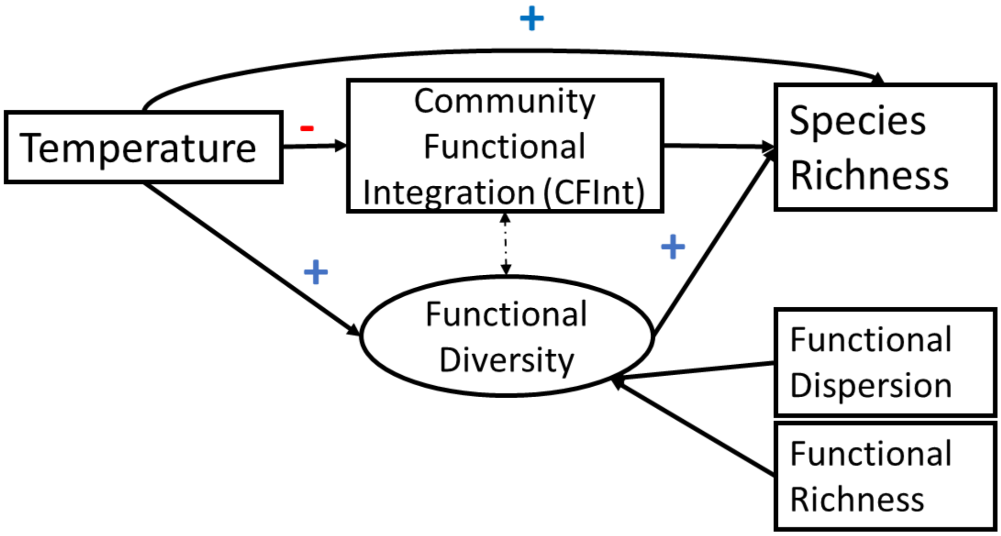


Figure 3-2: Graphical representation of the inferential model tested in this study. Arrows marked with "+" or "" represent the expected direction (positive and negative) of relationships. Rectangles represent observed (measurable) variables, while ellipses denote latent variables. One-way arrows indicate hypothesized causal relationships, whereas the two-way arrow represents an expected observational correlation between components.

3.3 Material and Methods

3.3.1 Field sampling, environmental data, and trait measurements

The Ontario Ministry of Natural Resources have sampled 707 lakes across Ontario as part of their Broadscale Monitoring Program (OBMP, Lester et al. 2020). Lakes were sampled during the summer months (June to September) from 2008 to 2012, spanning a broad latitudinal and longitudinal gradient. The OBMP employed a stratified sampling design on lake size classes and regions, with lakes randomly selected from within each size-region category.

Each lake was sampled following a standardized protocol that involved identifying all captured fish to the species level. The number of species per lake ranged from 2 to 25 (see Appleberg 2000 for general fish sampling; and Arranz et al. 2022 for further details on the OBMP sampling framework). For calculating correlations, only lake communities with more than four species were included in analysis (690 out of 707 lakes). In the subsequent analysis, the geographical boundaries of Ontario were used as the study area.

To demonstrate the usefulness of the concept of CFInt, we focused on climatic variables as climate is one of the main limiting factor for species distribution in the landscape (Minns & Moore 1995; Loewen et al. 2022). We selected four variables temperature-related variables: the number of ice-free days (reflecting winter length), maximum surface temperature, maximum month air temperature, and minimum monthly air temperature. To address collinearity among those variables, we conducted a principal component analysis (PCA). The first axis accounted for 80% of the variance, and its scores (multivariate coordinates) as our composite climate variable. Positive values of this axis correspond to high maximum and minimum air temperature, high surface temperature, and a greater number of ice-free days – effectively distinguishing warm lakes (positive scores) from cold lakes (negative scores).

We selected 15 traits (Table 3-1; see Supplementary Materials: Table S3-1 for details) that represent various aspects of species ecology, including diet, locomotion, and temperature preference. The trait data were sourced from FishBase (Froese & Pauly 2025). For Temperature preference, traits were mainly sourced from Ontario Freshwater Fish Life History Trait Base (Eakins 2025), and completed with data from FishBase (Froese & Pauly 2025) and existing literature (see details in Supplementary Materials

Table S3-2). Only species with full trait information were kept in the analysis (68 out of 87 species present in the dataset).

As is common in trait-based studies, these traits were summarized at the species level because detailed intraspecific variation are simply not available. Prior to analyses, all traits were standardized to a mean of zero and a variance of one, ensuring equal weighting among traits. We also applied the Gower's standardisation of matrices (Gower 1975; Peres-Neto & Jackson 2001) to balance the number of traits in each category. The standardization consists in scaling the traits so the sum of all the squared values of the category is one. This standardization does not change the covariation among traits (Peres-Neto & Jackson 2001).

Table 3-1: List of traits used in the analysis, categorized by their presumed ecological function. Traits marked with "*" are expressed as proportions relative to total body length (Length).

Function	Traits
Diet	Eye Diameter, Length, Head Length*, Preorbital Length, Trophic Levels
Locomotion	Standard Length*, Aspect Ratio, Body Depth*, Preanal Length*, Prepelvic Length*, Fork Length*, Predorsal Length*
Temperature Preference	Temperature Minimum, Temperature Maximum, Temperature interval

Our study explores two key aspects of CFInt: the spatial variation of pairwise trait correlations among communities and the influence of CFInt on local species richness.

Our hope is that these two case studies will illustrate the utility of CFInt as a framework for linking environmental gradients, trait correlations, and community assembly processes, thereby offering new insights into the mechanisms underlying biodiversity patterns. In the first part of our analysis, we calculate local (within lakes) correlation matrices among traits across species. In the second part, we introduce a new metric that quantifies the structure of these matrices, providing a measure of CFInt. A summary of our analytical framework is provided in the Supplementary Materials (Figure S3-1).

3.3.2 Describing variations in pairwise trait correlation

First, we computed the Pearson correlations for each pair of traits within every lake community, thus quantifying the linear correlation between two traits. A strong correlation - whether positive or negative correlation - indicates that the two traits vary synchronously, whereas a correlation near zero suggests that the trait vary independently. Consistently high correlations with minimal variation across lakes suggest that the relationship between these traits is robust and likely governed by fundamental biophysical or evolutionary constraints, rather than by local community assembly processes. In contrast, consistently low correlations with little variation indicate that the traits vary independently, implying a lack of functional linkage in the context of community assembly. Conversely, high variability in trait correlations across lakes may indicate that the relationship between those traits is subject to local selection pressures, such as environmental filtering or competitive interactions, thereby influencing community assembly processes. Our goal is to identify the most variable trait pairs and assess how this variability is structured along the latitudinal gradient.

To analyse the variation of the structure of trait associations along the latitudinal gradient, we used a Procrustes analysis (see Peres-Neto & Jackson 2001 for details). The Procrustes analysis determines the concordance between two matrices by rotating and superimposing them, thus estimating how different the two matrices' structures are. First, we calculated for each community a PCA of the traits – the PCA was set so the axes were calculated with correlation matrix – and extracted its first four eigenvectors: this captures the correlation structure of the traits within a community. Then, we calculated the pairwise procrustean distances among the communities' PCA: this distance describes how much two matrices (communities) differ from each other. We use the resulting pairwise Procrustes distance matrix to conduct a PCoA which arrange (ordinate) the communities according to their differences in correlation structure. Finally, we use the coordinates of the first two axes of the PCoA as new variables that describe the variation in the community trait structure.

3.3.3 Community functional integration: a metric to measure the variations in strength of correlations at the community level.

The second part of our analysis involved two steps (for graphical explanation, see Supplementary Materials, Figure S3-1). First, we developed a metric to summarise the overall structure of the correlation matrices, encapsulating the strength of trait correlations within each community: the absolute average correlation. We used the absolute values because, for CFInt, our focus is on the overall strength of trait associations rather than their direction. This metric is widely applied in evolutionary biology to study phenotypic integration (see Watanabe 2021 for a recent review). For each community, its pairwise trait correlation matrix was calculated. The lower triangle was extracted (to remove replicates due to the matrix symmetry), and calculated the average absolute correlation (Eq. 3-1):

$$Absolute\_average\_correlation_k = \frac{\sum |cor_{ij,k}|}{n_k} \text{ (Eq. 3-1)}$$

where $cor_{ij,k}$ is the correlation between trait *i* and trait *j* for the community *k*, n_k the total number of pairwise correlations present in the lower triangle of the correlation matrix of the kth community (105 in our case).

The second step consisted in calculating a Standard Effect Size (SES) for the metric described in Eq. 3-1 to control for the influence of species richness on the absolute average correlation - even in cases where traits are inherently uncorrelated. Traits can exbibit absolute correlations even when their associations are random, and smaller communities with fewer species tend to show stronger random correlations compared to larger communities (see Supplementary Materials, Figure S3-2). To account for this effect of sample size (richness) on absolute trait correlations, we used a permutation framework. For each community, we randomized the trait correlations independently shuffling each trait column. This approach maintains the number of species and the functional composition of the community (i.e., the average value for each trait remains unchanged), while eliminating any correlation patterns that arise solely from species richness.

We then computed the average absolute correlation from these randomized matrices and used these values to estimate the standardised effect sizes (SES) for each community (lake). SES was calculated by subtracting the mean expected absolute correlation under random trait association from the observed absolute correlation and dividing this difference by the standard deviation of the randomized values. We used 999 permutations to calculate the mean and standard deviation of the null distribution. Following standard practice, the observed correlation value was included as one of the permutations, resulting in a total of 1,000 values used to compute the mean and standard deviation for the randomized communities.

A positive SES indicates that the community's integration is higher than expected under random traits associations, whereas an SES close to zero suggests that the observed community integration is similar to what would be expected if traits were randomly associated. Conversely, a negative SES implies that the community is less integrated than expected based on random associations of traits. In our analyses, we refer to community functional integration solely in terms of its standardized effect size (SES.CFInt).

3.3.4 Variation of trait correlations across local communities and across the latitudinal gradient: contrasting variation of trait correlation with beta diversity

Patterns of functional structure can partly be explained by variation in local species composition, particularly when trait data are only available at the species level (see Arranz et al. (2022) for further discussion). To determine if our observed patterns of functional integration reflect solely taxonomic diversity or if they reveal additional dimensions of biodiversity patterns, we calculated compositional beta diversity among lakes. We employed the Jaccard-Chao distance to calculate pairwise differences in species composition among communities, as it is less sensitive to variations in gamma diversity (Cao et al. 2021). We then summarised these differences (beta-diversity) using a principal coordinate analysis (PCoA) and extracted the first two axes as new variables representing taxonomic beta diversity among lakes.

To contrast the patterns of CFInt with beta diversity, we first estimated the correlation between the patterns in trait structure (procrustean distances summarised with the PCoA as described in *Pairwise trait correlation and community functional integration*) and the patterns in beta diversity (summarised with the PCoA as described above). Relationships among taxonomic and functional diversity are not linear, we therefore estimated the correlation among the different metrics with Spearman's correlation. For both CFInt and beta diversity, we also fitted a general additive model with latitude as an explanatory variable. This allowed us to visually understand if the variations in trait correlations followed the same latitudinal trend as beta diversity.

3.3.5 Establishing the link between community functional integration and alpha diversity: evaluating the redundancy with other functional metrics

Many commonly used functional metrics tend to be highly correlated with one another (Mouchet et al. 2010). Therefore, before incorporating CFInt into our analysis of community functional structure, we first explored how CFInt relates to well-established measures of functional diversity: functional richness and functional dispersion. Specifically, we estimated functional dispersion based on the Hill numbers of the community trait distribution, and is used to assess assembly mechanisms in trait-based analysis especially through its SES (Chiu & Chao 2014; Mammola et al. 2021). Functional richness was also computed as the volume of the smallest convex hull (Cornwell et al. 2006) as is also used sometimes to describe functional structure. To calculate both metrics, we computed the Gower distance on the matrix containing all traits, as it can handle missing values (Gower 1971). As is routine in trait-based analysis of assembly mechanisms, we also computed its SES (Weiher & Keddy 1995; Münkemüller et al. 2012; Mason et al. 2013): we generated 999 random communities drawn from the regional species pool, and we calculated the mean and standard deviation for the random communities and contrasted the observed values with the expected values from the null communities. As before, the observed value was counted as one of the permutations, bringing the total to 1,000 values used to compute the mean and standard deviation for the random communities. The standardised effect size of functional dispersion will be referred as SES.Hill.

Assessing the correlations between CFInt and other functional metrics helps us determine whether our framework of CFInt reveals novel aspects of community functional structure that existing metrics do not capture. Although these metrics are derived from different mathematical formulations, their high empirical correlations often stem from shared sampling effects linked to species richness (Mouchet et al. 2010). By disentangling these effects, we can better assess the added value of CFInt in revealing novel ecological insights (see Supplementary Materials, Figure S3-3).

3.3.6 Establishing the link between community functional integration and alpha diversity: insights from structural equation modeling

Here, we aim to illustrate how CFInt can enhance our understanding of changes in a key and widely used community structure metric (taxonomic richness) across environmental (here, climatic) gradients. (Figure 3-2). To address this question, we used a structural equation model (SEM), which enable us to isolate both direct and indirect effects of multiple variables. In our SEM, we included functional dispersion as SES.Hill and CFInt as SES.CFInt as explanatory variables for species richness (Figure 3-2). Finally, we accounted for potential correlational error between SES.CFInt and functional diversity. Because SES.CFInt and the metrics underlying Functional Diversity can be somewhat correlated (see Supplementary Materials, S5), explicitly modeling this correlation in the SEM improves the accuracy of estimating the distinct effects of each variable on species richness.

To assess whether including CFInt improves our understanding of species richness patterns, we compared two SEMs: a baseline model that included all variables and the latent variable but excluded the path from CFInt to species richness, and a full model that included all paths. Because our primary interest lies in understanding how CFInt contributes to explaining species richness patterns, we report local estimation of model fit, specifically the R^2 value associated with the response variable, species richness. For global model evaluation, we followed the guidelines of Lefcheck (2016) by computing Fisher's C statistic, from which a p-value can be derived. Fisher's C evaluates the cumulative independence of variables across all model paths; a low p-value suggest that the model is missing a key path. This is particularly relevant for assessing the baseline model, as it allows us to test whether excluding the path from CFInt to species richness significantly reduces model fit. The AIC provides a criterion for selecting the most parsimonious model (Fan et al. 2016).

All analyses were conducted in R using RStudio (R Core Team 2020). Community phenotypic integration and standardized effect sizes (SES) for all trait metrics were computed using custom-made functions. Functional distance matrices and functional richness were calculated with the 'FD' package (Laliberté et al. 2022), while functional dispersion was calculated using the package ‘mFD’ (Magneville et al. 2022). Procrustes analysis and principal coordinate analysis (PCoA) were performed using the ‘vegan’ (Oksanen et al. 2020) and ‘ape’ (Paradis & Schliep 2019) packages, respectively. Structural equation models (SEMs) were implemented with the ‘piecewiseSEM’ package (Lefcheck 2016). All figures were produced in R using the ‘ggplot2’ (Wickham 2016) and ‘igraph’ (Csardi & Nepusz 2006) packages.

3.4 Results

3.4.1 Variation of trait correlations across local communities and across the latitudinal gradient.

Our first empirical analysis revealed marked variation in how traits co-vary within ecological communities—variation that is both widespread and structured in ecologically meaningful ways. By exploring patterns of trait integration across space, we found clear latitudinal gradients and distinct patterns of trait coordination among lake communities, suggesting that both local environmental conditions and broader climatic drivers play a role.

The empirical exploration of the concept of Community Function Integration (CFInt) examine how correlations between pairs of traits across local communities (Figure 3-3). The average pairwise correlation ranges from -0.64(between aspect ratio and fork length) and 0.79 (between temperature max and temperature min), with a median around -0.03. While some trait correlations show little variation (e.g. trophic levels and length), others vary substantially (e.g., fork length and aspect ratio). Among the 105 trait pairs, 32 exhibit a variance of correlation coefficients across communities greater than 0.1, and most of these highly variable pairs involve at least one locomotion trait (e.g., body depth, prepelvic length, fork length). These results suggest that local ecological or evolutionary processes may differentially shape how traits co-vary within communities, especially in relation to locomotion.

The first two axis of the PCoA, which capture variation in trait correlation networks across communities, summarise 43% of the total variation in trait structure, with the first five axes together accounting for 74% (Figure 3-3B). This suggests that while trait correlations vary across communities, the variation in certain trait pairs may be interdependent, implying the existence of distinct "types" or configurations of trait correlation networks.

Moreover, these differences in trait networks were only partially correlated with patterns in beta diversity (Figure 3-3C). Both axes of the trait network PCoA showed a moderate correlation with beta diversity (Spearman's $\rho = 0.39$, between the first axis of trait networks and the first axis of beta diversity Spearman's $\rho = 0.48$, also with the second axis of trait network). These findings suggest that variation in trait networks cannot be explained solely by differences in local species composition. Instead, they point to the possibility that local environmental filters or assembly processes may shape not just which species are present, but how traits co-vary within communities. This highlights the added value of considering CFInt as a distinct and informative dimension of community structure.

We examined the latitudinal trend in the variation of the trait correlation networks (Figure 3-3D) with generalized additive models (GAMs) explaining up to 13% of variance of in community trait correlation structure. A clear latitudinal gradient emerged: southern communities tended to cluster in the bottom-left quadrant of the PCoA presented (Figure

3-3C), while northern communities tended to be in the top-left quadrant – each reflecting distinct patterns of trait integration. Southern communities were characterized by a positive correlation between aspect ratio and minimum temperature, between head length and standard length and between preanal length and body depth, between eye diameter and maximum temperature, a strong negative correlation between maximum temperature and head length. In contrast, northern communities were characterised by positive correlations between aspect ratio and minimum temperature, between minimum temperature and length, and between temperature interval and preanal length and by a weak correlation between standard length and standard length, between body depth and preanal length, and between maximum temperature body depth. The peak in central Ontario (around Latitude of 47.5) shows that communities are characterised by strong positive correlations between minimum temperature and temperature interval, between temperature interval and aspect ratio, and by a negative correlation between eye diameter and maximum temperature, and a weak correlation between maximum temperature and head length. These contrasting patterns suggest that different trait coordination strategies may be favored along climatic gradients, potentially reflecting adaptation to local environmental constraints. This highlights CFInt varies not only across space but also in relation to broad-scale climatic drivers.

