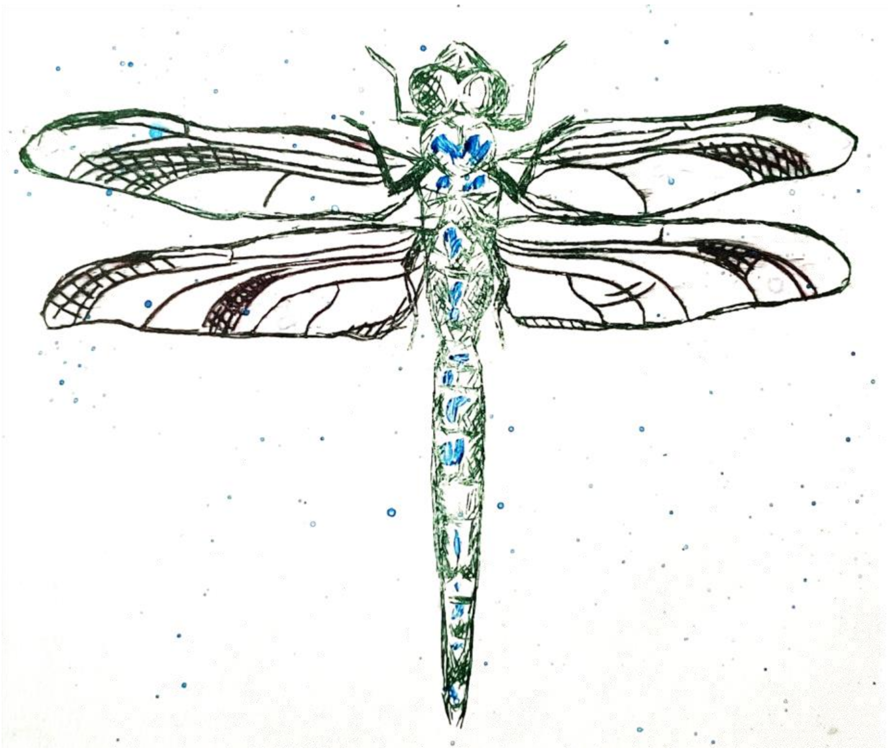
Effects of land use on the resilience of stream invertebrates to climate change



A thesis submitted for the degree of *Doctor of Philosophy*

by

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May 2023

Summary

Climate change and land use are recognised as primary drivers of global biodiversity decline, and pose a significant threat to freshwater ecosystems. The ecological, economic, and aesthetic importance of freshwaters necessitate urgent action to enhance their resilience to accelerating environmental change. Riparian broadleaf woodlands have been increasingly promoted for this purpose, but evidence demonstrating their effectiveness is scarce.

Using a 40-year macroinvertebrate dataset from 16 headwater streams in upland Wales, UK, this thesis aims to address the hypothesis that broadleaf woodlands enhance stream ecosystem resilience to climate change. Specifically, long-term community trends and multiple facets of ecological stability were assessed relative to water temperatures and discharge, water chemistry (acid *versus* circumneutral) and contrasting catchment character typical of upland management (sheep-grazed moorland, conifer plantations, and semi-natural broadleaf woodlands).

Since the start of monitoring (1981), progressive structural and functional changes have occurred in these streams, with indications that detritivores were among the taxa underlying these trends. While enhanced resilience of population- and community-level properties in broadleaf streams was evident, it was also apparent that changes were far-reaching. Extreme conditions including high temperatures and complex effects of dry weather were commonly associated with community change, but a large amount of unexplained variation remained. Particularly deleterious effects of conifer forestry were highlighted, in addition to vulnerabilities of rare taxa.

Despite the underlying complexities of stream communities and their dynamics, stream type remained the best predictor of taxonomic and functional diversity. Thus, coupled with their widely acknowledged benefits for biodiversity and stressor regulation, riparian broadleaves remain favoured candidates for climate adaptation. However, interventions may be required at broader scales than just riparian zones.