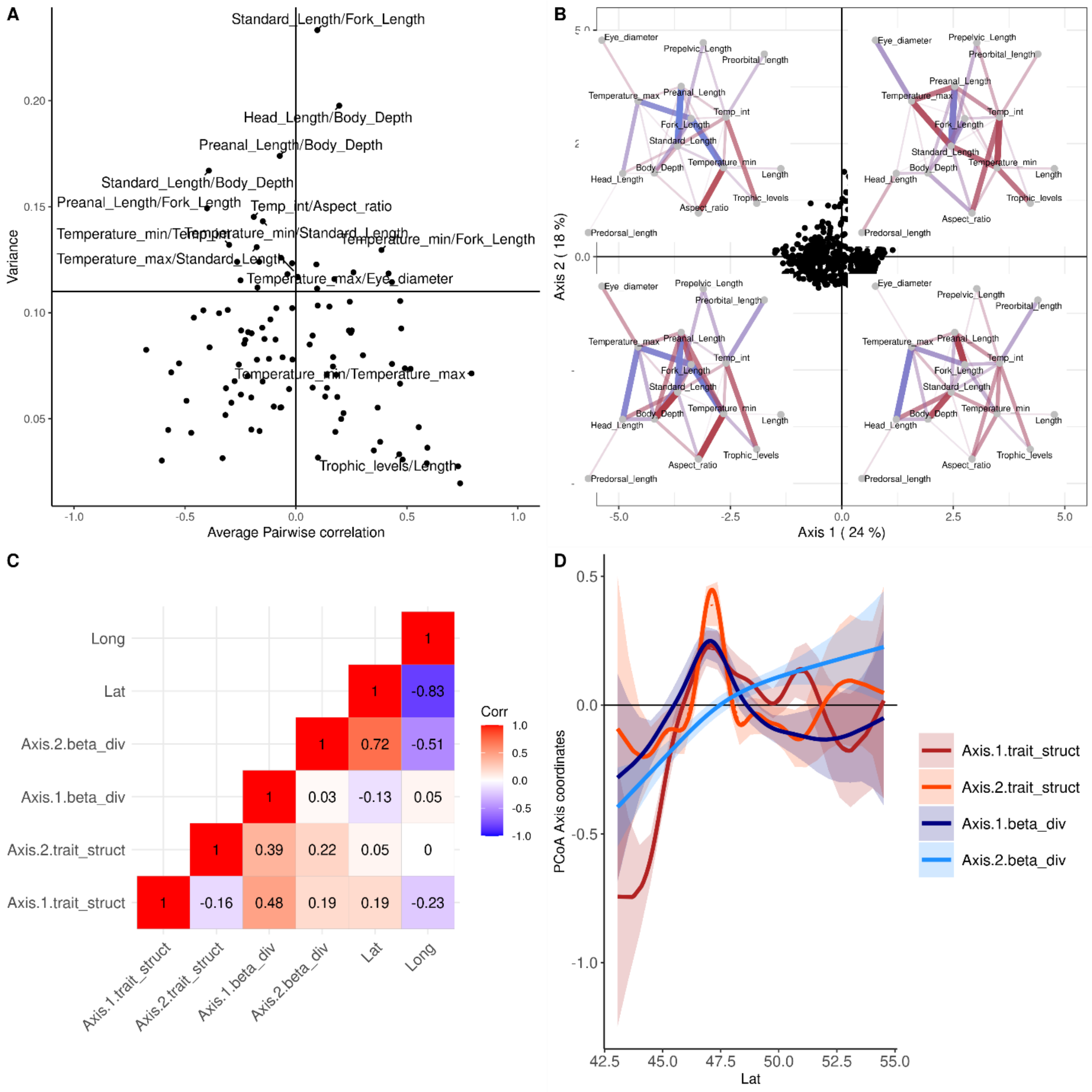


Figure 3-3: (A) Relationship between the mean and variance of pairwise trait correlations. Each point represents a trait pair. The vertical line indicates a variance of 0.1, corresponding to the 90th quantile of the variance distribution) **(B)** Principal Coordinates Analysis (PCoA) based on Procrustes distance between the different communities' eigenvector matrices from trait Principal Component Analysis (PCA), capturing variation in community-level functional integration. Each point represents a community. To facilitate interpretation, the average trait correlation network for each PCoA quadrant is displayed. Edge color indicates the direction of the correlation (blue = negative, red = positive), and edge thickness reflects the absolute strength of the correlation (thicker edges indicate stronger correlations). **(C)** Spearman correlation matrix showing associations between trait structure (Axis.1.struct.trait and Axis.2.struct.trait), taxonomic beta diversity (Axis.1.beta_div and Axis.2.beta_div), and

spatial gradients (latitude and longitude). Red indicates positive correlations, blue indicates negative correlations, and white indicates values near zero. **(D)** Generalized Additive Models **(**GAMs) depicting latitudinal trends in trait correlation structure and taxonomic beta diversity, based on the first two PCoA axes.

3.4.2 Linking community functional integration to alpha diversity

We introduce a new standardized metric of community functional integration, SES.CFInt, to quantify CFInt and explore its relevance for understanding species richness in lake-fish communities. Our results show that more functionally integrated communities tend to be richer in species and functionally more diverse. Incorporating SES.CFInt into structural equation models significantly improves model performance, revealing its added value in explaining richness patterns beyond traditional diversity metrics. These findings highlight the importance of considering trait integration as a distinct and informative dimension of community structure.

Our SES.CFInt metric ranged from -1.86 to 14.77, with a positive average at 4.35 (see Supplementary Materials, Figure S3-3, indicating that lake-fish communities in Ontario tend to exhibit strong function integration. We then evaluated the relationship between SES.CFInt and other functional diversity metrics by calculating pairwise Spearman correlations to capture non-linear relationships between the variables (details in Supplementary Materials, Figure S3-3). SES.CFInt was only correlated with the SES of functional dispersion (Spearman's $\rho = -0.10$). These results suggest that the most integrated communities also tend to be to some extent the most functionally underdispersed.

The next step was to test whether SES.CFInt, alongside functional diversity, modulate species richness (Figure 3-4B). We compared the performance of a model that includes SES.CFInt (Figure 3-4B) with a baseline model that excludes it (Figure 3-4A) to evaluate whether incorporating CFInt provides additional insights into variation in species across lake-fish communities. As expected, the baseline model showed a positive relationship between species richness and both climate (partial regression coefficient = 0.22) and the SES of functional dispersion (partial regression coefficient = 0.32): warm lakes and overdispersed communities tend to be richer. Similarly, SES.CFInt was associated with climate (partial regression coefficient = 0.31), indicating that communities in warmer lakes tend to be more functionally integrated. In the extended model, we included a direct path from SES.CFInt to species richness. This path was also positive (partial regression coefficient = 0.71), suggesting that CFInt is independently associated with higher species richness.

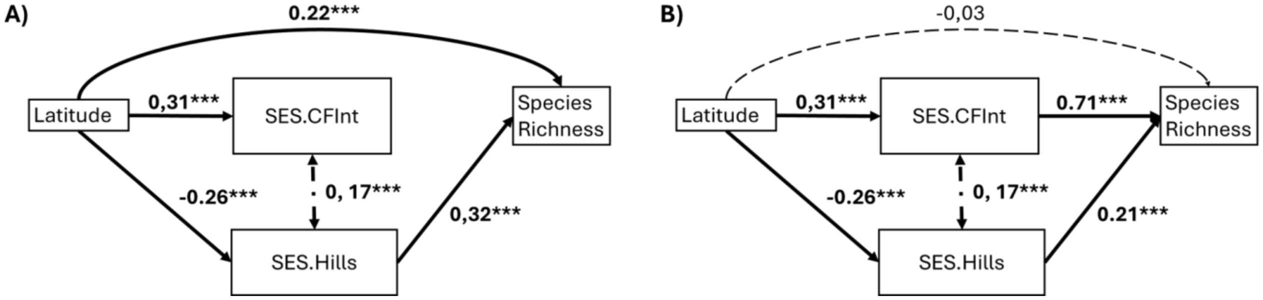


Figure 3-4: Visualisation of the Structural Equation Models (SEMs) applied to the full dataset. **(A**) Baseline model excluding the path between community functional integration (SES.CFInt) and Species Richness. **(B)** Extended model with the path. The number represents the partial slopes for the relationship represented as an arrow. Arrows represent modeled relationships, with values indicating standardized partial slope coefficients. Arrow thickness and asterisks denote the significance level of each relationship: thin arrows with no stars indicate non-significant relationships ($p > 0.05$); medium arrows with one star indicate marginal significance ($0.01 < p \leq 0.05$); thick arrows with three stars indicate high significance ($p < 0.001$).

To compare the performance of the two models, we assessed both local fit (using the R^2 associated to species richness) and global model fit (using AIC and Fisher's C for model A). Model B, which includes SES.CFInt as a predictor of species richness, outperformed the baseline Model A, with a higher R^2 for species richness (0.47 for Model B vs. 0.14 for model A). This indicates that including CFInt improves the model's explanatory power. However, model B also introduces an additional path, increasing mode complexity. To determine whether this added complexity is justified, we compared AIC values: Model B had a lower AIC (4913.280) than model A (5239.739), indicating better overall model performance. We also computed Fisher's C statistic for model A with to test for missing paths. The result (Fisher's C = 332.525 p-value < 0.00001) suggests a significant lack of fit, implying that a key relationship – specifically the path from SES.CFInt to species richness – is missing. Together, these results identify Model B, which includes the effect of CFInt, as the better-fitting and more informative model.

3.5 Discussion

We examined variation in trait correlations within local communities across a latitudinal gradient and a climatic gradient to evaluate the potential of CFInt as a meaningful biodiversity dimension. Our study followed to complementary lines of inquiry: a details exploration of community-level trait correlation networks and the introduction of a new metric quantifying CFInt (SES.CFInt), which quantifies the average strength of trait correlations within communities. We first described the structure and variation of these networks across space, highlighting the ecological significance of local differences in trait integration. We then assessed the added value of SES.CFInt in explaining species richness, relative to conventional functional diversity metrics. Together, our results demonstrate that patterns of CFInt vary systematically across environmental gradients, are only partially captured by existing metrics, and can enhance our understanding of community assembly processes.

3.5.1 Variations of pairwise correlations across communities

The initial question that motivated this work was whether trait-trait correlations varied across local communities, and if so, whether those patterns are structured in ecologically interpretable ways. Our analyses show that while many trait correlations are relatively conserved – likely due to intrinsic biological, including ecological, or evolutionary constraints (Messier, McGill, et al. 2017)– others vary markedly across communities, underscoring the context-dependence of functional relationships, suggesting they are modulated by ecological conditions such as climate and other spatial gradients.

As expected, some correlations were highly consistent (conserved), such as the well-documented positive relationship between body length and trophic levels (Romanuk et al. 2011). This widespread consistency supports the robustness of certain functional linkages across ecological contexts. However, we found approximately 32 trait pairs exhibited considerable variation across communities, particularly those involving morphometric traits linked to locomotion (Villéger et al. 2017). At the organismal level, these traits are known to form integrated morphological modules (e.g., head, trunk, back), and that their coordination affects swimming performance and ecological specialization (Peres-Neto & Magnan 2004; Larouche et al. 2015). Our results suggest that these integrative patterns may also emerge at the community level, potentially reflecting shared selective pressures or assembly constraints.

Beyond describing variation in the structure of trait correlation networks, we also found that this variation was geographically structured, with northern and southern communities displaying distinct configurations of trait relationships and topology. Key trait pairs distinguishing these regional patterns often involved thermal preferences – specifically, maximum and minimum temperature tolerances of the species present. This is consistent with the pronounced latitudinal climatic gradient in Ontario, where temperature remains a major constrain on species distribution and colonization (Loewen et al. 2022). These findings support the idea that trait integration may emerge as a product of local environmental filtering (Messier, McGill, et al. 2017). Similar patterns have been observed in plant communities, where trait correlations are shaped by local conditions such as climate (He et al. 2020), pollution (Delhaye et al. 2020), water availability (Sanaphre-Villanueva et al. 2022), and nutrient resources (Candeias & Fraterrigo 2020). In these systems, functional integration often reflects optimal trait combinations that are favored under specific environmental constraints.

While our trait data were compiled at the species level, and thus invariant across communities that have the same species composition, our results demonstrate that variation in trait correlations is not simply a byproduct of species turnover. The leading axis of variation in trait network structure – defined by correlations among trait such as temperature tolerance (max and min), body size (standard length), and shape (aspect ratio, fork length and prepelvic length) was moderately correlated with species composition (i.e., beta diversity). This finding reinforces the ideas that trait correlation networks capture unique structural properties of communities that are orthogonal to taxonomic composition.

3.5.2 A new dimension of functional structure

In the second part of our study, we evaluated whether SES.CFInt captures information distinct from existing measures of functional metrics. The development of novel metrics often risks redundancy, as many indices are influenced by species richness or reflect overlapping aspects of trait structure (Götzenberger et al. 2012; Scheiner et al. 2017). However, our results show that SES.CFInt adds complementary value. It was only moderately correlated with functional richness and with functional dispersion, suggesting that it captures a different facet of community organization. SES.CFInt quantifies the degree to which trait associations within a community deviate from expectations based on random trait assembly, given the community's observed species pool and trait distributions. The generally positive SES.CFInt values in our lake-fish dataset suggest that trait integration tends to be stronger than expected under null models, reflecting coordinated trait structures that may arise from ecological interactions, shared evolutionary history, or common environmental filtering.

While SES.CFInt is partially correlated with other functional metrics, these relationships are informative. Its positive association with functional richness suggests that communities occupying larger volumes of functional space also exhibit stronger internal coordination among traits. Likewise, the positive relationship with functional dispersion implies that integration is more likely in communities with broad trait distributions. One possible interpretation is that higher functional richness allows for more complex structuring of niches, which may, in turn, promote coordinated trait architectures along specific ecological axes.

3.5.3 Explaining species richness through community functional integration

Our final objective was to assess whether CFInt improves our capacity to explain local species richness. By comparing structural equation models with and without a direct path from SES.CFInt to species richness, we found consistent evidence that CFInt contributes meaningful explanatory power. The model including SES.CFInt had higher R^2 values for species richness, lower AIC, and a better global fit (as indicated by Fisher's C), demonstrating that CFInt is a relevant predictor of diversity patterns.

Importantly, the inclusion of SES.CFInt did not obscure existing ecological relationships. Well-established positive associations between climate and species richness were recovered in our models (Minns & Moore 1995) lending credibility to our framework. We also find a negative relationship between climate and functional dispersion due to the use of the SES instead of the raw functional dispersion. This negative relationship has been documented in Ontario by Lamothe et al. (2018): functional redundancy (functional dispersion controlled for species richness) is less important in northern boreal lakes than southern lakes. These results suggest that CFInt provides an additive contribution to our understanding of community assembly, rather than simply replacing or duplicating existing predictors.

We developed hypotheses on how SES.CFInt may interact with environmental filtering and influence species richness (Figure 3-2). Our first hypothesis drew from findings in plant studies (Messier, Lechowicz, et al. 2017; Delhaye et al. 2020), where stronger environmental filters – such as drought and heavy metal pollution – have been associated with greater functional integration within communities. In our study, we used temperature as a proxy for environmental filtering, given its well-documented role as a limiting factor for many species in Ontario (Minns & Moore 1995; Loewen et al. 2022). Contrary to expectations based on plant systems, we found that communities in warmer environments were more functionally integrated than those in colder regions. This patterns contrasts with studies in plants, where greater environmental stress is typically linked to stronger trait integration (Messier, Lechowicz, et al. 2017; Delhaye et al. 2020). A likely explanation for this discrepancy lies in differences between the environmental gradients examined and the ways in which different organisms respond to them. While previous studies focused on resource scarcity or stress (e.g. water availability), our study examined thermal gradients, which may act more as filters of physiological compatibility or ecological opportunity than as direct stressors.

Another hypothesis concerned the effect of CFInt on species richness. We proposed that SES.CFInt could act as a modulator of species richness. In our model, we found a positive relationship between SES.CFInt and species richness, suggesting that CFInt may facilitate species coexistence by influencing interspecific interactions. Gross et al. (2024) observed that plant communities were less integrated in arid regions, where species are more spatially scattered and interact less frequently; they interpreted lower integration as being associated with reduced lower competitive interactions. Although further theoretical and empirical work is needed to clearly establish the link between CFInt and interspecific competition, we propose that CFInt, for a given level of functional richness (i.e., a given volume in trait space), may help reduce competitive overlap by minimizing niche redundancy across multiple traits dimensions (Figure 3-5).

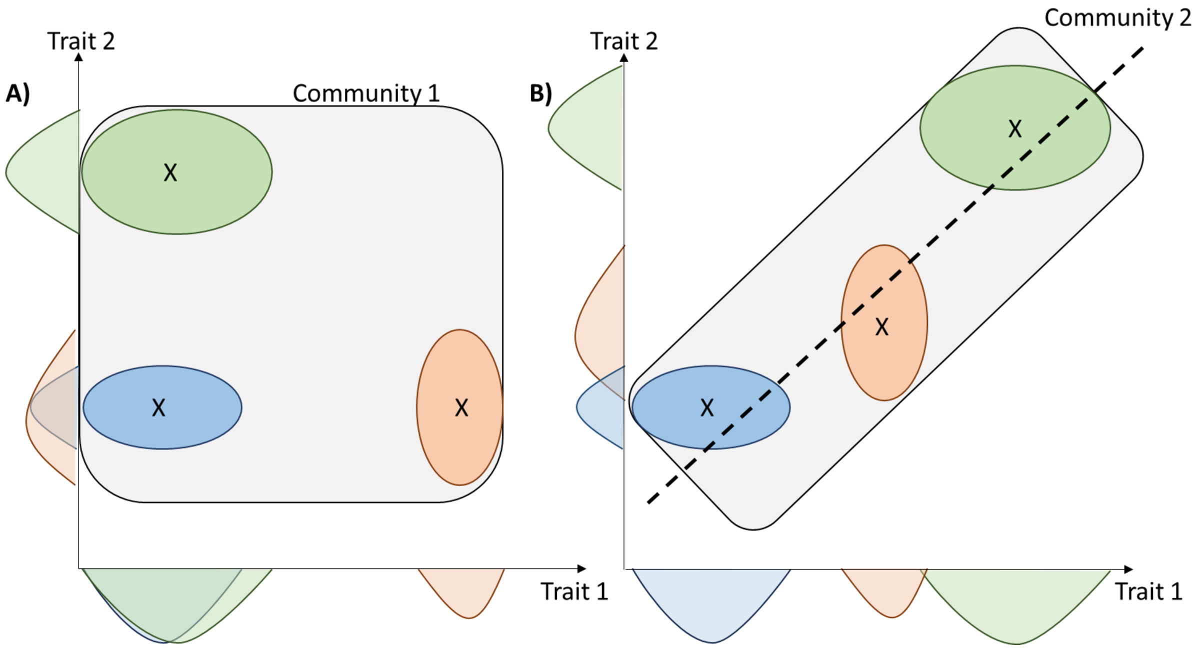


Figure 3-5: Conceptual illustration of the potential link between community functional integration and competitive interactions. In a two-dimensional functional trait space, two communities (grey rectangles) each consist of three species with niches

represented by the coloured ovals (blue, green, and orange). Trait-specific niche distributions are shown along each axis. **(A)** Community with low functional integration: niche overlap along individual trait axes (Trait 1 and Trait 2) is relatively high. **(B)** Community with functional integration: trait correlations align along a shared axis of integration (dashed line), resulting in reduced niche overlap on individual traits. This alignment may facilitate coexistence by minimizing competition across multiple trait dimensions.

3.6 Conclusion: Implications for the study of communities through the lens of Functional Ecology

Our objective was to demonstrate the value of incorporating an often-overlooked aspect of community functional structure - Functional Integration – into ecological analyses. More broadly, our findings suggest that functional integration represents a meaningful and previously overlooked axis of community structure. While functional ecology has traditionally focused on trait distributions and diversity metrics, the relationships among traits—how they covary within communities—can offer deeper insight into community assembly, niche differentiation, and the potential for species coexistence. As ecological research continues to move toward predictive frameworks, incorporating metrics of functional integration could improve our ability to forecast community responses to environmental change, especially in systems where trait coordination plays a critical role in ecological performance or resilience. We encourage future studies to explore the role of functional integration across different ecosystems, taxa, and environmental gradients to further uncover its generality and ecological significance.