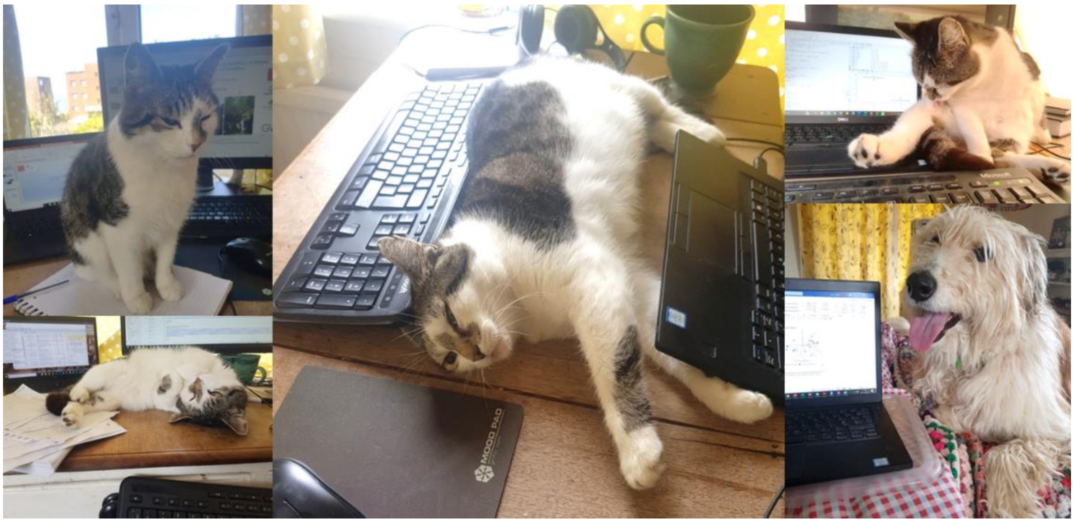
Overall, this research provides sought-after evidence of climate and catchment character effects that enhances our understanding of ecological resilience, with important implications for river management in the face of global environmental change.

Acknowledgements

My first and foremost thanks go to Dr. Ian Vaughan for his supervision, and his unwavering optimism and encouragement. Without him, I would not have had this opportunity nor the depth of knowledge I now possess – especially for R! I am forever grateful. Thanks also to Prof. Steve Ormerod for the supervision, freshwater expertise, and for his lifelong commitment to the ecological monitoring that was the foundation of this research. And to the rest of my supervisory team, Prof. Jane Memmott, Prof. Bill Symondson, and Dr. Tom Nisbit, your support and kindness will always be remembered. I am incredibly grateful to my funders, UKRI NERC and the GW4 FRESH CDT, and particularly to Prof. Isabelle Durance. Through this experience, I have gained invaluable skills, connections, and friends.

I would also like to thank my family and friends who have been my biggest support, and who underpin my resilience in unstable times. To my brother, Michael, thanks for your undying belief in me and your over-dedication to teaching me maths. To Richard, thanks for introducing me to the world of social sciences and Critical Animal Studies, and embracing my love for tiny creatures. To James, who kept me tanked up on coffee and biscuits, and gave me a safe home in which to write, I cannot express how appreciative I am. And to my parents, Kate Dunbar, and Brendan Joyce; thank you for teaching me what it means to respect and nurture life on this planet, in all of its complexity. To my mum especially (my ultimate role model), thank you for proofreading this entire thesis, or as you put it, being 'bludgeoned' by science. And to Dad, you always wanted me to become a 'doctor'… so I dedicate this to you.

My final thanks go to Archie and Jack; the brains (and the beauty) behind it all…



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"… there was abundance of wood in the mountains. Of this … the traces still remain … the land reaped the benefit of the annual rainfall, not as now losing the water which flows off the bare earth into the sea, but, having an abundant supply in all places, … it let off into the hollows the streams which it absorbed from the heights, providing everywhere abundant fountains and rivers, of which there may still be observed sacred memorials in places where fountains once existed".

Plato, 360 BCE (Taylor 1929)

Chapter 1: General Introduction

1.1 Overview

Human activities have exerted a profound impact on ecosystems worldwide, spanning freshwater, marine, and terrestrial environments. Even the most remote and seemingly untouched areas, such as the polar regions, have not been spared from human influence (e.g., Mishra, Singh and Mishra, 2021). The extensive development and exploitation of nature over the past centuries have reached a magnitude where some propose the recognition of a new geological epoch, the Anthropocene, in which humans are the primary drivers of global change (Crutzen 2002; Lewis and Maslin 2015). The global environmental transformations anticipated in the coming decades pose significant threats to the stability of socio-ecological systems, biodiversity, and the well-being of billions of people (Costello et al. 2009; IPBES 2019; IPCC 2021). Thus, the conservation or enhancement of ecological resilience in ecosystems—their capacity to maintain their current state in the face of disturbances (Holling 1973)— is a pressing, and perhaps the greatest challenge in human history.

As arguably amongst the most important, sensitive, and threatened of all ecosystems, freshwaters are a central priority in this challenge (Dudgeon et al. 2006; Scheffer et al. 2015; Gleick 2018; Reid et al. 2018). With the exclusion of large ice sheets, freshwater habitats cover less than 10% of land surface area and just 0.8% of the whole surface of Earth (Gleick 1996; Lehner and Döll 2004). Despite their small extent, these habitats contain disproportionately high biodiversity, supporting around 9.5% of all described animal species (Balian et al. 2008). Specifically, macroinvertebrates, which include Arthropods (exoskeletal animals such as insects and arachnids), Annelids (including leeches and other segmented worms), Molluscs (gastropods and bivalves) and Platyhelminthes (flatworms), comprise 85% of all animal species described for freshwaters (Balian et al. 2008). As the dominant animal group, they are responsible for many major ecological functions (Wilson 1987), including processing, storage, and transfer of large quantities of carbon and nutrients, filtering water, and providing food for many other organisms both in and out of the freshwater habitat (Cummins and Klug 1979; Vannote et al. 1980; Burdon and Harding 2007; Bartels et al. 2012; Battin et al. 2023).

Moreover, macroinvertebrates are effective bioindicators, given their ubiquitous nature, diversity, and range of sensitivities (Hodkinson and Jackson 2005; Bonada et al. 2006).

Concerns over climate change and its impacts on freshwater ecosystems have been recognised for decades (Gleick 1989). Yet, unprecedented warming in recent years alongside reports of global biodiversity declines have sparked new interest (WWF 2020; IPCC 2021). Already subject to an array of anthropogenic stressors, including pollution, abstraction, channel modification, fishing, and invasive species, climate change is considered a leading threat to freshwater ecosystems, alongside land use (Reid et al. 2018). However, owing to these multiple threats, assessing the specific effects of climate change remains a challenge, and responses are likely to be complex, unpredictable, and interacting (Ormerod et al. 2010; Jackson et al. 2016; Birk et al. 2020). Response to climate can depend on the type of disturbance (pulse or press) (Ratajczak et al. 2017; Harris et al. 2018; Inamine et al. 2022), features of the habitat (heterogeneity, connectivity, and resource dynamics) (Mantyka-Pringle et al. 2014; Van Looy et al. 2019; Murdoch et al. 2020), and the level of biological organisation (community versus population, taxa versus functional traits) (Hillebrand and Kunze 2020). Moreover, despite rapid rates of decline seen for freshwater vertebrate populations, long-term dynamics of freshwater macroinvertebrates are highly varied (Vaughan and Ormerod 2012; Jourdan et al. 2018; Baranov et al. 2020; van Klink et al. 2020; Outhwaite et al. 2020).

In recent years, a range of management strategies have been suggested to adapt rivers for climate change. These include catchment and riparian land use, and restoring water quality (Gerber et al. 2013; Scheffer et al. 2015; Ellison et al. 2017; Griscom et al. 2017; IPCC 2022). For example, riparian broadleaf trees have been widely promoted for their ability to reduce temperatures, regulate flow, and potentially support aspects of ecological resilience (Palmer et al. 2008; Ormerod 2009; Broadmeadow et al. 2011; Thomas et al. 2016). Management strategies that improve water quality and support biodiversity, for example, could offset some of the effects of warming and enhance resilience (Vaughan and Gotelli 2019; Tracy et al. 2022). However, there remains considerable uncertainty over the available options and their efficacy, largely due to a poor understanding of resilience and its mechanisms, and a lack of empirical evidence based on tangible measures rather than proxies (Pimm et al. 2019; Prober et al. 2019).

Considering these issues, this thesis investigates the effects of climate change and land use on stream macroinvertebrate resilience, as both long-term change and ecological stability. Stability is applied an umbrella term encompassing multiple measures that together describe ecosystem dynamics, allowing a more detailed understanding of response and recovery in relation to disturbance (Donohue et al. 2013). In this study, a 40-year dataset from upland headwater streams in mid-Wales was used. Such long-term data sets are rare but allow vital insights into long-term trends and dynamics across a range of temporal scales (Jackson and Füreder 2006).

The upland location used for this research provided key insights into the impacts of climate change unobscured by downstream intensive agricultural and urban pressures (Ormerod et al. 2010). Nevertheless, the Welsh uplands have a long history of human activity, and have experienced various processes, including acid deposition (Weatherley and Ormerod 1987; Donald and Gee 1992), and alterations driven primarily by intensive sheep farming and coniferous forestry (Simmons 2003; Holden et al. 2007). Small areas of semi-natural broadleaf woodland remain, allowing its assessment as a management strategy in contrast with the prevailing management for timber and sheep. The results of this study contribute to sought-after evidence required to guide policy and management strategies to maintain the long-term ecological resilience of freshwaters, and contribute to a collective effort to ensure a global safe operating space for humanity (Rockström et al. 2009).