3.7 Supplementary materials for Chapter 3

Table S 3-1: Details of the traits used for the analysis. Traits have been extracted from FishBase (Froese & Pauly 2025) and from the Ontario Freshwater Fishes Life History Trait Base (Eakins 2025) for the thermal traits

Trait	Unit	Meaning
Aspect Ratio	NA	Caudal height/Caudal fin area
Body Depth	Percentage of Total Length	Height of the body/Length
Eye Diameter	Percentage of Head Length	Eye diameter/Length of the head
Fork Length	Percentage of Total Length	Proportion of length to the fork over total length
Head Length	Percentage of Total Length	
Length	Cm	Common total length
Maximum Temperature	Celsius	Maximum preferred Temperature
Minimum Temperature	Celsius	Minimum preferred Temperature
Preanal Length	Percentage of Total Length	Length between the mouth to pre-anal fin/Length
Predorsal Length	Percentage of Total Length	Length between the mouth to the pre-dorsal fin /Length
Preorbital Length	Percentage of Head Length	Length between the mouth to eye /Length
Prepelvic Length	Percentage of Total Length	Length between the mouth to pre-pelvic fin/Length
Standard Length	Percentage of Total Length	Length to the tail
Temperature Interval	Celsius	Minimum Temperature – Maximum Temperature

Table S 3-2: List of species considered in the study with the source from which thermal data were extracted. Ontario Freshwater Fishes Life History Trait Base (Eakins 2025) is noted with the anagram OFFLHTB. We also report the source from which FishBase extracted their data.

Species (scientific name)	Species (common name)	Source for the Temperature traits
Alosa pseudoharengus	Alewife	Ontario Freshwater Fish Life History Trait Base (OFFLHTB)
Amblopites rupestris	Rock bass	OFFLHTB
Ameiurus melas	Black Bullhead	Fishbase (Baensch & Riehl 1991)
Ameiurus natalis	Yellow Bullhead	OFFLHTB
Amia calva	Bowfin	Fishbase (Baensch & Riehl 1991)
Aplodinotus grunniens	Freshwater Drum	OFFLHTB
Carpiodes cyprinus	Quillback	OFFLHTB
Catostomus catostomus	Longnose Sucker	OFFLHTB
Catostomus commersonii	White Sucker	OFFLHTB
Chrosomus eos	Northern Redbelly Dace	(Stauffer et al. 1980)
Coregonus artedi	Cisco (lake herring)	OFFLHTB
Coregonus clupeaformis	Lake Whitefish	OFFLHTB
Cottus bairdii	Mottled Sculpin	OFFLHTB
Cottus cognatus	Slimy Sculpin	OFFLHTB
Cottus ricei	Spoonhead Sculpin	OFFLHTB
Couesius plumbeus	Lake Chub	Fishbase (Baensch & Riehl 1991)
Culaea inconstans	Brook Stickleback	Fishbase (Baensch & Riehl 1991)
Cyprinella spiloptera	Cyprinella_spiloptera	(Mathur et al. 1983)
Cyprinus carpio	Common Carp	(Wismer & Christie 1987)
Dorosoma cepedianum	Gizzard Shad	OFFLHTB
Esox lucius	Northern Pike	OFFLHTB
Esox masquinongy	Muskellunge (muskie)	OFFLHTB
Etheostoma exile	Iowa Darter	OFFLHTB
Etheostoma nigrum	Johnny Darter	Fishbase (Baensch & Riehl 1991)
Fundulus diaphanus	Banded Killifish	Fishbase (Baensch & Riehl 1991)
Gasterosteus aculeatus	Threespine Stickleback	OFFLHTB
Hiodon alosoides	Goldeye	OFFLHTB
Hiodon tergisus	Mooneye	OFFLHTB
Ictalurus punctatus	Channel Catfish	OFFLHTB
Labidesthes sicculus	Brook Silverside	Fishbase (Baensch & Riehl 1997)
Lepisosteus osseus	Longnose Gar	OFFLHTB
Lepomis cyanellus	Green Sunfish	OFFLHTB
Lepomis gibbosus	Pumpkinseed	OFFLHTB
Lepomis macrochirus	Bluegill	OFFLHTB
Lepomis megalotis	Longear Sunsfish	(Wismer & Christie 1987)
Lota lota	Burbot (ling)	OFFLHTB
Luxilus cornutus	Common Shiner	(Ulvestad & Zar 1977)

Micropterus dolomieu	Smallmouth Bass	OFFLHTB
Micropterus salmoides	Largemouth Bass	OFFLHTB
Morone chrysops	White Bass	OFFLHTB
Moxostoma erythrurum	Golden Redhorse	OFFLHTB
Moxostoma acrolepidotum	Shorthead Redhorse	OFFLHTB
Neogobius melanostomus	Round Goby	OFFLHTB
Notemigonus crysoleucas	Golden Shiner	OFFLHTB
Notropis atherinoides	Emerald Shiner	OFFLHTB
Notropis bifrenatus	Bridle Shiner	Fishbase (Baensch & Riehl 1985)
Notropis hudsonius	Spottail Shiner	OFFLHTB
Oncorhynchus mykiss	Rainbow Trout	OFFLHTB
Oncorhynchus tshawytscha	Chinook Salmon	OFFLHTB
Osmerus mordax	Rainbow Smelt	OFFLHTB
Perca flavescens	Yellow Perch	OFFLHTB
Percina caprodes	Logperch	(Singkran 2007)
Percopsis omiscomaycus	Trout-perch	OFFLHTB
Pimephales notatus	Bluntnose Minnow	OFFLHTB
Pimephales promelas	Fathead Minnow	OFFLHTB
Pomoxis nigromaculatus	Black Crappie	OFFLHTB
Prosopium coulterii	Pygmy Whitefish	OFFLHTB
Prosopium cylindraceum	Round Whitefish	Fishbase (Scott & Crossman, 1973)
Pungitius pungitius	Ninespine Stickleback	OFFLHTB
Rhinichthys atratulus	Eastern Blacknose Dace	OFFLHTB
Rhinichthys cataractae	Longnose Dace	OFFLHTB
Salvelinus fontinalis	Brook (speckled) Trout	(Wismer & Christie 1987)
Salvelinus namaycush	Lake Trout	OFFLHTB
Sander canadensis	Sauger	OFFLHTB
Sander vitreus	Walleye	OFFLHTB
Semotilus atromaculatus	Creek Chub	(McMahon 1982)
Umbra_limi	Central Mudminnow	(Wismer & Christie 1987)

Figure S 3-1: Analytical framework detailing the steps for the analysis of community functional integration (CFInt) (1), for the computation of the Standardised Effect Size of the CFInt (2) and the calculation of the other Functional Diversity metrics (3)

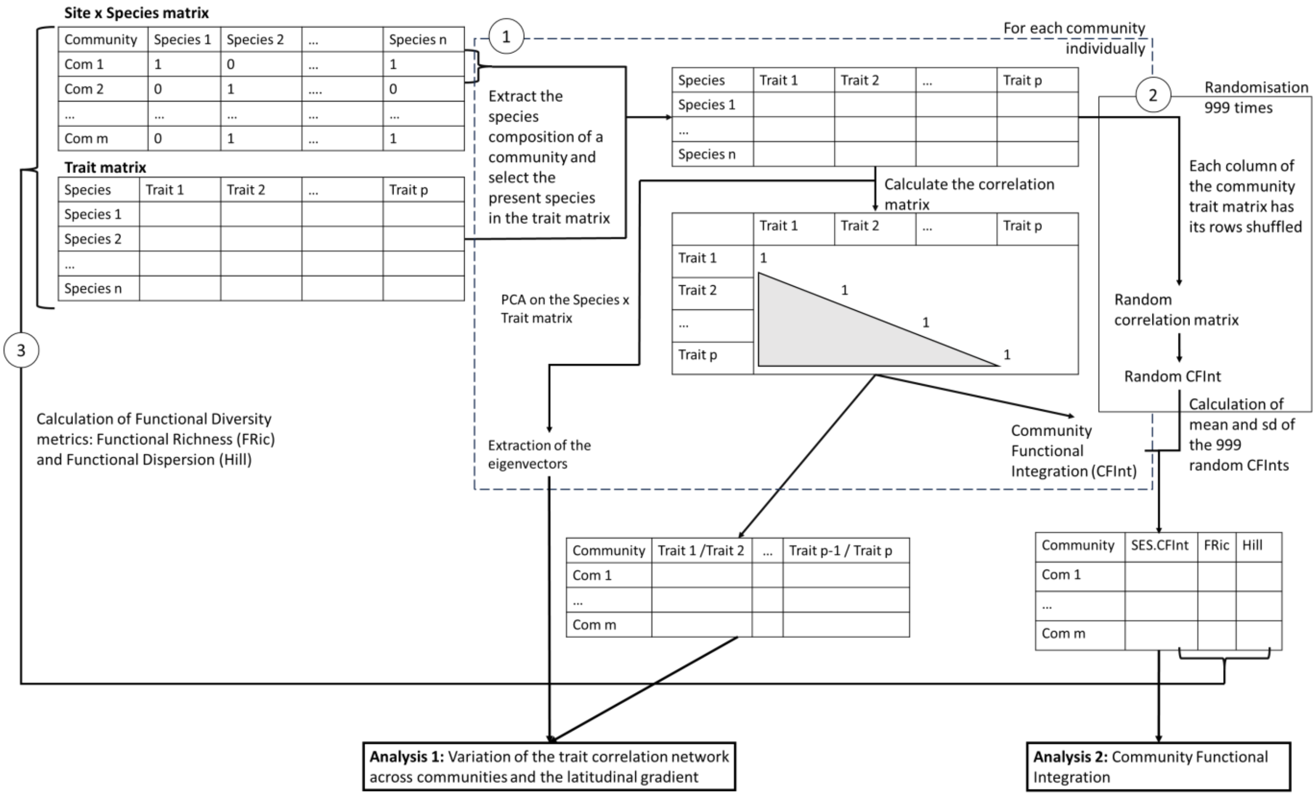


Figure S 3-2: Average Absolute Correlation (AAC) for simulated trait matrices with different number of species (from 3 to 40 species) (in black) and the correction (SES.AAC in red). Fifteen traits were simulated by a normal distribution (mean =0, sd=1), and no association among traits was computed in the simulation.

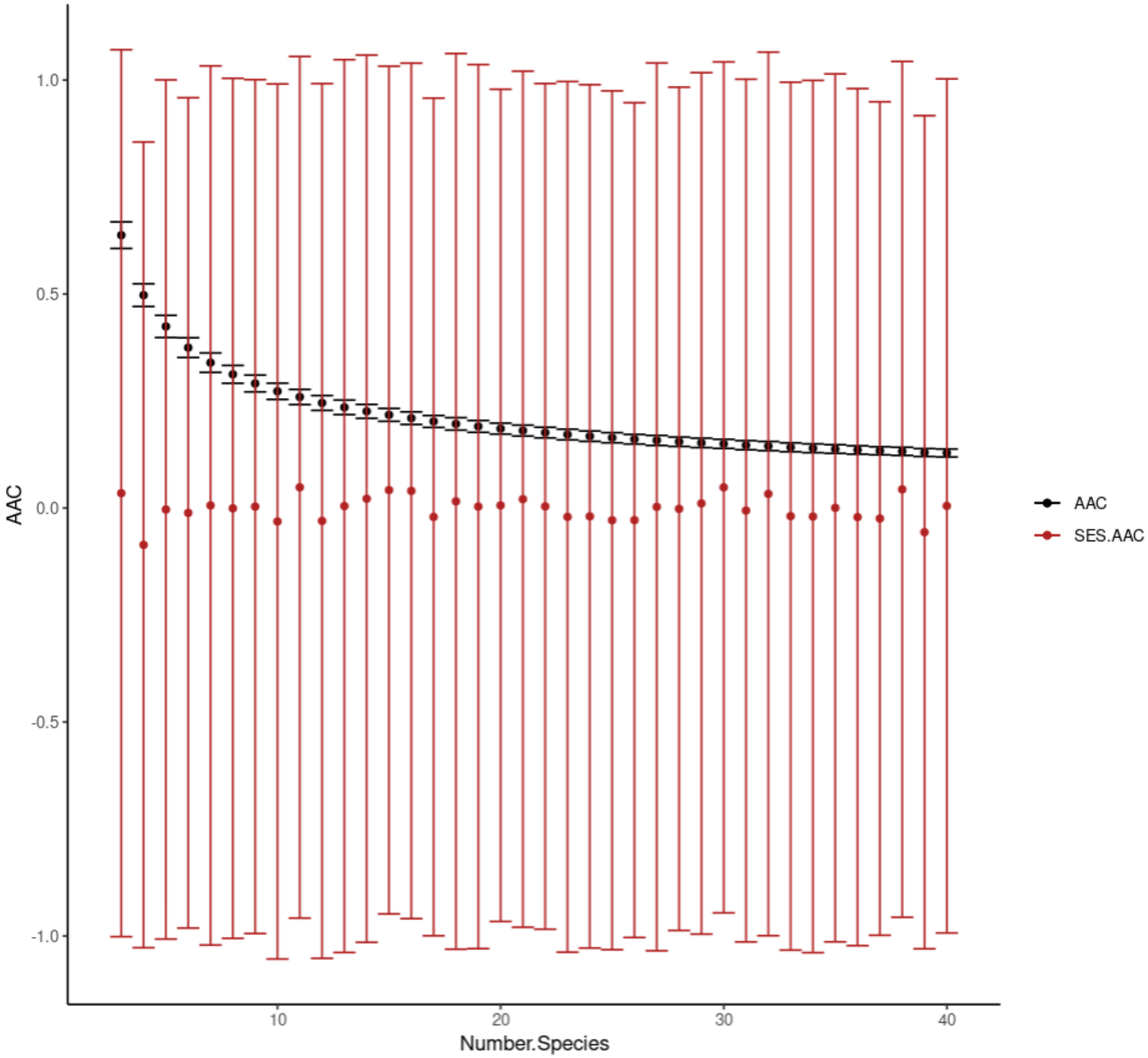


Figure S 3-3: **(A)** Distribution of the different functional metrics. In red, Community Functional Integration (CFInt), in orange the Standardised effect size of CFInt (SES.CFInt), in yellow, Functional Richness (FRic) and in blue, Functional Dispersion (Hill). **(B)** Distribution of the standardised effect size (SES) of different functional metrics. **(C)**: Correlation matrix of the different metrics. The color of the tiles represents the correlation between two metrics: dark blue represents strong negative correlations, bright yellow, strong positive correlations and correlation close to 0 are represented in teal.

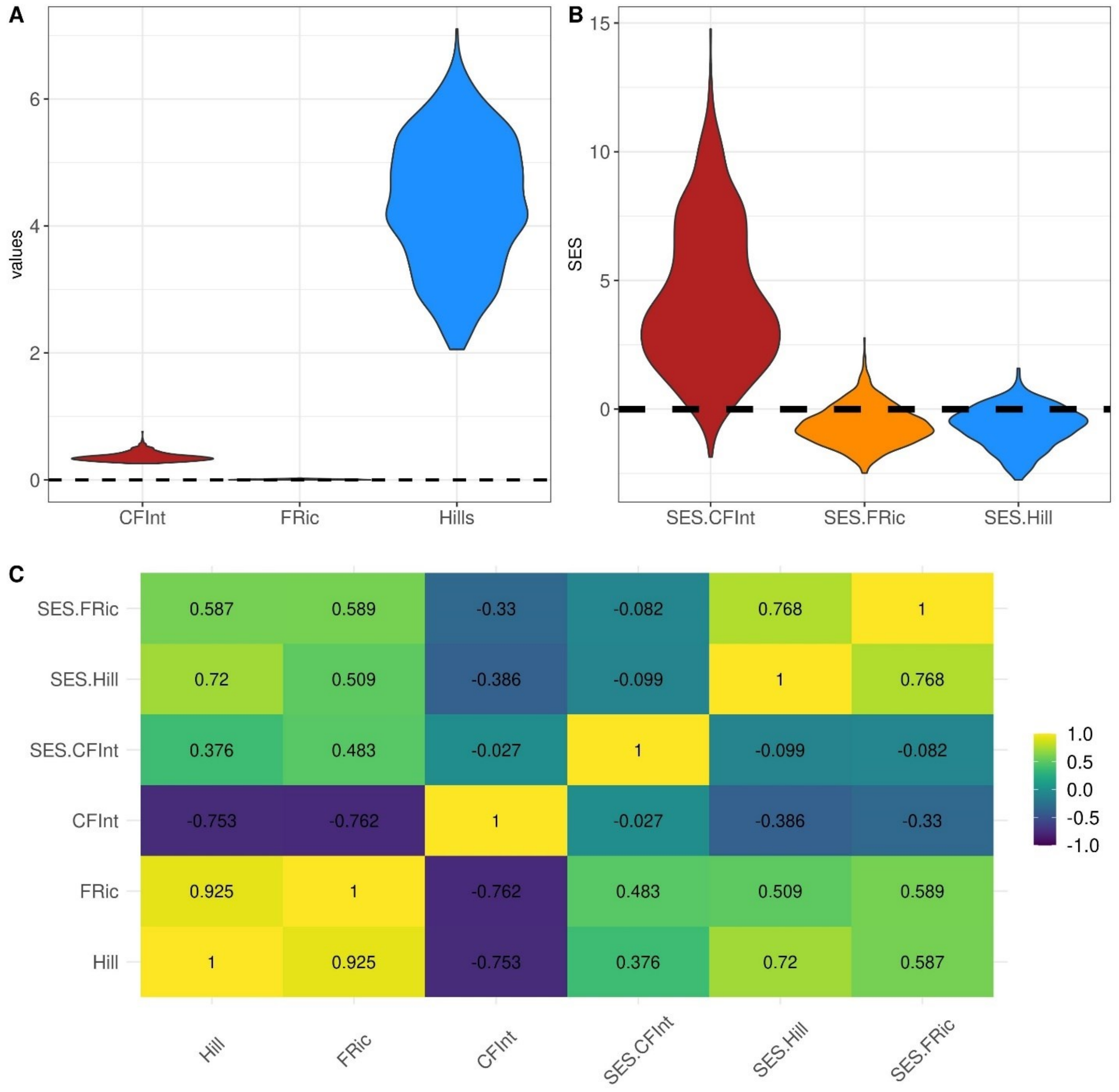
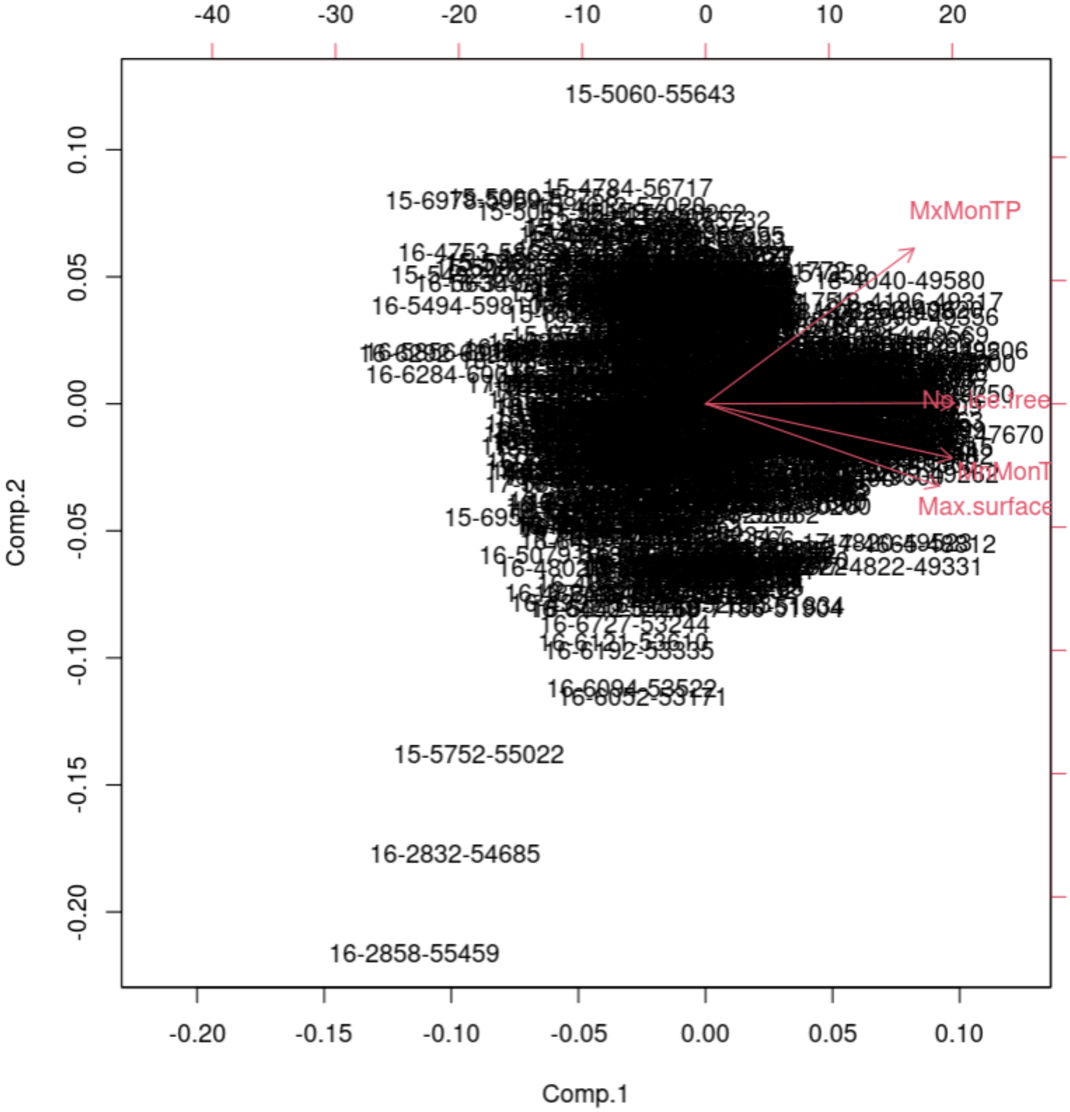