1.2 Research objectives

The overall aim of this study was to determine how catchment land use and climate affect the long-term trends and ecological stability of stream macroinvertebrate communities, and in particular whether broadleaf woodland enhances resilience in response to climate variability. To address this, individual objectives of this research (contextualised in Figure 1.1) were to determine:

1) The long-term trends in stream community structure and function and their relationship with climate change and land use.
2) The effects of climate and land use on the ecological stability of communities.
3) The species-specific versus environmental factors that influence the stability of populations, and how their dynamics relate to community stability.

Chapter 2 establishes the contextual framework for this project, beginning with an overview of ecological resilience concepts and their relevance in scientific research and policy. It proceeds with a thorough review that explores the connection between broadleaf woodlands and the resilience of stream ecosystems. This review encompasses the interrelationships between the riparian zone, the broader catchment area, and their impacts on the biotic and abiotic characteristics of streams. Additionally, it investigates the influence of climate change on these ecosystems, as well as the potential of broadleaf trees in mitigating climate-related effects and promoting resilience. Furthermore, this chapter establishes the specific terms and definitions that are employed throughout the thesis and identifies research gaps that warrant further investigation.

Chapter 3 focuses on analysing long-term trends in stream macroinvertebrate community structure and function. The study employs nonlinear statistical methods to model changes over time, and the connections between biodiversity and in-stream temperature and flow conditions, which are directly influenced by climate factors. By examining these relationships, the research estimates the impact of land use and climate change on patterns of long-term biodiversity change and considers the implications for future climatic trends.

In Chapter 4, a novel multidimensional approach is employed to assess the ecological stability of upland stream communities across different stream types. This comprehensive assessment includes multiple components, such as resistance, engineering resilience, temporal variability, food web robustness, and persistence, considering both taxonomic and functional attributes. The unique aspect of this study lies in the simultaneous evaluation of these components, which is a rare practice in the field. Furthermore, nonlinear modelling techniques are used to assess relationships between key components of ecological stability and climate, and changes over time.

Chapter 5 focuses on the assessment ecological stability at population-level within each stream community. Similar to Chapter 4, multiple components of stability were calculated. Mixed-effect models were employed to examine the influence of various taxon characteristics, including rarity, resistance and resilience traits, and functional feeding guild, compared with the environment, i.e., stream type. Subsequently, the chapter explores the relationships between diversity, population stability, and community stability, with a particular emphasis on exploring asynchrony as a potential mechanism underlying patterns at the community-level.

The final discussion, Chapter 6, integrates and contextualises the insights from all chapters to address the overall hypothesis that broadleaf woodland increases the resilience of stream invertebrates to climate change compared to other land use types. This chapter considers the implications of the research findings, limitations, and potential routes for further research. Together, these analyses seek to enhance our understanding of ecological resilience in upland streams, and provides valuable insights for policy and conservation in the face of climate change.

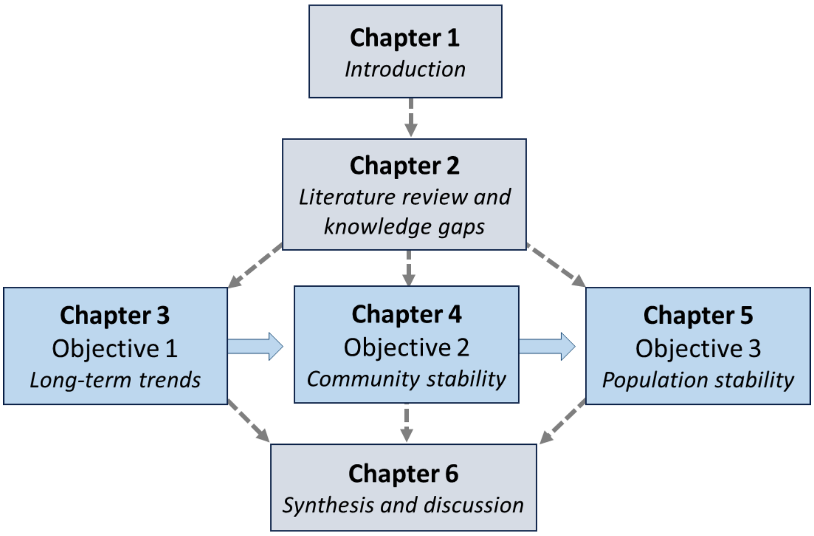


Figure 1.1 *Flowchart of thesis chapters. Dashed arrows represent development of thesis structure and flow of information towards final discussion. Boxes and arrows in blue highlight chapters addressing main research objectives and their sequence (low to high resolution of communities and their dynamics).*

1.3 Study area and sampling

Sixteen perennial headwater streams surrounding the Llyn Brianne reservoir in the Cambrian mountains of mid-Wales, UK (52°8′N 3°45′W) were used for this research (Figure 1.2). These streams, all of second and third order, cover a catchment area of around 300 km^2 that drains into the Afon Tywi, the longest river in Wales. At around 35 km inland and 215-410 m above sea level, regional climate is maritime and temperate, with mean daily stream temperatures rarely outside 0-20°C, and a mean annual rainfall of around 1900 mm (Weatherley and Ormerod 1990; Durance and Ormerod 2007). The underlying geology comprises Ordovician and Silurian shales, mudstones and grits that are base-poor, while soils are a mixture of brown podzolic, stagnopodzols and peats with low buffering capacity. Surface runoff is therefore soft (mean total hardness 4-20 mg CaCO3 L^{-1}) and generally acidic (mean pH 4·8-6·9).

Stream sub-catchments range from 15-264 ha, which are mainly dominated by sheep-grazed acid grassland or conifer plantation, though some semi-natural deciduous woodland remains. Moorlands consist mostly of grass (*Molinia caerulea*) and bracken (*Pteridium* sp.), while conifer plantations, extensively planted in the 1950s and 60s and which undergo periodic clear-felling, comprise densely packed non-native conifers, Sitka spruce (*Picea sitchensis* Carriere) and lodgepole pine (*Pinus contorta* Douglas). Conifer plantations have notorious issues with acidity due to heavy metal accumulation, and interception of atmospheric pollutants by needles (Ulrich 1983). Deciduous woodlands in the uplands are a mix of oak (*Quercus*), birch (*Betula*), hazel (*Corylus*), rowan (*Sorbus*), and ash (*Fraxinus*) (Rutt et al. 1989).

Within streams, substrates range from gravel (2-16 mm) to bedrock, with aquatic plants *Juncus* spp and *Sphagnum* spp, and bryophytes present (Rutt et al. 1989; Weatherley and Ormerod 1990). Streams also support a mixture of epilithic diatoms and algae (Round 1991; Winterbourn et al. 1992). Overall, macroinvertebrate community composition varied considerably over an acid gradient, from species-rich communities of mayflies (Ephemeroptera), caddisflies (Trichoptera), and stoneflies (Plecoptera) in circumneutral streams, to species-poor communities dominated by acid-tolerant taxa, including Plecoptera (Weatherley and Ormerod 1987).

In this study, streams were characterised by acid-base and land use types, forming four stream types. These were seven acid moorland streams (AM: CI1, CI2, CI3, CI4, CI5, CI6, and LI5), two circumneutral moorland streams that were buffered by small calcite veins (CM: LI6 and LI7, pH >6.9), five acid conifer streams (AC: LI1, LI2, LI3, LI4, and LI8), and two semi-natural broadleaf woodland sites (GI1 and GI2) (Figure 1.2). Over the course of sampling, land use remained relatively stable, though in 1987-8, three streams (LI4, CI2 and CI5) were artificially limed. However, no lasting effects were seen, and both AM and AC streams continue to be chronically or episodically acidic, a legacy from the industrial revolution and poor management (Rutt et al. 1989; Donald and Gee 1992; Bradley and Ormerod 2002b).

Each spring (typically April or May) since 1981, benthic macroinvertebrates have been sampled using a quality-assured, standardised three-minute kick-sample (two minutes within the riffle and one-minute at the stream margin) with a 0.9mm mesh hand net (230 mm x 255 mm) (Bradley and Ormerod 2002a) - noting that the number of streams sampled each year reflected access difficulties and resource availability (Figure 1.3). Animals were preserved and identified to the lowest taxonomic level possible each year, and standardised across years by pooling taxa to the minimum taxonomic resolution in any given year (see Durance and Ormerod, 2007). For the purposes of this study, data were further pooled to genus-level or higher (e.g., family) for comparability to ecological trait data, specific details of which are given in each chapter.