Figure S 3-4: PCA for the 4 climate variables: in the analysis, we extracted the coordinates of the first axis to represent the variation in climatic variables across Ontario. The first axis of the PCA summarise 80% of the variations of the climatic variables. On the first axis, communities with positive coordinates are characterised by high maximum month temperature (MxMonTP), high minimum monthly temperature (MinMonTP), high maximum surface water temperature (Max.surfaceTP), and large number of ice-free days (No_icefree). Positive coordinate, therefore, characterise warm lakes while negative coordinates characterise cold lakes.



4 CHAPTER 4: Functional indicators of change: quantifying and predicting temporal shifts in lake-fish communities along an extensive environmental gradient

4.1 Abstract

Functional diversity encompasses multiple dimensions, including functional composition, functional dispersion and community functional integration (CFInt). Each of these dimensions captures different aspects of community functional structure and may reflect distinct ecological mechanisms shaping local communities. Yet, it remains unclear how congruent temporal changes in these dimensions are, especially under ongoing biodiversity change. In this study, we analysed temporal shifts in functional composition, functional dispersion, and community functional integration across 56 lake-fish communities in Ontario, Canada, spanning an extensive environmental gradient that includes strong climatic and ecological variation. Using data from two time periods (1960–1980 and 2008–2012), we assessed how functional structure has changed over time across this diverse landscape. We found that all three dimensions exhibited significant temporal shifts, with community functional integration showing the strongest temporal overall change and that the temporal shifts in the three dimensions were poorly correlated to one another. This highlights that no single dimension of functional structure can serve as a reliable proxy for the others. Temporal shifts across different dimensions of functional structure and taxonomic composition were weakly correlated, indicating that shifts in functional structure are not a product of shifts in functional composition alone. Spatial structuring of these temporal shifts also varied markedly across dimensions: shifts in taxonomic composition and community functional integration were

influenced by both broad-scale and fine-scale spatial structures, while shifts in functional composition were primarily explained by broad-scale patterns. In contrast, temporal shifts in functional dispersion showed no significant spatial structuring and could not be explained by the spatial models. Together, the results highlight the importance of considering multiple dimensions of functional structure to fully capture how communities' dynamics change over time. They further suggest that much of the variation in temporal shifts likely reflect stressors and ecological processes that are not strongly spatially structured, such as localised habitat changes, biotic interactions, or stochastic events.

4.2 Introduction

It is accepted that biodiversity has entered its Sixth Mass Extinction, with a degradation of biodiversity and ecosystems worldwide (Ceballos et al. 2015). Despite covering around 0.1% of Earth's surface, freshwater ecosystems are home to about 10% of the world's animal species (Balian et al. 2008). These ecosystems are exceptionally biodiverse yet disproportionally threatened: extinction rates among freshwater species exceed those of their terrestrial and marine counterparts (Costello 2015; Reid et al. 2019; Sayer et al. 2025). This vulnerability is driven by a combination of threats, varying in type and acting across multiple spatial scales (Olden et al. 2007; Strayer & Dudgeon 2010; Reid et al. 2019): from local pressures such as habitat degradation and overexploitation, to pervasive global drivers like climate change and land-use intensification. Although there is growing interest in incorporating multiple components of biodiversity into conservation science and policy (Pollock et al. 2017; Stephenson et al. 2019), biodiversity is still often framed primarily through the lens of taxonomic diversity, such as species richness.

Species composition reflects just one facet of biodiversity change (Olden et al. 2016; Cadotte & Tucker 2018; Campbell & Mandrak 2020), and conservation strategies focused only taxonomic diversity may overlook critical components of diversity (Devictor et al. 2010). These overlooked components such as functional and phylogenetic diversity, play key roles in shaping community dynamics and ecosystem processes, and their loss can potentially have cascading effects beyond what is captured by taxonomic measures alone (Duffy 2003; Baiser & Lockwood 2011). Spatial and temporal mismatches between taxonomic and functional diversity are well documented (e.g. Devictor et al. 2010; Barnagaud et al. 2017): these dimensions often respond differently to environmental change and thus cannot reliably serve as proxies for one another.

Functional diversity is a key aspect of biodiversity, as it captures the range, value, and distribution of species' traits that shape community dynamics and influence ecosystem functioning and resilience (Biggs et al. 2020). Consequently, measures of functional structure have been proposed as valuable indicators for understanding and tracking biodiversity change (Statzner et al. 2001; Vandewalle et al. 2010). The functional structure of communities typically encompasses two well-known components - functional composition and functional diversity – as well as a less commonly examined one: community functional integration (CFInt), which reflects the patterns trait correlations among species within communities (see Chapter 3). When assessing temporal shifts in functional structure, ecologists often focus on either functional composition (e.g. Lima et al. 2017; Receveur et al. 2024) or functional diversity (e.g. McLean et al. 2019; Campbell & Mandrak 2020). In fish communities, few studies have simultaneously investigated temporal changes across multiple dimensions of functional diversity (e.g. Toussaint et al. 2018) and the discrepancies in the temporal dynamics among these dimensions remain poorly understood.

Each functional diversity dimension provides unique insights into community function. Historically, functional composition describes the presence and representation of different functional groups (e.g. different trophic guild, botanical groups) within a community (e.g. Tilman et al. 1997; Díaz & Cabido 2001). And today, functional composition is typically quantified as the community-weighted mean (or unweighted) of each trait, representing the “average” species in terms of function (Ricotta & Moretti 2011) and is used to identify the dominant ecological strategy within the community (Grime 1974; Vandewalle et al. 2010). In temporal analyses, this dimension can reveal shifts in the ecological strategies of communities (Vandewalle et al. 2010). For example, a shift from slow-growing, long-lived fish species toward fast-growing, short-lived species has been observed in the North Sea (Beukhof et al. 2019).

Another key component of functional structure is functional diversity, which can be quantified using a range of metrics (Scheiner et al. 2017; Mammola et al. 2021). Among these, functional dispersion is widely used to infer assembly mechanisms, such as environmental filtering and density-dependent interactions, based on patterns of trait distribution (HilleRisLambers et al. 2012; Adler et al. 2013; Mammola et al. 2021). More recently, the concept of community functional integration (CFInt) has emerged, which describes the variation in the strength and structure of pairwise correlations among traits within and across communities (see Chapter 3 for more details). This approach has been primarily explored in plant communities within the framework of the Leaf Economic Spectrum, offering insights into species strategies for resource optimization (Messier et al. 2010; Messier, McGill, et al. 2017). Yet, research on community functional integration remains limited, and the mechanisms linking trait integrations to community assembly processes are not well resolved. Nonetheless, emerging evidences indicate that trait correlations within communities are shaped by environmental filters (Flores-Moreno et al. 2019; Candeias & Fraterrigo 2020; Delhaye et al. 2020; He et al. 2020), underscoring the important of further investigating this overlooked dimension of functional structure.

In this study, we integrate multiple dimensions of functional structure - functional composition, functional dispersion, and community functional integration – into the analysis of temporal shifts of freshwater fish communities across a large climatic and environmental gradient. Specifically, we reanalyze the lake-fish dataset used by Cazelles et al. (2019) to track temporal shifts in functional structure and to disentangle the spatial scales that underpin these patterns along an extensive environmental gradient.

We focus on three key questions: (1) Do freshwater fish communities show temporal shifts in functional composition, dispersion, and integration? (2) Are these shifts interrelated; such that changes in one dimension correspond with changes in others? (3) At what spatial scale does landscape structure explain variation in these temporal patterns? To further disentangle these patterns, we conduct analyses of functional dispersion across different trait sets, recognizing that aggregating traits may obscure important signals (Bower & Winemiller 2019; Côte et al. 2019 and Chapter 2). Although the spatial structure of temporal shifts in functional structure does not directly measure environmental gradients, it can serve as a latent variable capturing underlying environmental heterogeneity (Dray et al. 2012). For example, previous studies have interpreted broad-scale spatial patterns as indicative of dispersal limitation of large-scale environmental filtering, while finer-scale patterns are more likely to reflect local processes such as microhabitat filtering or species interactions (Biswas et al. 2016). In our system, a well-established spatial axis—the South–North gradient—aligns with multiple key environmental variables, including climatic conditions and historical patterns of post-glacial recolonization (Jackson & Harvey 1989; Loewen et al. 2022). By linking the spatial structure of temporal shifts in functional composition, dispersion, and integration, we aim to determine whether broad-scale processes (e.g., dispersal limitation, environmental filtering) or fine-scale local dynamics (e.g., microhabitat filtering, species interactions) drive changes in community assembly in freshwater ecosystems.

Our study system comprises lake-fish communities in Ontario, which support a range of human activities, including fishing, navigation, and recreation. These lakes are routinely monitored by the Ontario Ministry of Natural Resources, whose mandate is to "estimate the current state and changes over time of Ontario's fisheries" and to "identify natural and human-caused stresses affecting fisheries" (Ontario Ministry of Natural Resources 2016). Similar to lake ecosystems worldwide, Ontario's lakes are subject to multiple stressors, including local stressors such as invasive species, chemical pollutants, regional stressors such as land-use changes within their watersheds, and global stressors like climate change (Jones et al. 2017; Campbell & Mandrak 2019; Cazelles et al. 2019; Gutowsky et al. 2019; Sinclair et al. 2021). As such, this study advances our understanding of the dynamics of a large-scale freshwater ecosystem and offers a framework for future research on spatial and temporal variations in functional structure.

4.3 Material and Methods

4.3.1 Contemporary and historical communities, functional trait data and environmental data

Contemporary and historical communities' datasets

Lakes in Ontario have been extensively monitored by the Ontario Ministry of Natural Resources, resulting in two major databases suitable for spatiotemporal analyses of functional structure: the Aquatic Habitat Inventory (hereafter referred to as 'historical') and the Broad-scale Monitoring Program (hereafter referred as 'contemporary'). The Aquatic Habitat Inventory included data on fish presence-absence data, water chemistry, and physical habitat characteristics collected from approximately 10,000 lakes across Ontario between 1960 and 1982. The Broad-scale Monitoring Program (Lester et al. 2020) Ontario's current inland lake monitoring initiative, collected data on fish abundance and biomass, as well as a large set of water chemistry and other physical habitat features. For this study, we used contemporary data collected between 2008 and 2012, comprising records of 89 fish species across 704 lakes. It has been noted that small-bodied prey fishes were likely under-sampled in the historical surveys (Alofs & Jackson 2015). To account for this, we followed the species list identified by Cazelles et al. (2019), which included 39 species that were reliably detected in both the historical and contemporary datasets. We supplemented this list with additional species of ecological interest, including invasive species such as Common Carp (*Cyprinus carpio*), resulting in a total of 49 species included in the initial list of species. We filtered out species for which trait data were not available: the final list of species included 38 species (see Supplementary Materials, Table S4-1). To investigate temporal shifts in functional structure, we focused on lakes that were sampled during both historical and contemporary periods. Given that certain functional metrics, such as trait correlation analyses, required a minimum of species observations, we excluded lakes containing fewer than 3 species. After this filtering step, 569 lakes remained for further analysis (Figure 4-1).

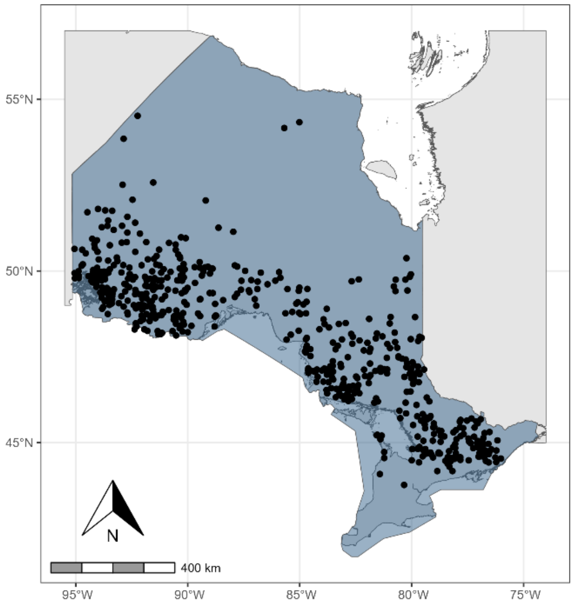


Figure 4-1: Locations of the 569 lakes surveyed in both the historical (1960 to 1980) and contemporary (2008 to 2012).

Functional traits

We extracted 15 functional traits from FishBase (Froese & Pauly 2019; see Supplementary Materials, Table S4-2). When relevant, the traits were grouped into three functional categories based on their ecological roles (Table 4-1): diet, Locomotion

(Loco). As many species in Ontario are limited by their thermal limits (Minns & Moore 1995; Loewen et al. 2022), we included measures of the species' thermal preference (TP): we used the estimation of lower and upper thermal preference (minimum and maximum temperature), extracted from Ontario Freshwater Fish Life History Trait Base (Eakins 2025), completed with FishBase (Froese & Pauly 2025) and existing literature..

Table 4-1: List of 15 traits used in the calculation of functional metrics. The traits are categorised according to their function in the organism: diet, locomotion and temperature preferences. The '*' shows which traits are a ratio (details in Supplementary Materials Table S4-1)

Function	Traits
Diet (5 traits)	Length, Eye diameter*, Trophic level, Preorbital length*, Head Length*
Locomotion (7 traits)	Standard length*, Fork length*, Preanal length*, Predorsal length*, Prepelvic length*, Body depth*, Aspect Ratio
Temperature preference (3 traits)	Minimum temperature, maximum temperature, interval between minimum and maximum temperature

In addition, we created a combined (pooled) trait set including all traits, hereafter referred as to "All". It is important to note that traits in FishBase and Ontario Freshwater Fish Life History Trait Base are reported at the species level, without accounting for intraspecific variability. Accordingly, following common practice in trait-based studies in ecology, we assumed that intraspecific variation is negligible relative to interspecific differences.

To calculate functional metrics, all traits were standardized to a mean of zero and a standard deviation of one, to account for differences in measurement scales among traits. In addition, for the calculation of functional dispersion of the ‘All’ set, we applied the Gower standardisation of matrices to balance the different numbers of traits in each category (Gower 1975): this standardization consists in scaling the traits so the sum of all the squared values of the category is one.(Gower 1975; Peres-Neto & Magnan 2004).

Describing patterns of changes in the functional structure of fish communities

4.3.2 Functional metrics

In this study, we focused on temporal shifts in the functional structure of lake-fish communities, which we decomposed into three dimensions: functional composition, functional dispersion, and community functional integration. To quantify these dimensions, we used three complementary metrics: the community trait mean (CTM) to capture functional composition (Ricotta & Moretti 2011), the Hill number to represent functional dispersion (Chiu & Chao 2014), and the average of absolute correlation between traits to describe community functional integration.

For functional dispersion, we calculated the Gower distance on the trait matrix (Gower 1971) to estimate the pairwise similarities among species and then estimated the Hill number based on this distance matrix. Functional dispersion is sensitive species richness - a source of sampling effect (Mouchet et al. 2010; Mason et al. 2013) - because lower-richness communities inherently occupy a more restricted trait space, which constrains observed dispersion independently of ecological processes. As a result, communities with different richness levels, or even similar richness but differing species identities, cannot be directly compared without accounting for this richness effect. To meaningfully compare different communities, we calculated the Hill numbers for both the contemporary and historical communities and controlled for species richness with a null model. For each lake community, we generated 999 random communities by independently permuting columns of the trait matrix and, as is standard practice, included the observed community to reach a total of 1000 communities for analysis. This allowed us to estimate the expected Hill number for each species richness level under random assembly, from which we calculated the standardized effect size (SES) of the functional dispersion across all communities (Eq.4-1).

$$SES_{metric} = \frac{(metric_{observed} - \overline{metric_{null}})}{sd(metric_{null})} \quad \text{(Eq.4-1)}$$

where SES_{metric} is the standardised effect size of a given functional dispersion metric, $metric_{observed}$ is the observed value of the metric of interest, $metric_{null}$ the values of the metric calculated with the null model. A negative SES reflects lower-than-expected functional dispersion relative to randomly assembled communities of the same richness, characterizing the community as functionally underdispersed. A positive SES reflects higher-than-expected functional dispersion relative to randomly assembled communities of the same richness, characterizing the community as functionally overdispersed. A key part in the analysis of functional dispersion and the interpretation of SES was the definition of trait sets we used four different sets of traits (as defined in the section *Functional traits*). We calculated the observed Hill numbers and the associated SES independently for each set.