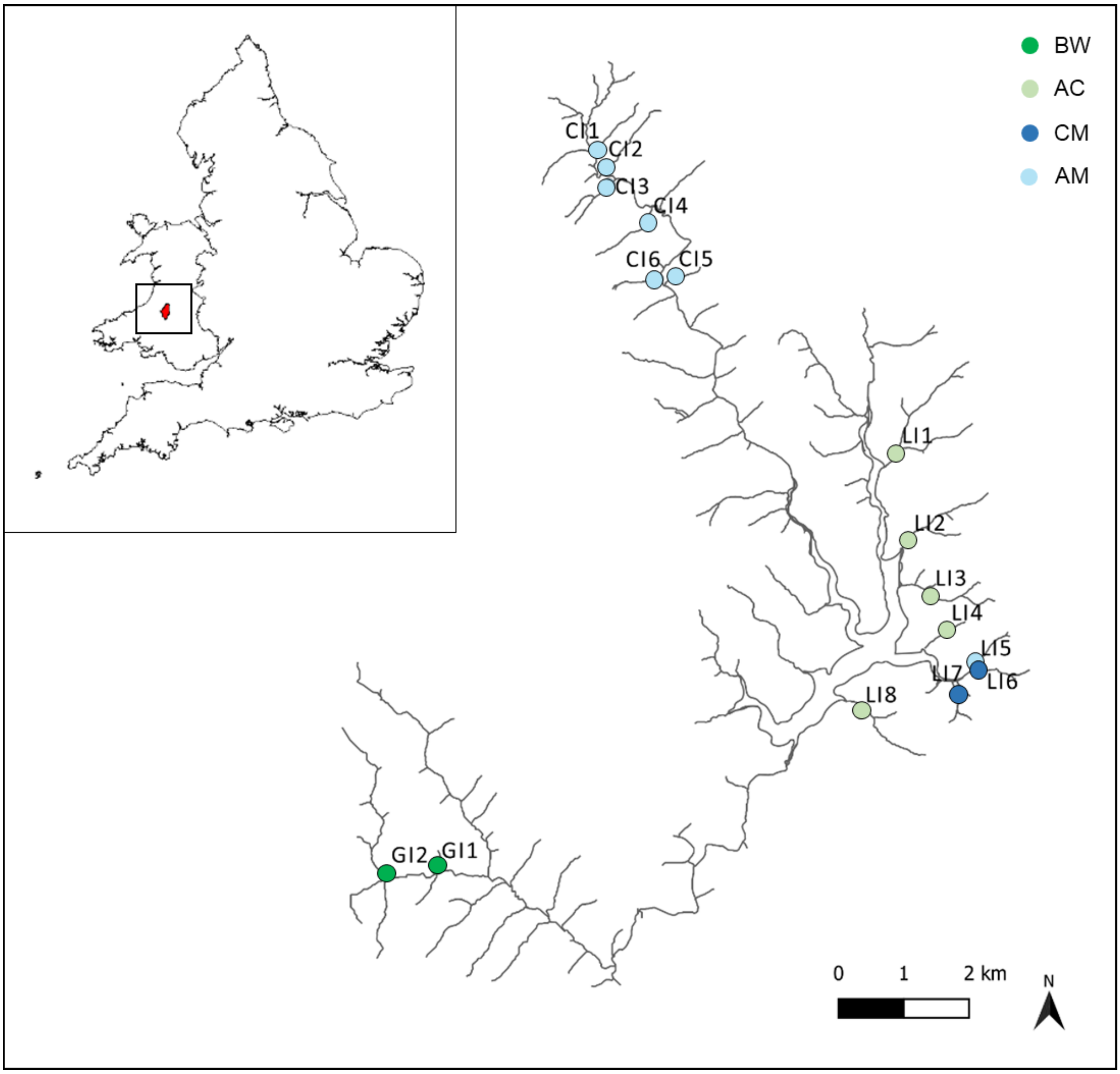


Figure 1.2 *The location of streams within the Llyn Brianne stream observatory in upland Wales, UK. BW = Broadleaf woodland, AC = Acid conifer, CM = Circumneutral moorland, AM = Acid moorland. Map contains EDINA Digimap Ordinance Survey geospatial data.*