To quantify community functional integrations (CFInt), we extracted the trait matrix for each community and calculated its correlation matrix, from which we derived the average absolute correlation using the lower triangle. Absolute correlations are also sensitive to the number of observations (here species) used in their calculation; specifically, samples of absolute correlations drawn from larger populations (with the same underlying correlation) tend, on average, to be higher. Therefore, rather than using the raw values of the average of absolute correlations for functional integration, we calculated its standardised effect size (SES). To compute SESs, we permuted values of each trait independently within each community, thereby simulating expected average absolute correlation values under a null model of random trait association (details of the procedure in Supplementary Materials, Figure S4-1). We generated 999 random permutations and, as customary, included the observed value in the distribution, resulting in a total of 1000 values used to calculate the SES according to the equation above (Eq.4-1). A positive SES for CFInt indicates that the traits within a community (lake) are more strongly correlated than expected by chance (i.e., under random association of species), suggesting elevated functional integration. Conversely, a negative SES for CFInt indicates that traits withing the community (lake) are less strongly correlated, indicating lower functional integration within the community (lake) are less strongly correlated than expected under random assembly, reflecting lower functional integration.

4.3.3 Detecting temporal changes in the functional metrics and taxonomic composition

The temporal shifts for each metric were calculated independently for each community (lake). Specifically, we computed the difference for each community between its contemporary state (from the Broadscale Monitoring Program dataset) and its historical state (from the Aquatic Habitat Inventory dataset), as follows (Eq. 4-2):

$$difference_i = Metric_{contemporary.i} - Metric_{historical,i} \quad \text{(Eq.4-2)}$$

where metric refers to one of the three functional structure metrics described above, and *i* indexed individual (lakes) communities. A positive difference indicates that the metric of interest is higher in the contemporary community compared to its historical state, while a negative difference indicates that the contemporary community exhibits a lower value than in the past. A difference close to zero suggests little or no change in the functional structure of the community over time.

For functional composition, we identified variation across community trait means (CTM) values, with Partial Least Square Discriminant Analysis (PLS-DA). PLS-DA is an extension of Linear Discriminant Analysis that identifies the linear combination of variables (here CTM values for each trait) that best separates predefined groups – in our case, the contemporary and historical datasets - while accounting for repeated measures, such as the same lake sampled at different time points (Westerhuis et al. 2010). We chose to assess traits separately, rather than combining them into composite axes of variation (e.g., the first few axes from a principal coordinate analysis of CTM values), to preserve trait-specific interpretations of temporal changes and to capture variation in some traits that might not be adequately represented by the dominant axes alone. Specifically, we applied PLS-DA to maximize the separation between contemporary and historical communities based on their CTM values. The analysis summarized variations in CTM across communities along two components of the PLS-

DA given that we only have two time periods. We quantified temporal shifts in functional composition based on from PLS-DA scores (from the first and second component) by computing the differences in the scores between contemporary and historical scores (Eq 4-2).

For functional dispersion and functional integration, we calculated the difference between the SES values (described in the section *Functional metrics*) from the contemporary and historical communities (Eq. 4-2). For functional dispersion, a positive difference meant that the contemporary community is more overdispersed than its historical state, a negative difference meant that the contemporary community is more underdispersed than in its historical state. For CFInt, a positive difference meant that the contemporary communities are more integrated than the historical communities, a negative difference shows that contemporary communities were less integrated than their historical state.

Lastly, we quantified changes in taxonomic composition to assess how much of the shifts in functional structure could be attributed changes in species composition. Because trait values were fixed for each species across time, any changes in functional structure directly result from changes in species composition. By quantifying taxonomic turnover as well, we can assess whether shifts in functional structure simply reflect random species replacement through time, or whether they result from non-random turnover that selectively removes or adds species with particular trait profiles. For example, a lake may experience substantial taxonomic turnover over time, but if the species lost and gained have similar traits, the resulting change in functional structure will be minimal. Conversely, even moderate taxonomic turnover can lead to large shifts in functional structure if the turnover disproportionately affects species with particular trait values. By comparing shifts in taxonomic composition and functional structure between two time periods within the same lake, we can disentangle whether observed functional changes are simply proportional to species turnover, or whether they reflect non-random, trait-based processes driving community change. To do this, we calculated the Chao's Jaccard distance between communities to capture changes in taxonomic composition (Cao et al. 2021). The resulting distance matrix was then subjected to Principal Coordinate Analysis (PCoA). We retained the first five PCoA axes, which were subsequently used in a repeated measure PLS-DA (see above) to maximize differences in taxonomic composition between historical and contemporary communities (Westerhuis et al. 2010). The resulting PLS-DA scores where then used to describe changes in taxonomic composition over time (Supplementary Materials: Figure S4-2): we extracted the scores of communities on both axis and calculated the difference between contemporary and historical communities using Eq. 4-2.

4.3.4 Describing temporal shifts along the latitudinal gradient

Before analysing in detail, the spatial patterns of temporal shifts in the different dimensions of functional structure, we described the variations in the temporal shifts across the latitudinal gradient. Many environmental broadscale gradients are structured along the South-North axis, such as climate. By studying the latitudinal gradients of the temporal shifts in the functional structure can help us understanding where changes in functional structure are more important. To study the latitudinal gradient of the metric, we ran a general additive model (GAM) to capture non-linear relationships between the temporal shifts in the functional structure and latitude. In details, we used the latitude as the explanatory variable. The number of splines was set at 20, and smoothing parameters were extracted with the method of restricted maximum likelihood (REML). We reported the adjusted R^2 as an estimate of the model's fit. The GAMs were run on temporal shifts in each functional dimension separately.

Predicting temporal shifts in community structure using spatial patterns

Our next objective was to assess whether temporal shifts in community structure follow spatial patterns, and to determine the spatial scale at which these shifts emerge. Clarifying the spatial structuring of temporal changes illuminate whether broad-scale forces, such as climate gradients or dispersal limitation, shape community dynamics, or whether local-scale processes, such as habitat filtering or biotic interactions, are more influential (Legendre & Fortin 1989; Biswas et al. 2016). Recognizing these spatial patterns is essential for understanding the drivers of community change and for designing conservation strategies that are responsive to dynamics across spatial scales. The spatial analysis followed three main steps: (1) calculation of the Moran's Eigenvector Maps (MEMs; Dray et al. 2006), which generated spatial variables based on the spatial relationships among lakes, allowing us to capture spatial patterns at multiple scales — from broad, landscape-level gradients (e.g., climate or post-glacial history) to fine-scale local structures (e.g., watershed-level variation); (2) selection of MEMs that could effectively describe spatial structure among our studied lakes; and (3) evaluation of which MEMs (from large to small spatial scales) explained variation in temporal shifts of different functional components.

4.3.5 Deriving predictors of spatial structuring and scales

Moran’s Eigenvector Maps (MEMs) decompose the spatial configuration of the lakes into orthonormal components, each representing spatial patterns at different scales, based on geographic distance matrices among lakes. We estimated the geodesic distance among lakes using Vicenty’s ellipsoid method, which provides accurate distance estimates based on geographic coordinates (longitude and latitude). Using this distance matrix, we computed a Moran’s Eigenvector Map (MEMs) to represent spatial patterns across multiple scales (Dray et al. 2006; Griffith & Peres-Neto 2006). MEMs are orthonormal by design, meaning that each represents an independent spatial pattern, with no redundancy or any correlation between MEMs. A total of 131 positively autocorrelated MEMs and 437 negatively autocorrelated MEMs were extracted and used as explanatory variables in subsequent analyses to investigate the spatial structuring and scale dependency of temporal variation in functional structure. Importantly, the order of the MEMs indicates the spatial scale they represent lower-numbered MEMs (e.g., 1st MEM) capture broad-scale spatial patterns, whereas higher-numbered MEMs (e.g., 568th MEM) represent finer-scale spatial variation.

4.3.6 Selecting spatial predictors to retaining meaningful structures

Although all Moran’s Eigenvector Maps (MEMs) capture some degree of spatial variation, some represent patterns that are too weak to constitute meaningful spatial structuring. As described by Diniz-Filho et al.(2003), orthonormal spatial eigenvectors (including MEMs) can capture three types of spatial patterns. The first type exhibits strong positive autocorrelation or strong negative autocorrelation at longer distances, typically associated with broad large-scale environmental gradients. The second type shows positive autocorrelation only at short distances, characteristic of patchy spatial distributions. The third type includes MEMs that exhibit extremely weak spatial autocorrelation. To identify and exclude MEMs that captured extremely weak spatial structures, we calculated the Moran's *I* coefficient of each MEM across a range of spatial scales, using 20 distance classes. This approach allowed us to assess whether a given MEM describes spatial autocorrelation at different scales. We retained only those MEMs with an absolute Moran's *I* values greater than 0.05 in at least one distance class. Following this selection step, 197 of the original 567 MEMs were retained for further analysis (see Supplementary Materials: Figure S4-3 for the retained MEMs). Additionally, by calculating Moran's *I* for the temporal shifts in functional structure across the same distance classes, we were able to evaluate whether these shifts were spatially structured (autocorrelated), and at which scales. As with the MEM selection, we applied a threshold of |Moran's *I*| > 0.05 to identify meaningful spatial structure, beyond weak or negligible levels of spatial autocorrelation.

4.3.7 Understanding the spatial structures and scales underlying temporal community change

Each Moran's Eigenvector Maps (MEMs) captures a distinct spatial scale and can be integrated into models and sub-models (i.e., scale-classified subsets, e.g., broad, intermediate, and fine scales) to investigate the spatial structuring of response variables (Legendre & Legendre 2012; Dray et al. 2012), specifically the temporal shifts in community structure investigated in our study. We quantified the proportion of variation in temporal shifts of functional and taxonomic metrics explained by multiple linear regression models, using temporal shifts in functional structure (i.e., the functional metrics) (Eq.4-2) as response variables and MEMs as spatial predictors. Each functional metric was analyzed in an independent regression model against the full set of MEM predictors. To achieve this, we applied a variable selection using the relaxed LASSO approach, which improves model selection performance compared to traditional forward selection methods (Hastie et al. 2020) and allowed us to retain only the most relevant MEMs for each the temporal shifts of the different functional metrics. The selected MEMs were then classified into three categories based on their spatial scale: broad-scale, intermedia-scale, and fine-scale structures. We subsequently performed a variation partitioning to quantify the proportion of variation explained by the full model and each spatial category, i.e., broad-scale, intermediate-scale, and fine-scale structures (Dray et al. 2012; Dray et al. 2024). Model performance and explained variation were reported using adjusted R^2 values for each spatial category (Peres-Neto et al. 2006).

All analyses were conducted in R Core Team 2024) using RStudio. Community Weighted Means and functional dispersion were calculated using the ‘FD’ (Laliberté et al. 2014) and ‘mFD’ (Magneville et al. 2022) packages, respectively. The PLS-DA was performed using the ‘mixOmics’ package (Rohart et al. 2017). Community functional integration (CFInt) and associated null models were computed using customs functions. Geodesic distances were calculated with the ‘geosphere’ package (Hijmans 2010). GAM were run with the package ‘mgcv’ (Wood 2025). Spatial analyses, including MEM computation, were conducted using ‘adespatial’ (Dray et al. 2024). The relaxed LASSO procedure for variable selection was performed using ‘glmnet’ (Friedman et al. 2010), variation partitioning with ‘vegan’ (Oksanen et al. 2020), and visualizations were produced with ‘ggplot2’ (Wickham 2016).

4.4 Results

4.4.1 Quantifying temporal shifts in lake-fish communities

We began by quantifying the extent of temporal restructuring in lake-fish communities, quantifying how their functional attributes have shifted over time (Figure 4-2 and Figure 4-3 and Table S4-3 for the table with all the average values of temporal shifts). The results suggest that lake-fish communities have experienced substantial shifts in functional composition and CFInt over time, while other components of community structure, such as functional dispersion and taxonomic composition, have remained comparatively somewhat more stable.

For the functional structure, 5 out of 7 metrics had an average change significantly different from 0 (complete table of the paired t-test's results, Supplementary Materials Table S4-3): the first component of functional composition with an average difference of 1.77 (results of a paired t-test between the contemporary and historical values: *t-value* = 16.02, *p-value*$< 2.2 \times 10^{-16}$), the second component of functional composition with an average shift of -0.53 (*t-value*= -5.47, *p-value*= 6.68×10^{-8}), functional dispersion of diet traits with an average shift of -0.16 (*t-value* = –4.41, $p = 1.12 \times 10^{-5}$) and community functional integration (CFInt) with an average shift of 0.82 (*t-value* = 9.26, *p-value* $< 2.2 \times 10^{-16}$). Of the two axes of the PLS-DA representing taxonomic composition (the first component captured 30% of the variation, and the second component captured 17%), only the first showed a significant change between historical and contemporary communities (shifts in the first component of taxonomic composition: mean = 1.24, $t = 17.75$, $p < 2 \times 10^{-16}$).

The PLS-DA applied to the CTM successfully discriminated between contemporary and historical communities with two main axes of trait combinations. The first component (Figure 4-2A), which explained 20% of the variation in functional composition, primarily differentiated contemporary and historical communities based on body depth, head length, maximum temperature, minimum temperature, and standard length. Specifically, contemporary communities were characterized by species that, on average, have deeper bodies, larger heads and higher minimum temperature preference (Figure 4-2B). The second component of the temporal PLS-DA explained 9% of the variation in functional composition and separated historical and contemporary communities based on their average aspect ratio, prepelvic length, maximum temperature, and trophic levels (Figure 4-2C). Contemporary communities along this axis tended to be composed of species with higher aspect ratios, but smaller prepelvic lengths, lower maximum temperature preferences, and lower trophic positions (Figure 4-2D). Overall, these results indicate that contemporary lake-fish communities have shifted on average, toward species with warmer temperature preferences, deeper bodies and larger heads, higher aspect ratios, and lower trophic levels.

Shifts in functional composition exhibited a clear latitudinal trend (Figure 4-2E). Specifically, the second component of functional composition showed the strongest latitudinal trend the greatest changes along the second axis occurred in southern lakes. Specifically, southern lakes shifted toward communities of more pelagic, cool-water species. Temporal shifts in the first axis of functional composition had a less pronounced latitudinal trend. However, some of the biggest changes were found in northern communities. These patterns suggest that the restructuring of community functional composition is spatially structured, likely reflecting underlying latitudinal gradients in climate and environmental conditions across the region.

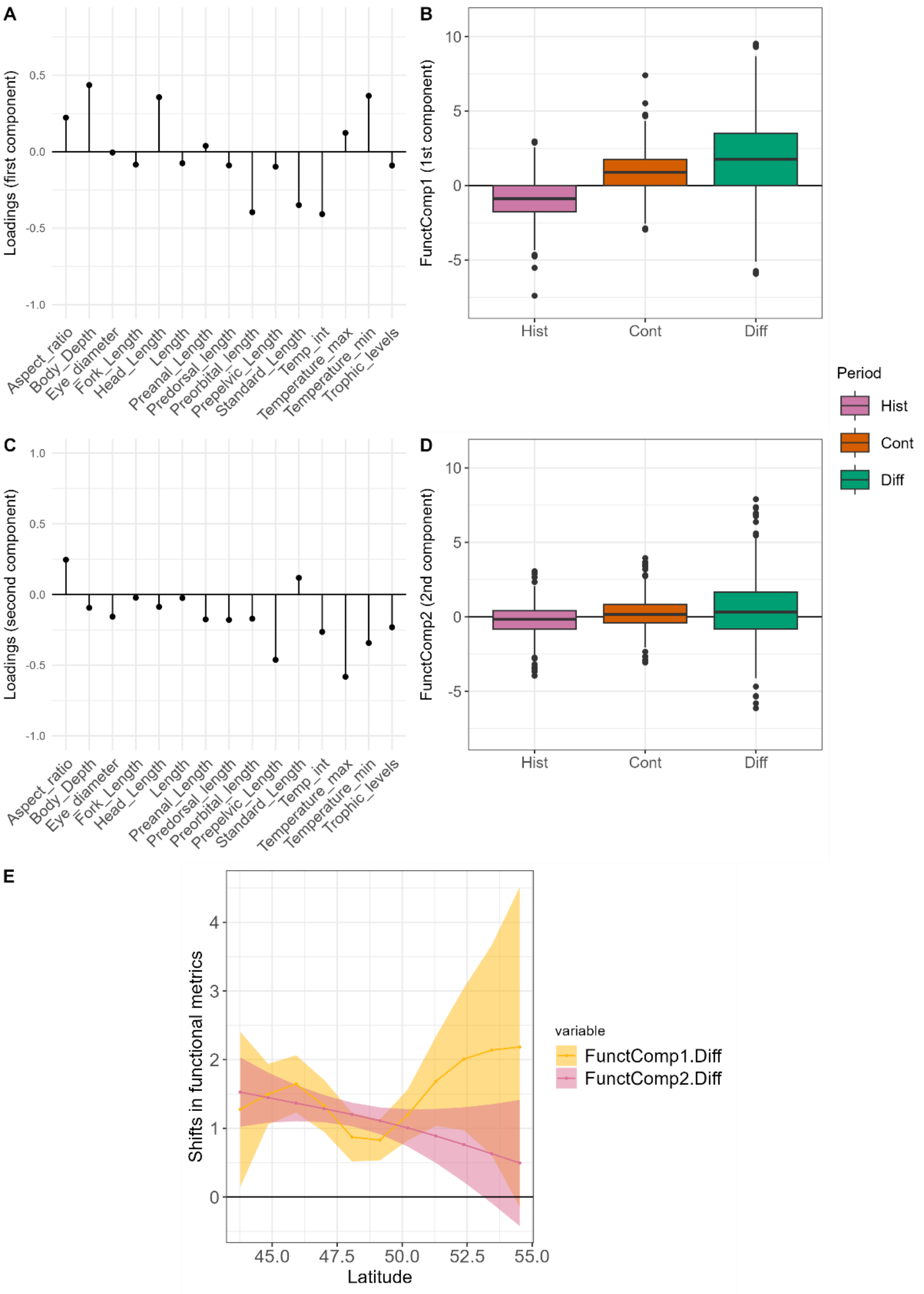


Figure 4-2: Temporal shifts in functional composition of lake-fish communities. Functional composition was quantified by applying a PLS-DA to the CTM of each trait. The PLS-DA identified combinations of traits that maximised differences between Historical (Hist) and Contemporary (Cont) communities. Panels **(A)** and **(C)** show the **l**oadings of each trait on the first the two components of the PLS-DA, respectively; positive loadings indicate traits positively associated with the given component. Panels **(B)** and **(D)** display the distribution of

community scores along the two components of the PLS-DA (FunctComp1 for the first component and FunctComp2 for the second component). Temporal difference (Diff) between historical and contemporary were calculated from community scores on each PLS-DA component. Colours represents either the time period (“Cont”, or “Hist”) or magnitude of temporal change (Diff). Panel **(E)** illustrates the latitudinal gradient of temporal shifts in functional composition, derived from a generalized additive model (GAM). Adjusted R^2 for the GAM associated with the shifts in the first component: R^2=0.002; in the second component: R^2= 0.01

For functional dispersion, the direction of temporal shifts did not vary depending on the trait (Figure 4-3A). For diet traits, in average, historical communities showed pronounced overdispersion (average SES.Diet in historical communities =1.06) and tended to become underdispersed over time (average shift in SES.Diet = -0.16). The average shifts between contemporary and historical communities, were negative for functional dispersion of both the locomotion and temperature preference trait sets (average shifts in dispersion of locomotion trait: -0.05; of temperature preference: -0.39). Historical communities for these two trait sets were, on average, underdispersed (mean historical functional dispersion of locomotion traits: –0.31, of temperature preference: –0.36). Collectively, these patterns suggest an average convergence toward more random trait distributions in contemporary communities for diet, and more underdispersion for locomotion and temperature preference: this indicates a weakening of biotic interactions and a strengthening of environmental filtering.