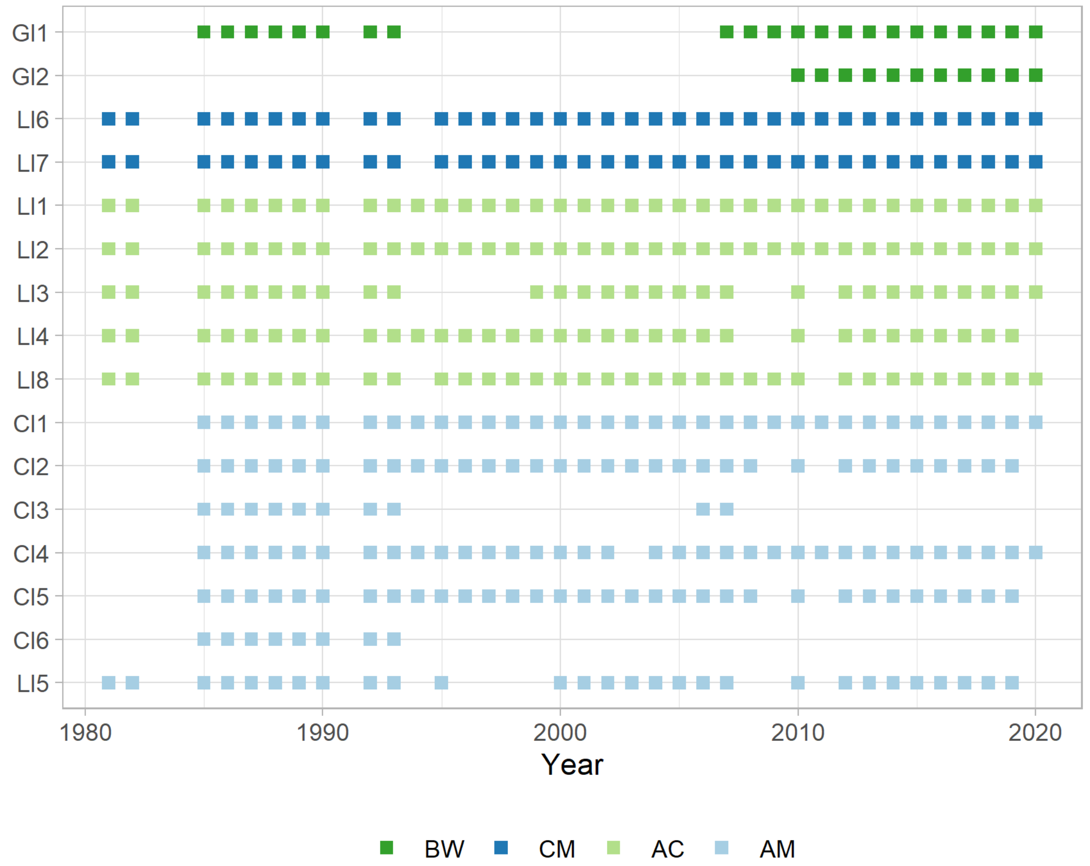


Figure 1.3 *Macroinvertebrate sampling history for each stream. Points represent years that samples were collected each spring, between the first (1981) and most recent (2020) year. BW = Broadleaf woodland, AC = Acid conifer, CM = Circumneutral moorland, AM = Acid moorland.*

Chapter 2: Literature Review: The role of riparian broadleaf woodland in river ecosystem resilience to climate change

2.1 Introduction

Nature demonstrates remarkable capacities for resilience in spite of adversity. From natural to anthropogenic disasters such as flooding or volcano eruptions, or hunting species to near-extinction, life can recover if the opportunity allows (Mlot et al. 2011; Ripple et al. 2014; Wagner 2020). Resilience is not always predictable, however, particularly if disturbances are novel or extreme. The unprecedented challenges posed by the current climate and biodiversity crisis mean that the world's crucial ecosystems are facing increasing threat (Scheffer et al. 2015; IPBES 2019). Understanding the factors governing resilience in natural systems is therefore critical.

Among the ecosystems facing significant threats, freshwaters are particularly vulnerable, already burdened by an array of stressors. These include land use change, pollution, abstraction, channelisation, invasive species, and fishing, with agriculture and urbanisation as prominent contributors (Reid et al. 2018; IPBES 2019). In England, for example, not a single river currently meets the criteria for 'good chemical status', and just 14% are considered to have 'good ecological status' as a result of these many stressors (Environment Agency 2019). Climate change is predicted to exacerbate these issues further, presenting significant and escalating risks to freshwater ecosystems already strained at local scales (Ormerod et al. 2010; Jackson et al. 2016; Reid et al. 2018). Rivers may also be particularly vulnerable, given their dependence on hydrology, sensitivity to temperature (Daufresne et al. 2004; Durance and Ormerod 2007), and the large numbers of ectothermic species they support (Balian et al. 2008).