For community functional integration (CFInt), contemporary communities were generally more integrated than historical communities (Figure 4-3B). Historical communities had an average a CFInt of 2.98, and the average difference between contemporary and historical communities was 0.81, indicating a notable increase in trait correlations over time. Together, these results suggest that contemporary lake-fish communities are marked by stronger trait integration but reduced functional dispersion, indicating a convergence toward more homogenised functional community structures.

Latitudinal trends of temporal shifts in functional dispersion depended in the trait set (Figure 4-3B). For Locomotion and All traits, In, changes in dispersion were minimal (values close to zero) in southern and central Ontario, whereas northern communities showed strong patterns toward more underdispersion. For Diet and Temperature preference sets, stronger changes were observed in the southern lakes compared to northern lakes. However, even though the effect of the latitude was significant, the adjusted R^2 were low (R^2 = 0.03 for temporal shifts in dispersion of diet traits and R^2= 0.04 for the temporal shifts in dispersion of temperature preference traits). For temporal shifts in CFInt, we observed a pronounced latitudinal gradient (Figure 4-3D): communities in the central regions of Ontario become more integrated over time, while northern communities a decrease in trait integration. Similarly, as with the shift patterns observed for locomotion and temperature preferences, the fit of the latitudinal trend for CFInt was modest (adjusted R^2 = 0.08).

Together, these results highlight that spatial patterns in functional restructuring are trait-dependent, with temperature preferences and locomotion traits showing contrasting latitudinal trends, while CFInt displays a distinct spatial dynamic centred in Ontario’s mid-latitudes. However, despite apparent latitudinal trends, the low adjusted R^2 reported for the latitudinal gradient suggests a poor predictive power of spatial gradient. The weak explanatory power of these trends suggests that latitude alone is insufficient to explain the observed patterns of functional shifts, instead pointing to the influence of additional local or region-specific factors shaping these changes.

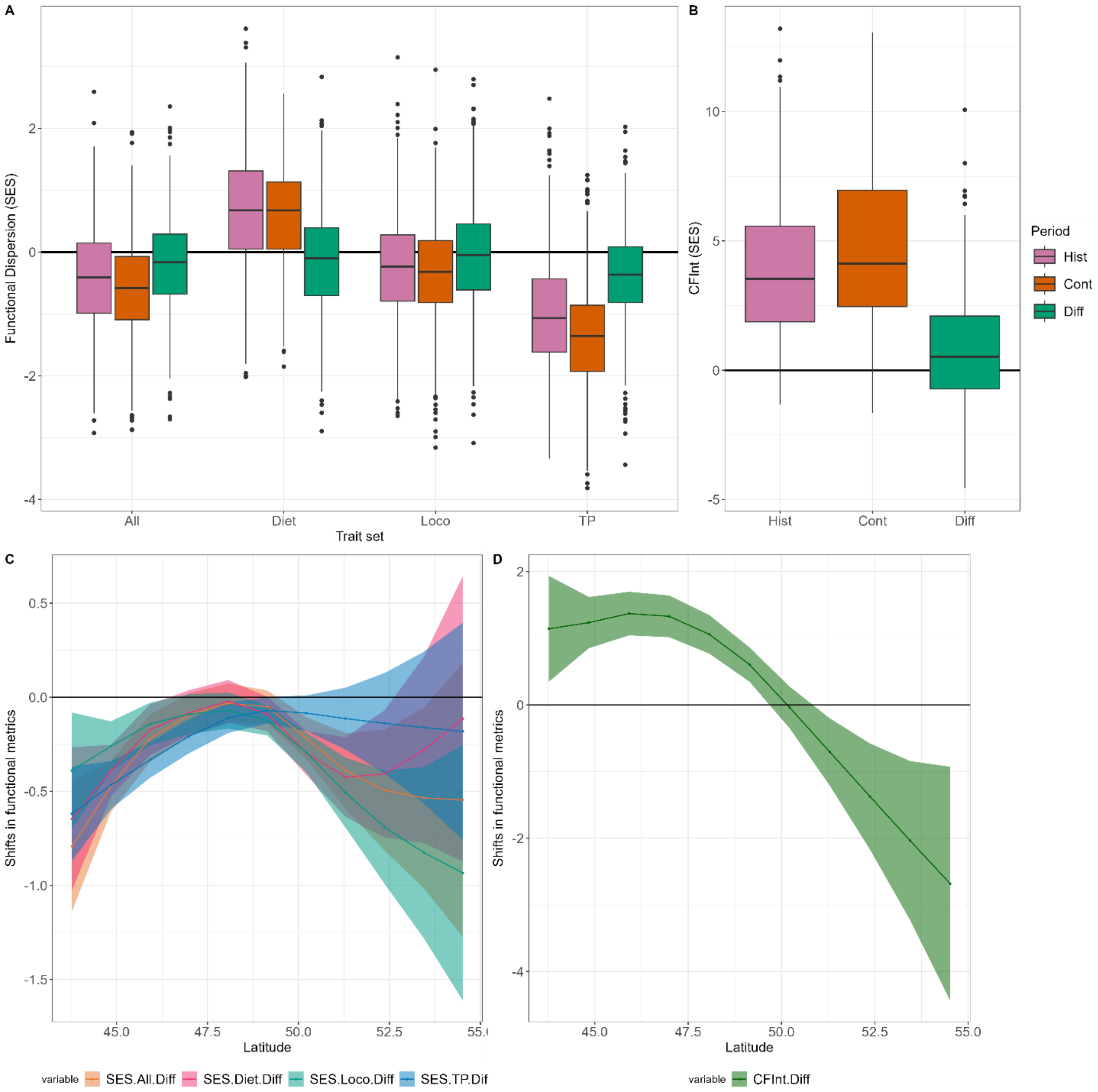


Figure 4-3: Temporal shifts in functional dispersion and community functional integration (CFInt). (A): Distribution of the standardized effect sizes (SES) for functional dispersion, calculated across four trait sets: *All* (all 15 traits combined), *Die*t (diet-related traits only), *Loco* (locomotion traits only), and *TP* (temperature preference traits only). **(B):** Distribution of community functional integration (CFInt) calculated as the SES of the average absolute correlation within each community. Boxplot colours indicate data period (contemporary (“Cont”), historical (“Hist”), or the temporal differences between the two (“Diff”). **(C) and (D):** Latitudinal gradients for functional dispersion and CFInt, based on generalized additive model. Colours represent different metrics: orange for shifts in functional dispersion across all traits (SES.All.Diff), pink shif in diet traits (SES.Diet.Diff), light green for shifts in locomotion traits (SES.Loco.Diff), blue for shifts in temperature

preference traits (SES.TP.Diff), and dark green for shifts in CFInt. Fit in panels (C) and (D) were derived from a generalized additive model (GAM). Adjusted R^2 for the model for shifts in dispersion of All traits: R^2= 0.06; for diet traits: R^2= 0.03; for locomotion traits: R^2=0.02; for Temperature Preference: R^2= 0.04; for CFInt: R^2= 0.09

4.4.2 Comparing shifts in functional structure and taxonomic composition

The next step in our analysis was to assess the degree of congruence among the temporal shifts in the different metrics of functional structure (Figure 4-4). We used Spearman's rank correlation to assess the strength and direction of association between temporal shifts in the different functional metrics to detect monotonic relationships without assuming linearity. The strongest correlations were observed among the different measures of functional dispersions: differences in functional dispersion of all traits were strongly correlated with differences in functional dispersion of locomotion traits (Spearman's correlation between the temporal shifts in dispersion of all traits and locomotion traits: ρ= 0.76) and were also moderately correlated with differences in functional dispersion of diet traits (Spearman's correlation between the temporal shifts in dispersion of all traits and temperature traits = 0.46). Overall, temporal shifts in the remaining functional metrics were weakly or moderately correlated to one another: every metrics had their unique temporal patterns.

We also assessed the congruence between temporal shifts in functional structure and shifts in taxonomic composition to evaluate whether observed changes in taxonomic composition could explain the observed functional temporal dynamics (Figure 4-4). Temporal shifts in taxonomic composition were moderately correlated with shifts in functional composition (correlation between the second axis of functional composition and the second axis of taxonomic composition: Spearman's ρ = 0.-52 These findings indicate that while changes in species composition contribute to functional restructuring, they only partially explain the observed shifts in functional structure, suggesting that other factors beyond taxonomic turnover are also at play.

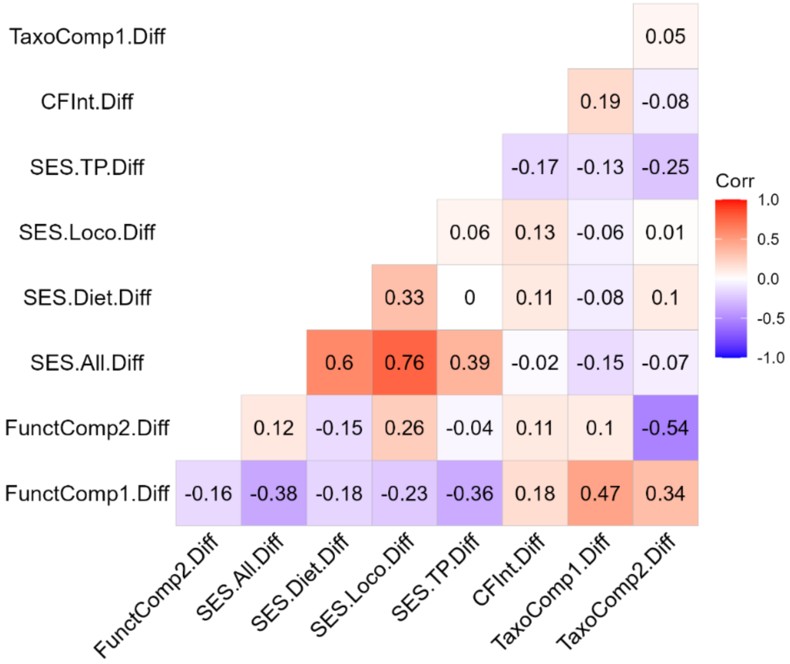


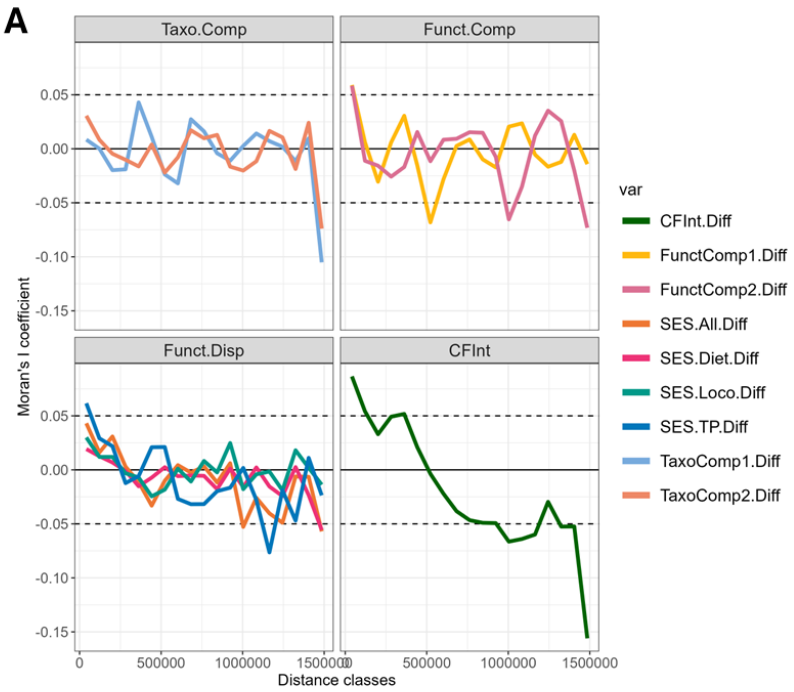
Figure 4-4: Spearman correlations among temporal shifts in the different functional dimensions and taxonomic composition. The matrix shows Spearman correlation coefficients among temporal shifts in functional composition (FunctComp1.Diff and FunctComp2.Diff, representing the first and second components of the PLS-DA applied to CTM), functional dispersion (SES.All.Diff, SES.Diet.Diff, SES.Loco.Diff, Diff.SES.TP), and community functional integration (CFInt_Diff). Correlations with temporal shifts in taxonomic composition (TaxoComp1.Diff and TaxoComp2.Diff, representing the first and second components of the PLS-DA applied to taxonomic composition). Colours indicate both the strength and direction of the correlation: dark blue represents strong negative correlations, dark red represents strong positive correlation, and white indicates weak or no correlation.

4.4.3 Spatial structure of temporal shifts in functional structure and taxonomic composition

Our spatial analysis involved two steps: first, assessing the spatial autocorrelation of each metric across different distance classes; second, using spatial predictors (Moran's Eigenvector Maps – MEMs) to capture the spatial patterns and scales associated with temporal shifts in functional and taxonomic structure (Figure 4-5).

The correlogram revealed diverse patterns of spatial autocorrelation across the metrics and their temporal shifts (Figure 4-5A). Positive values of Moran's *I* indicate that communities at similar distances experiences similar temporal shifts, whereas negative Moran's *I* values reflect dissimilarities in temporal shifts between geographically close communities. Notably, community functional integration (CFInt) exhibited clear spatial patterns, with positive autocorrelation at short distances that shifted to negative autocorrelations at broader spatial scales (Figure 4-5A). In contrast, the remaining metrics displayed weaker or less distinct spatial structuring in their correlograms, suggesting limited spatial dependence in their temporal shifts (Figure 4-5A).

The variation partitioning analysis (Figure 4-5B) revelated that MEMs explained varying proportions of the temporal shifts in both functional structure and taxonomic composition. Models for the first component of taxonomic composition, the second component of functional composition, functional dispersion (all traits combined), and community functional integration (CFInt) accounted for over 10% of the variation, with the model for community functional composition explaining up to 23% of the observed variation in temporal shifts. By contrast, the spatial models explained very little variation in temporal shifts of functional dispersion for specific trait sets (Figure4-5B). The lowest explanatory power was observed for shifts in the dispersion of diet traits and locomotion, which accounted for only 3% of the variation. When examining the variation explained by each scale-classified subsets (i.e., broad, intermediate, and fine scales), broad-scale MEMs consistently accounted across all functional metrics for the largest share of variation in temporal shifts (Figure 4-5B), reaching an adjusted R^2 as high as 0.12 for the model describing temporal shifts in CFInt. Fine-scale MEMs accounted for part of the variation in temporal shifts in some metrics, notably for shifts in the functional dispersion of diet traits (adjusted R^2=0.13), the first component of functional composition (adjusted R^2=0.08), and in CFInt (adjusted R^2=0.05). In contrast, fine-scale MEMs explained very little variation in other metrics. In some cases, fine-scale MEMs were not selected at all by the LASSO procedure, as observed in the models for shifts in the dispersion of diet traits and locomotion traits. These differences in the proportions of explained variations across metrics emphasize that temporal shifts in community structure exhibit distinct spatial patterns and point to the likelihood that different ecological processes are driving these temporal dynamics across the various dimensions of community structure.



B

Dimension	Metric	Broadscale	Intermediate scale	Fine scale	Total R^2
Taxo.Comp	TaxoComp1.Diff	0.01	0.009	0.08	0.10
	TaxoComp2.Diff	0.06	0.02	0.05	0.13
Funct.Comp	FunctComp1.Diff	0.09	0.04	0.08	0.23
	FunctComp2.Diff	0.00^+	0.00^+	0.00^+	0.00
Funct.Disp	SES.All.Diff	0.03	0.00^+	0.00^+	0.03
	SES.Diet.Diff	0.06	0.01	0.13	0.20
	SES.Loco.Diff	0.03	0.00^+	0.00^+	0.03
	SES.TP.Diff	0.03	0.00^+	0.00^+	0.03
CFInt	CFInt.Diff	0.12	0.00^+	0.05	0.17

Figure 4-5: Spatial patterns and explanatory power of spatial models for temporal shifts in functional structure and taxonomic composition - (A): Spatial autocorrelation across distance classes for the different metrics of temporal shifts in functional structure and taxonomic composition. Temporal shifts in taxonomic composition are shown in the panel labelled 'Taxo.Comp': shifts along the first axis are shown in light blue (TaxoComp1.Diff) and shifts along the second axis in light orange (TaxComp2.Diff). Temporal shifts in functional composition are displayed in the 'Funct.Comp' panel, with the first axis shown in yellow (FunctComp1.Diff) and the second axis in pink (FunctComp2.Diff). Shifts in functional dispersion are show in the panel labelled 'Funct.Disp': dispersion of all traits in orange (SES.All.Diff), diet traits in dark pink (SES.Diet.Diff), locomotion traits in green (SES.Loco.Diff), temperature preference traits in dark blue (SES.TP.Diff). Shifts in community functional integration are shown in the CFInt panel in dark green (CFInt.Diff). Autocorrelation is expressed using Moran's *I* coefficients; the horizontal line indicates the threshold for considering meaningful autocorrelation (|Moran's I| = 0.05). **(B)**: Adjusted R^2 values associated with different blocks of MEMs, representing broad, intermediate, and fine spatial scales, for each functional and taxonomic metric. The

symbol “+” indicates that no MEM from the corresponding category (broad-scale, intermedia-scale, or fine-scale structures) was selected by the LASSO procedure.

4.5 Discussion

In this study, we conducted a comprehensive analysis of temporal shifts in the functional structure of lake-fish communities across a large latitudinal gradient. Our results revealed that the various dimensions of functional structure exhibited divergent temporal shifts, with each associated with distinct spatial scales of variation. While broad-scale spatial patterns accounted for most of the explained variation in these temporal shifts, our results suggest that fine-scale spatial patterns could play an important role in driving changes in some community-level functional dimensions over time.

4.5.1 Mismatches between temporal shifts in functional dimensions and taxonomic composition.

It is well established that biodiversity is a multifaceted concept, and focusing on a single dimensions fails to capture the full extent of biodiversity variation across landscapes (Heino et al. 2007; Devictor et al. 2010; Kuczynski et al. 2018; Doxa et al. 2020) or through time (Purschke et al. 2013; Beiroz et al. 2018; Kuczynski et al. 2018; Campbell & Mandrak 2020). Consistent with this, our results showed limited correlations between temporal shifts in taxonomic composition and the various dimensions of functional structure in lake-fish communities. Although our traits were assigned at the species-level, changes in taxonomic composition alone did not fully account for the observed shifts in functional metrics. This suggests that while species turnover contributes to functional change, additional processes such as trait filtering or differential species gains and losses (and their associated traits) are also shaping the functional temporal shifts in trajectories of these communities. Taken together, functional shifts in these communities are not merely by-products of taxonomic turnover but reflect more complex dynamics likely driven by selective processes acting on species traits (Olden 2006).

While many studies have highlighted mismatches between taxonomic, functional, and phylogenetic structure of the communities (Devictor et al. 2010; Doxa et al. 2020; Campbell & Mandrak 2020), it remains uncommon for functional structure itself to be assessed across multiple dimensions (composition, dispersion, and integration) simultaneously. Few studies have explored how different dimensions of functional structure — such as composition, dispersion, and integration — covary or diverge over time. For example, Kuczynski et al. (2018) reported a spatial mismatch between functional richness and evenness in freshwater fish communities in Europe. Similarly, our findings reveal temporal mismatches among functional indices: the temporal shifts in different dimensions of community functional structure were only weakly correlated. These low correlations suggest that each dimension of functional structure responds to changes in environmental conditions or abiotic processes through time in a distinct way, and importantly, that no dimension can reliably serve as a proxy for the others.

Assessing only a single dimension of functional structure risks oversimplifying community dynamics and may fail to detect important aspects of biodiversity change. Similarly to conservation policies which focus on taxonomic diversity and overlook functional and phylogenetic diversity (Devictor et al. 2010; Pollock et al. 2017), conservation strategies focused solely on one facet of functional diversity — for example, monitoring functional composition— may inadvertently overlook significant shifts in other dimensions, such as trait dispersion or functional integration. Those dimension capture different facets of community responses to changes in environmental and biotic conditions that may be of interest for monitoring and define conservation efforts (Vandewalle et al. 2010). Our results highlight the importance of adopting multidimensional frameworks for biodiversity monitoring, ensuring that ecological indicators more comprehensively reflect changes in ecosystem structure and function, and thereby informing more effective conservation actions.

4.5.2 Changes in functional composition: a shift toward deep-bodied and warm-water species

On average, lake-fish communities in Ontario have undergone notable changes in their functional composition between the historical time and contemporary periods. Specifically, shifts toward warm-water fish communities, pervasive across Ontario, were consistent with expectations under climate warming in Canada (Chu et al. 2003; Van Zuiden et al. 2016). For the second component of functional composition, Ontario's fish communities showed an overall shift toward species with pelagic traits and low trophic levels. This trend was particularly pronounced in southern lakes, while northern lakes exhibited more modest shifts on this dimension.

Climate change is widely associated with the proliferation of warm-water species and the erosion of functional diversity in freshwater ecosystems (Daufresne & Boët 2007; Buisson et al. 2013). Predatory species such as smallmouth bass are known to benefit from warming temperatures (Jackson & Mandrak 2002; Chu et al. 2003; Van Zuiden et al. 2016), whereas prey species like the redbelly dace may be negatively affected by the expansion of these predators (Jackson & Mandrak 2002; Alofs & Jackson 2015b). The expansion of large-bodied sport fishes could help explain the pronounced shifts toward higher trophic levels and morphological compositional changes observed in southern lakes (Cazelles et al. 2019).

4.5.3 Shifts in functional structure reflect changes in community assembly mechanisms

Additionally, shifts in functional dispersion of diet traits were, on average, significantly different from zero – indicating consistent directional change over time. Specifically, we observed a negative shift in the dispersion of diet traits. For Temperature preference and 'All trait' trait sets, average changes across all communities were also significantly different from zero: on average the communities became more underdispersed. Notably, northern communities showed more pronounced signs of underdispersion in locomotion traits, while southern communities are becoming more underdispersed in their temperature preference traits.

These patterns suggest important shifts in community assembly processes over time. Overdispersion in functional traits is often associated with competitive interactions (HilleRisLambers et al. 2012), particularly when considering traits linked to resource use. The observed decline in dispersion of diet traits — which were historically overdispersed — likely reflects a weakening of biotic interactions, with reduced competitive exclusion among species. In contrast, underdispersion is commonly linked to environmental filtering (HilleRisLambers et al. 2012), especially for traits associated to environmental tolerances. The negative shifts in the dispersion of locomotion and temperature preference traits suggest that environmental filters are becoming stronger through time. Southern communities becoming more underdispersed in their thermal traits may indicate stronger environmental filtering, while northern communities had less pronounced shifts. This seemed to confirm interpretations of functional composition, which suggested that the climatic barriers may be maintained in northern communities.

Finally, we detected a general increase in community functional integration over time. Functional integration can reflect environmental constraints on community structure (Messier, Lechowicz, et al. 2017), but recent research showed that it can be also sensitive to biotic interactions, with higher trait correlations often associated with intensified competition (Gross et al. 2024). The observed positive shifts in community functional integration may reveal a strengthening of both environmental constraints and biotic interactions. The observed positive shift in functional integration may therefore signal a simultaneous strengthening of environmental constraints and biotic interactions. This pattern could arise if environmental conditions are increasingly favouring certain combinations of traits, or if competitive dynamics are leading to tighter trait convergence within communities. For example, warming temperatures and habitat modifications may simultaneously constrain viable ecological strategies while intensifying competition for limited resources, both of which would drive stronger trait integration. Collectively, our findings point to potential substantial changes in the balance of environmental filtering and competitive interactions shaping Ontario’s lake-fish communities over time.

4.5.4 Spatial structure of temporal shifts in functional structure and taxonomic composition

MEMs, by capturing complex spatial structure, can be a powerful tool to predict variation in biodiversity patterns: Dray et al. (2012) explained 42.9% of the variation in taxonomic composition of plant communities in Panama. However, MEMs can also capture weak spatial patterns or spatial noise. To avoid including those spatially non-significant MEMs, we selected them based on their Moran's *I* across different distance classes (Diniz-Filho et al. 2003). This ensured that MEMs included in the spatial analysis represented meaningful spatial patterns at different scales. To our knowledge, this study is the first one attempting to predict shifts in communities' functional structure with MEMs.

Temporal shifts across the different metrics displayed highly variable spatial autocorrelation patterns. Most correlograms, particularly those for functional dispersion metrics, did not exhibit clear or consistent spatial structures. Moreover, the explanatory (predictive) power of the spatial models based on MEMs varied depending on the metric considered, with broad-scale spatial structures generally accounting for the largest proportion of variation in temporal shifts of both functional structure and taxonomic composition. Together, the correlogram and the spatial models show the complexity of the temporal shifts in the functional structure of fish communities.

The generally weak spatial patterns observed, therefore, suggest that temporal shifts in functional structure and taxonomic composition may be shaped by factors that are not strongly spatially structured, such as stochastic processes or very local environmental or biotic changes that are not well represented by spatial scales. This highlights the importance of integrating non-spatial drivers and context-dependent factors in future analyses. The overall weak spatial patterns suggest that conservation strategies cannot rely solely on spatial prioritisation to predict or manage community changes. Instead, conservation efforts will need to be adaptive and locally informed, accounting for site-specific dynamics and the potential influence of non-spatial drivers such as local habitat conditions, species interactions, and stochastic events.

Broad-scale spatial patterns underlie shifts in functional composition

Although overall spatial patterns in shifts in the first component functional composition were relatively weak, temporal shifts in the second component of functional composition exhibited clearer and interpretable spatial structuring. The temporal changes in the first component in functional composition showed a spatial signature characterised by positive autocorrelation at short distances, negative autocorrelation at intermediate scales, and little to no structure at the broadest spatial scales — a pattern suggestive of patchy, spatially aggregated processes, potentially driven by regional habitat mosaics or local species pools that are not strictly aligned with large-scale environmental gradients (Legendre & Fortin 1989; Diniz-Filho et al. 2003). In contrast, the second axis displayed a more classic – although modest – signature of broad-scale environmental structuring, with positive spatial autocorrelation at short distances that gradually shifted to negative autocorrelation at broader scales (Legendre & Fortin 1989; Diniz-Filho et al. 2003).

The spatial models did not corroborate these findings, with the second axis of functional composition not being explained by any spatial scale. On the other hand, the first axis of functional composition was explained partially with broadscale structure. The first axis of functional composition was characterised in part by thermal preference traits (minimum temperature) and could capture the changes more closely aligned with Ontario’s pervasive climatic gradient. Ontario’s climatic gradient remains one of the most influential drivers of fish community composition in the region (Jackson & Harvey 1989; Loewen et al. 2022), and our results suggest that it continues to shape the trajectory of functional change in these lake-fish communities. By contrast, the spatial pattern of the second component of functional composition likely reflects more complex, spatially heterogeneous processes, such as habitat alteration or landscape-scale management practices that operate independently of broad climatic gradients (Minns & Moore 1995; Loewen et al. 2022).

Shifts in community functional integration: the role of fine-scale structures

The correlograms for the temporal shifts in community functional integration (CFInt) displayed spatial patterns characteristic of large-scale gradients, with positive autocorrelation at short distances transitioning to negative autocorrelation at large scales (Legendre & Fortin 1989; Diniz-Filho et al. 2003). However, our spatial models revealed that these temporal shifts were also partly explained by spatial predictors (MEMs) with negative eigenvalues. Negative eigenvalue MEMs capture patterns of negative autocorrelation, where high and low values in functional space are juxtaposed, often reflecting fine-scale spatial heterogeneity driven by patch dynamics or localised ecological processes (Diniz-Filho et al. 2003; Biswas et al. 2016).

Fine-scale environmental variation has been documented as an important driver of freshwater fish distributions. For instance, Loewen et al. (2022) showed that localized (fine-scale) gradients such as water quality can be more influential for species like brook trout than broad-scale (e.g., climatic) gradients. In addition, fine-scale spatial predictors (MEMs) may also reflect biotic interactions, such as localized competitive dynamics (Biswas et al. 2016). Cazelles et al. (2019), working with the same dataset, found that temporal changes in thermal composition of lakes were more strongly associated with the dispersal of gamefishes than with broad environmental factors like temperature. Both habitat quality and biotic interactions in Ontario’s lakes have likely been altered over time through habitat degradation from pollutants (Reid et al. 2019), as well as through natural and human-assisted dispersal of species such as smallmouth bass (Alofs & Jackson 2015a; Van Zuiden et al. 2016).

4.6 Conclusion

Our study provides a comprehensive, multi-dimensional perspective on the temporal restructuring of lake-fish communities across Ontario. We demonstrate that functional composition, dispersion, and integration exhibit largely independent temporal dynamics, underscoring that no single dimension fully captures the complexity of community change. These dimensions also varied markedly in their spatial structure, with functional composition and community functional integration showing clearer spatial patterns than functional dispersion. Broad-scale environmental gradients, particularly Ontario’s climatic gradient, continue to shape patterns of functional change, while fine-scale processes — including habitat heterogeneity, species introductions, and local environmental changes — play a key role, especially for taxonomic composition and functional integration. The generally weak spatial structure of temporal shifts highlights the influence of non-spatial or highly localised drivers of community change.

Together, our findings emphasize the need for biodiversity monitoring, management, and conservation strategies that are both multi-dimensional and scale explicit. Recognising the distinct and sometimes decoupled dynamics of different components of functional structure will be essential to effectively detect, understand, and respond to biodiversity change in freshwater ecosystems under ongoing environmental pressures.

4.7 Supplementary materials for Chapter 4

Table S 4-1: List of 44 fishes targeted during the AHI sampling effort (bait and sport fishes) and of interest (invasive species). In bold, the 38 species that were kept in the analysis. The other fishes were filtered out of the analysis either because they were absent from both datasets or because not enough data on their functional traits were available.

Common_Name	Scientific_Name	Type of fish
Blackchin Shiner	Notropis_heterodon	Bait fish
Blacknose Shiner	Notropis_heterolepis	Bait fish
Bluegill	**Lepomis_macrochirus**	Sport fish
Bluntnose Minnow	**Pimephales_notatus**	Bait fish
Brook Trout	**Salvelinus_fontinalis**	Sport fish
Brook Stickleback	**Culaea_inconstans**	Bait fish
Brown Bullhead	**Ameiurus_nebulosus**	Bait fish
Burbot	**Lota_lota**	Sport fish
Lake Herring	**Coregonus_artedi**	Bait and Sport
Common Shiner	**Luxilus_cornutus**	Bait fish
Creek Chub	**Semotilus_atromaculatus**	Bait fish
Fathead Minnow	**Pimephales_promelas**	Bait fish
Golden Shiner	**Notemigonus_crysoleucas**	Bait fish
Johnny Darter	**Etheostoma_nigrum**	Bait fish
Lake Trout	**Salvelinus_namaycush**	Sport fish
Lake Whitefish	**Coregonus_clupeaformis**	Sport fish
Largemouth Bass	**Micropterus_salmoides**	Sport fish
Logperch	**Percina_caprodes**	Bait fish
Longnose Dace	**Rhinichthys_cataractae**	Bait fish
Longnose Sucker	**Catostomus_catostomus**	Bait fish
Mimic Shiner	Notropis_volucellus	Bait fish
Mottled Sculpin	**Cottus_bairdii**	Bait fish
Muskellunge	**Esox_masquinongy**	Sport fish
Ninespine Stickleback	**Pungitius_pungitius**	Bait fish
Pearl Dace	**Margariscus_nachtriebi**	Bait fish
Northern Pike	**Esox_lucius**	Sport fish
Northern Redbelly Dace	**Chrosomus_eos**	Bait fish
Pumpkinseed	**Lepomis_gibbosus**	Sport fish
Rainbow Smelt	**Osmerus_mordax**	Bait fish
Rock Bass	**Ambloplites_rupestris**	Sport fish
Sauger	**Sander_canadensis**	Sport fish
Shorthead Redhorse	**Moxostoma_macrolepidotum**	Bait fish
Slimy Sculpin	**Cottus_cognatus**	Bait fish
Smallmouth Bass	**Micropterus_dolomieu**	Sport fish

Spottail Shiner	**Notropis_hudsonius**	Bait fish
Walleye	**Sander_vitreus**	Sport fish
White Sucker	**Catostomus_commersonii**	Bait and Sport
Yellow Perch	**Perca_flavescens**	Sport fish
Common Carp	**Cyprinus_carpio**	Invasive
Goldfish	Carassius_auratus	Invasive
Round Goby	Neogobius_melanostomus	Invasive
Rudd	Scardinius_erythrophthalmus	Invasive
Tubenose Goby	Proterorhinus_semilunaris	Invasive
Tench	Tinca_tinca	Invasive
Ruffe/Eurasian Ruffe	Gymnocephalus_cernua	Invasive
Black Crappie	**Pomoxis_nigromaculatus**	Sport fish
Lake Sturgeon	Acipencer_fulvescens	Protected but has subsistence fishery
Northern Sunfish/Longeared Sunfish	**Lepomis_megalotis**	**Sport fish**
Green Sunfish	**Lepomis_cyanellus**	Sport fish

Table S 4-2: List of functional traits used in the analysis of the functional structure of fish communities. Traits have been extracted from FishBase, and from the Ontario Freshwater Fishes Life History Trait Base (Eakins 2025) for the thermal traits. The values are reported at the species level.

Trait	Unit	Meaning
Aspect Ratio	NA	Caudal height/Caudal fin area
Body Depth	Percentage of Total Length	Height of the body/Length
Eye Diameter	Percentage of Head Length	Eye diameter/Length of the head
Fork Length	Percentage of Total Length	Proportion of length to the fork over total length
Head Length	Percentage of Total Length	
Length	Cm	Common total length
Maximum Temperature	Celsius	Maximum Temperature in the species range
Minimum Temperature	Celsius	Minimum Temperature in the species range
Preanal Length	Percentage of Total Length	Length between the mouth to pre-anal fin/Length
Predorsal Length	Percentage of Total Length	Length between the mouth to the pre-dorsal fin /Length
Preorbital Length	Percentage of Head Length	Length between the mouth to eye /Length
Prepelvic Length	Percentage of Total Length	Length between the mouth to pre-pelvic fin/Length
Standard Length	Percentage of Total Length	Length to the tail
Temperature Interval	Celsius	Minimum Temperature – Maximum Temperature

Table S 4-3: Results of the paired t-test to compare the values of different metrics of functional structure and taxonomic composition between the contemporary and historical states of the communities. The null hypothesis is that the difference between contemporary and historical is equal to 0: that there is no change on average between contemporary and historical communities.

Dimension	**Metric**	**Mean**	**t-value**	**p-value**
Taxonomic composition	TaxoComp1.Diff	1. 67	22.617	<2.2e-16
	TaxoComp2.Diff	-0.13	-1. 7408	0. 08227
Functional composition	FunctComp1.Diff	1. 90	16.209	<2.2e-16
	FunctComp2.Diff	0.48	5.6673	2.309e-08
Functional dispersion	SES.All.Diff	-0.20	-6.2679	7.242 e-10
	SES.Diet.Diff	-0.12	-3.4776	0.0005447
	SES.Locomotion.Diff	-0.05	-1.4344	0. 152
	SES.TP.Diff	-0.39	-12.165	<2.2e-16
CFInt	CFInt.Diff	0.74	7.854	2.034 e-14

Figure S 4-1 Analytical framework to compute Community Functional Integration in two steps: 1/ calculate the average absolute correlation for each community. 2/ compute null trait matrices to estimate the average absolute correlation of the community in a scenario where traits are not associated with one another. The last step is to calculate the SES of the average absolute correlation.

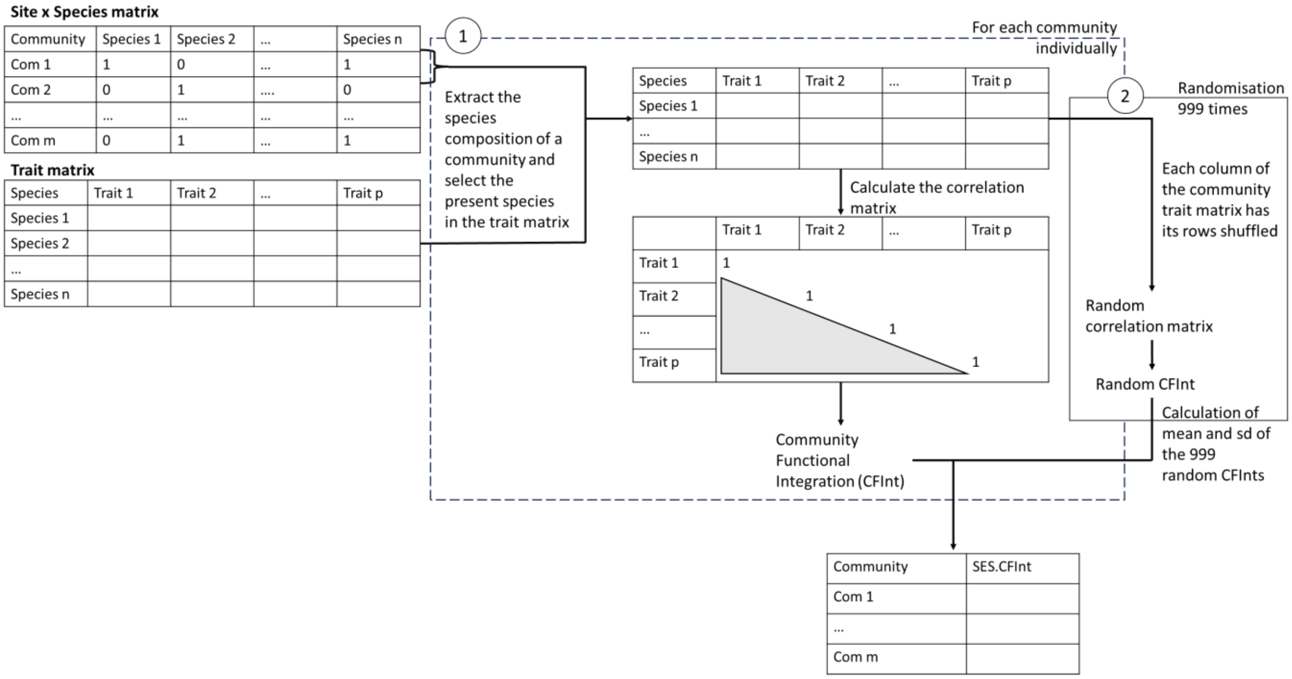


Figure S 4-2: Results of the PLS-DA on the taxonomic composition. We calculated changes taxonomic composition across communities with Jaccard’s similarity and computed a PCoA to summarise the distance matrix. The first three PCoA axis were extracted to calculate the PLS-DA that maximises the differences between historical and contemporary communities.

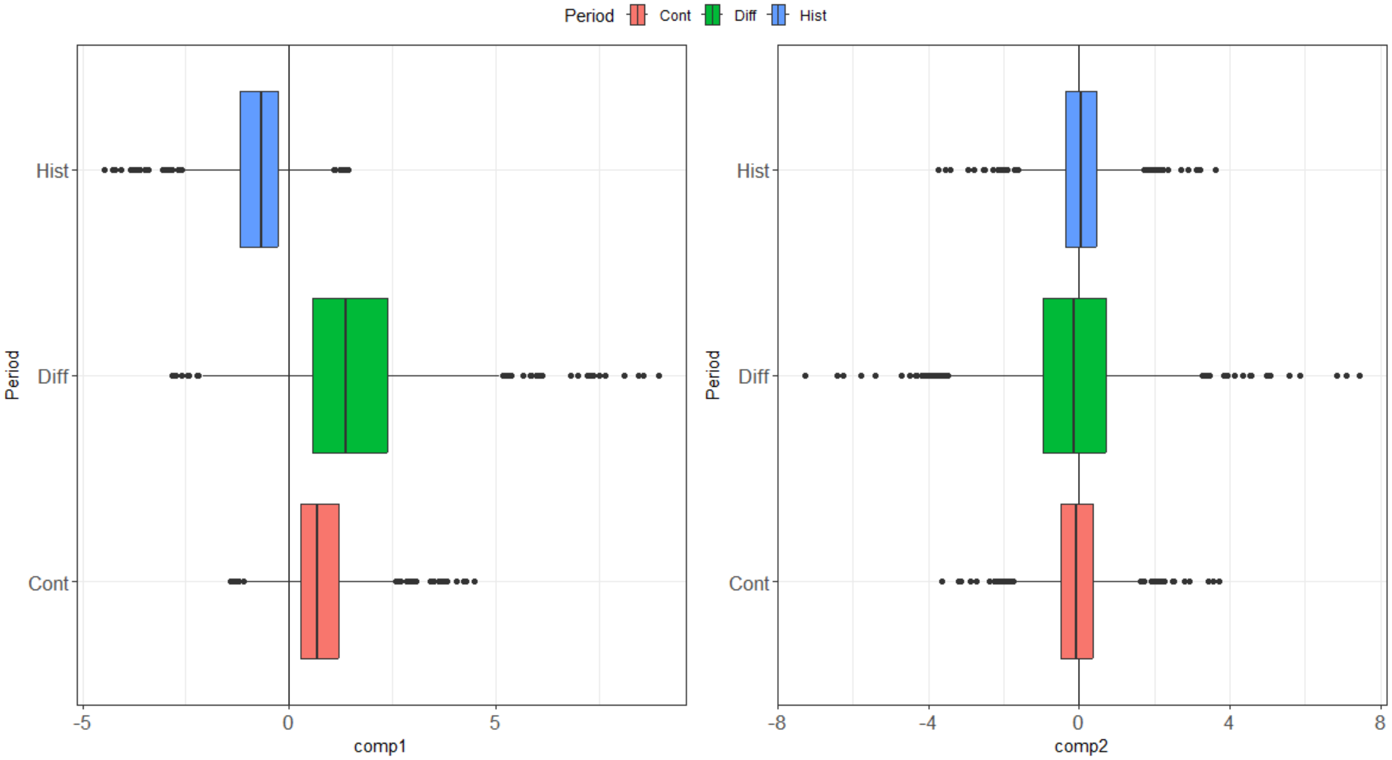
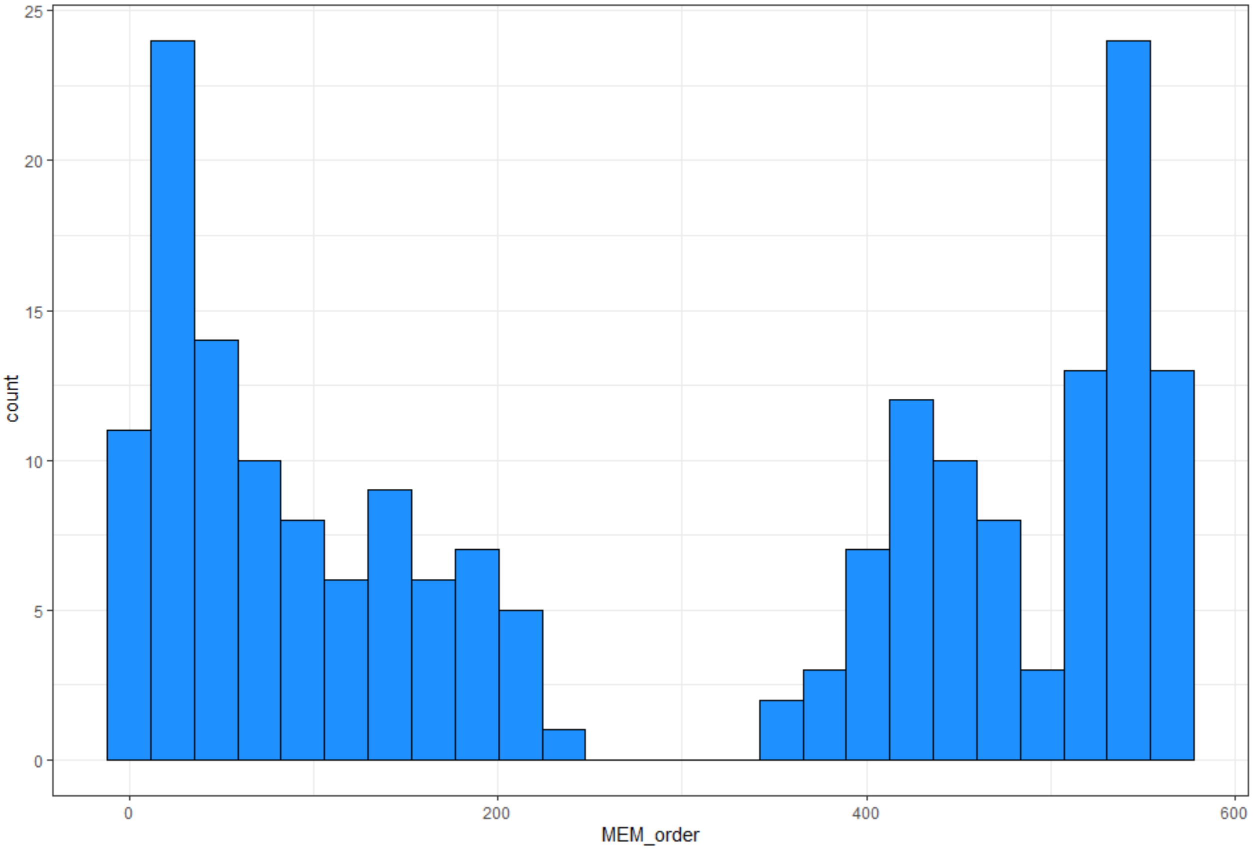


Figure S 4-3: 197 MEMs which have a Moran's *I* above 0.05 for at least one distance among 20 distances. On the x-axis, the order of the selected MEM put in bins, and on the y-axis the number of MEM filtered within each bin. The MEMs' orders are binned in an interval of 25 (for instance, the first bin counts how many MEMs from MEM1 to MEM25 have been selected)



5 GENERAL CONCLUSION

5.1 Concluding remarks

The main goals of the thesis were to challenge parts of the current functional ecology framework for the study of community assembly mechanisms and to improve the predictive power of the models, by reframing the current framework or by including new concepts. We achieved this using Ontario's lake-fish communities as a case study. Chapter 2 and 3 explored some conceptual blind spots of the analytical framework used in functional ecology, by developing novel ways to think about common problems or by introducing new concepts within community functional ecology. The fourth chapter was a direct application of the different concepts developed in the previous chapters to answer to conservation problems.

5.1.1 What trait to choose for community functional ecology?

Chapter 2 focused on the choice of traits used in the analysis of trait dispersion patterns to infer assembly mechanisms. Far from the purely methodological approach often used to answer such question (e.g. Mouillot et al. 2021), we proposed a conceptual framework in which the selection of traits is based on a-priori knowledge of the function of the traits or on the dispersion patterns those traits show in the communities (*a posteriori* selection). We highlighted that even though combining traits could be necessary to observe specific dispersion patterns, pooling traits without careful considerations would simply blur any signal of under or over-dispersion and therefore limit our capacity to infer assembly mechanisms, and the predictive power of environmental models.

The results of Chapter 2 were echoed in Chapter 4 where we used the *a priori* categorisation of the traits to understand the temporal changes in the functional structure of fish communities. In Chapter 4, we demonstrated that the different sets of traits showed different temporal shifts: we only detected significant average temporal changes for diet traits. Pooling all the traits together obscures important change in the diet traits and therefore our ability to detect changes of assembly mechanisms over time. Additionally, we demonstrated that even though the temporals shifts were not very pronounced on average, we could detect some latitudinal patterns: echoing results of Chapter 2, that even though patterns of functional dispersion may not be very strong, we could still observe some distinctive patterns.

Overall, our work challenges the frequent practice in functional ecology consisting in pooling many traits together, without proper consideration about the role specific traits play in the assembly of communities. We proposed two frameworks to categorise traits; one based on *a priori* knowledge and one on the optimisation of pattern observation. Both methods allow scientists to move forward by either improving their hypotheses (with *a priori* categorisation) or the predictive power of their model (with the algorithm-based categorisation).

5.1.2 Community Functional Integration: what trait-trait correlation can tell about community's structure?

Chapter 3 explored a dimension of the functional structure that is often overlooked in the study of communities outside plant ecology: the trait-trait correlation patterns. To achieve this, we developed the definition of community functional integration (CFInt) and an analytical framework to describe variations of community functional integration. We then used two empirical examples to demonstrate the usefulness of such concept in the analysis of communities. We showed that correlations patterns were structured across the landscape; with Southern communities displaying specific pattern in their trait-trait correlation structure compared to the most Northern communities. The second example showed that community functional integration’s variations were strongly associated with environmental gradient (e.g. temperature) and with patterns of species richness. Those results showed that including community functional integration into the study of communities revealed interesting patterns that could potentially improve our capacity to predict local biodiversity.

The concept of community functional integration was also used in Chapter 4 where we described the temporal shifts of many functional indices in lake-fish communities. Chapter 4 can be used as a third empirical study to demonstrate the usefulness of including community functional integration in the analysis of community: community functional integration had the most pronounced temporal shifts among all the dimensions studied in Chapter 4. Temporal shifts in community functional integration were also the easiest to predict with spatial patterns, with broadscale spatial patterns (reflecting large-scale environmental gradients) explaining most of the variations. As such, we further demonstrated that community functional integration could be a product of environmental conditions.

Overall, we demonstrated that trait correlations patterns are not static both across the landscape (from one community to another) and in time. Even though more work is necessary to unveil the theoretical interpretations of such patterns, the results of

Chapter 3 and 4 underscored the relevance of community functional integration as a meaningful concept to describe communities’ variations across space and time.

5.2 Limitations in the data available

5.2.1 Limitation of the trait data

An important limitation of the trait-based approach of biodiversity is the available data for traits, that led us to make important assumptions. As is common in functional ecology, the data we used in this analysis are data available in databases (e.g. Ontario Freshwater Fish Life History Trait Base (Eakins 2025), FishBase (Froese & Pauly 2025), Temperature Relationships of Great Lakes Fishes: A Data Compilation (Wismer & Christie 1987)).

Thus, we considered that traits aggregated at the species level were representative of our system, and that intraspecific variation of a trait was negligeable compared to the interspecific variation of the same trait. In addition to the intraspecific variation of traits that can be relevant to better understand the functioning of communities, other studies highlight the importance of taking into consideration differences of traits from different life stages (Nakazawa 2015; Ramachandran et al. 2023): a notorious ontogenic shift in fish species is the shift in diet and trophic position. In our study, and as is usual in functional ecology, we only considered adult traits, and thus we may have overlooked important environmental filters that only apply to the other life stages. A way forward would be to collect robust trait data across different ontogenic stages and conduct the same analysis.

Another important limitation from our work comes from the availability of trait data. We gathered complete trait data for 68 out of 87 species present in the dataset (5 species were missing locomotion data and 14 were missing temperature data). Usually, incomplete data are handled through the Gower distance (Gower 1971): the pairwise functional distances among species are only calculated based on available data present for each pair. Our analytical design does not allow for such a method to be applied, thus we decided to consider only species with full trait coverage as is common in functional ecology (Májeková et al. 2016; Côte et al. 2019; Scherer et al. 2023). Our metrics are necessarily impacted by such choice, with 245 communities being effectively truncated (of 1 to 3 species). However Májeková et al. (2016) showed that not all functional metrics presented the same sensitivity to such truncation, and Rao’s entropy, which Hill numbers are closely related to (Chiu & Chao 2014), is the least sensitive among functional diversity metrics. And even though results from data deletion and data imputation methods were different, Scherer et al. (2023) showed that they still had the same directionality: we could still capture some of the signal with omitting the incomplete data.

To improve the trait coverage, imputation can be a way forward: the idea is to estimate missing values based on closely related species (e.g. Kuczynski et al. 2018; Cooke et al. 2019; Scherer et al. 2023). However, imputation can only be effective when missing data are random; in our case, many species with missing data were from the same families. For instance, 5 species of Redhorses (*Moxostoma sp.*) are present in our dataset, only 2 have thermal traits. Similarly, 8 species of shiners (*Notropis sp.*) were present, and only 4 had complete trait data. Moreover, some scientists have warned not to use one species to approximate the thermal preference of another (example for two shiners: Reemeyer et al. 2024).

5.2.2 Limitations of the sampling protocol

Our analysis was also constrained by the sampling protocol: the Ontario Ministry of Natural Resources sampled fish communities using different multi-mesh gillnets (benthic gillnets with a mesh > 20cm for large fishes and a standard multi-mesh gillnet for smaller fishes) (Lester et al. 2020). Gillnets are known to bias sampling based on the size of the fishes: bigger fishes tend to be capture more than smaller fish, even from the same species (Prchalová et al. 2009). Gillnets, as a passive sampling gear, are also highly sensitive to the “probability of encounter”, the probability a fish swims into the net (Portt et al. 2006). Some families, such as percids, seemed to be over-sampled by gillnets compared to other sampling gears (Prchalová et al. 2008; Jurvelius et al. 2011). In general, larger fishes are likely to be better represented in our dataset compared to smaller species such as shiners and minnows.

Those sampling biases are especially important in the historical dataset used in Chapter 4. To account for those sampling biases, and as was done in previous studies, we ran our analysis on truncated communities: our final species list was made of 38 species instead of 87 species present in the contemporary dataset. Therefore, for Chapter 4, conclusions are done on incomplete community data.

5.3 Potential avenues for future work

5.3.1 Defining fish communities: between operational and oversimplification

Throughout the whole thesis, I made few important assumptions or simplifications about our systems, that may prevent deeper understanding of their functioning. The most important one is how we defined communities. As presented in the General Introduction (section *1.5.1*), properly defining the boundaries of a community is not straightforward. I chose to respond to this problem with a very operational approach, and to use the geographic limits of lakes as the communities' boundaries: one lake equals one community.

Assuming that the limits of a community are not bigger than the one of the lakes is sound: natural dispersal is rather limited between lakes (Olden et al. 2001), so environmental requirements and all biotic interactions should be accounted for, by using the lake's limits to define the fish communities. However, it is possible that one lake is home of several communities; indeed, some lakes can be big enough that individuals from one part of it will not interact with individuals living in another part. For instance, in the lake Erie (Canada), Sinclair et al. (2021) have explicitly defined multiple communities based on their geographical location, to better understand the dynamic of each sub-community. Even though, our dataset did not include the Great Lakes, for which such refinement of the definition of communities would be necessary, we can not exclude that some of the bigger and deeper lakes actually contain several communities and considering them as one may have blurred some signals of assembly mechanisms.

Another way our definition of community may be limiting is that fish communities tend to be multi-trophic; therefore, fishes from the same lake are not part of the same trophic guild (e.g. planktivorous vs predators). Therefore, they may not directly compete with one another, and thus, pooling species exploiting different resources may blur some signal of competitive interactions. Moreover, the biotic interactions within the community is not limited to competitive interactions but also comprised predation. Seibold et al. (2018) advocates for explicit multi-trophic communities, in order to better understand the dynamics of communities and highlight the importance of trophic interactions over competitive interactions. Some studies have defined multi-trophic communities for this purpose, however it is often done across taxa (e.g. zooplankton with fish) rather than within a taxa *per se* (e.g. Pecuchet et al. 2020). By defining sub-communities within fish communities by the individuals' trophic level or by the species' guild, signal of competitive interactions may be easier to detect since it will not be diluted by the signals of competition from the other trophic levels. Dividing the current communities into trophic sub-communities may also able us to explicitly take into consideration the predation pressure by including the abundance or biomass of predators in the variables determining the variations of trait dispersion patterns of prey sub-communities for instance.

Overall, the definition of the community used in this thesis was practical, but some refinement around it may allow for more precise hypotheses, more nuanced interpretations of the observed patterns, and better predictions from the models.

5.3.2 Scale: Which mechanism are we able to detect?

A second limitation of the work is the scale at which the patterns were studied. The patterns of functional diversity and their interpretation are scale dependent, and the question of the scale is even more relevant when using null models and species pools (Weiher & Keddy 1995; Lessard et al. 2015). Species pools defined at finer scale are expected to be less diverse and therefore using them may reveal more easily patterns of competitive interactions. While species pools defined at large scale will highlight the role of environmental filtering on the assemblage of local communities.

For chapter 2, the question of the scale was fully accounted for and results showed similar patterns than previous studies: the larger the species pool was, the harder it was to detect over-dispersion. In fact, the species pools defined at the Primary Watershed seemed to be a good compromise to detect both signal of environmental filtering and competitive interactions. For species pools defined at Secondary Watershed scale, under-dispersion was not much detected and for the Province species pool, over-dispersion was hardly observed.

Such sensitivity analysis was not conducted for Chapter 3 and 4. For the calculation of community functional integration, there was no species pool, or more precisely each community was its own species pool, therefore the question of the scale of species pool is not necessarily relevant for this metric. Contrasting the results of community functional integration found at the local scale and regional scale may reveal if communities follow the same functional integration as regional or global species pool and what discrepancies among the different scales may tell us about the constraints within which communities are assembled. Indeed, Messier et al. (2017) states that environmental filtering is the main process shaping trait correlations at local level, while biophysical laws are more likely to play a role at any scale. Trait correlations do not automatically scale down (from global to local) or scale up (from local to global), and by contrasting functional integration across scales, we may be able to disentangle how much of the local integration is constrained. Studying functional integration across scales and understanding the discrepancies across scales may help better understand how biodiversity is shaped and assembled.

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