Reflecting the vulnerabilities, recent studies have revealed an alarming 83% decline in freshwater vertebrate populations since 1970, a rate faster than any other ecosystem type (WWF, 2020). The situation for invertebrates (the dominant animal group), however, is more nuanced, with variations in trends observed across different regions and taxa, and contrasting with observed declines in terrestrial insects (Vaughan and Ormerod 2012; Jourdan et al. 2018; Baranov et al. 2020; van Klink et al. 2020; Outhwaite et al. 2020). Dirzo et al. 2014; Hallmann et al. 2017; Hallmann et al. 2020). For example, a meta-analysis by van Klink et al (2020) revealed a 9% decline in terrestrial insect abundance per decade, but an 11% increase in freshwaters.

Given the threats to freshwater ecosystems, their preservation and scientific understanding are imperative for a host of reasons. They play a crucial role in many ecological functions. Not only are their diverse communities responsible for processes such as water purification, organic matter processing and nutrient cycling within food webs (Cummins and Klug 1979; Wilson 1987), but rivers serve as intricate networks for the receipt, processing, transport, and storage of substantial quantities of organic materials within and across the landscape (Battin et al. 2023). Thus, they are thought to play a crucial, and previously underestimated role in regulating carbon cycles and the climate (Butman et al. 2016; Battin et al. 2023). Considering these facts, human wellbeing and survival is intrinsically linked to freshwater ecosystem resilience (Millennium Ecosystem Assessment, 2005; Palmer et al. 2008).

In recent years, nature-based solutions for climate mitigation and resilience have gained prominence (Scheffer et al. 2015; Prober et al. 2019; Williams et al. 2020). Specifically, management strategies aimed at stress reduction and enhanced resilience at local scale could prove most effective, while contributing incrementally to global goals (Rockström et al. 2009; Scheffer et al. 2015). Riparian broadleaf woodlands are one such strategy proposed as a practical, cost-effective solution to this challenge, offering multiple benefits with relative ease (Nisbet et al. 2011; Thomas et al. 2015; Thomas et al. 2016; Williams et al. 2020).

Despite the availability of practical guidance (e.g., Woodland Trust 2016) and the widespread promotion of expanding riparian woodlands, there is a lack of empirical evidence supporting their effectiveness in enhancing ecosystem resilience (Prober et al. 2019). While the benefits of broadleaf woodlands in river ecosystems are widely acknowledged, it is crucial to evaluate their specific contributions and to understand their potential role in river ecosystem resilience. Moreover, with the increasing use of the term ‘resilience’ in science, policy and legislation, there is a need for a clear definition and practical measurement methods to ensure its meaningful application (Newton 2016; Pimm et al. 2019; Sanderson Bellamy et al. 2021).

This chapter begins with a review of definitions of resilience in both scientific and policy contexts, ensuring a clear understanding of the concept. Furthermore, current knowledge regarding the impacts of climate change on rivers is investigated, identifying key threats and vulnerabilities. Subsequently, this chapter aims to provide a comprehensive understanding of how broadleaf woodlands can influence river ecosystems and potentially enhance their resilience against climate change. Lastly, evidence gaps are identified where further research would aid management and policy decisions, and enhance our understanding of resilience in these dynamic systems.

2.2 Resilience in science and policy

Over recent decades, the term 'resilience' has become widely used in scientific and political language (Walker et al. 2004; Folke 2006; Brown 2012; Baggio et al. 2015), and 'resilience thinking' is now central to climate change mitigation and adaptation strategies in law and policy (Wenta et al. 2019). Not only has the term appeared in global governance goals, such as the United Nations climate mitigation report (IPCC 2022), and the Aichi Biodiversity Targets (target 15), but has been mandated in legislation, such as the Well-being for Future Generations (Wales) Act 2015, and the Environment (Wales) Act 2016 (Sanderson Bellamy et al. 2021).

Despite its prolific use and legally binding targets, there is no clear definition of resilience or consistent means of measurement. In its conceptual sense, resilience is often defined as the capacity to withstand or recover from disturbances, or for complex socio-ecological systems to absorb or withstand perturbations and maintain structure and function, arising through self-organisation, learning, and adaptation (Holling 1973; Gunderson 2000; Walker et al. 2004; Biggs et al. 2012). Current guidance for its measurement includes assessing attributes such as diversity, habitat extent, condition, connectivity, and 'adaptability' (Sanderson Bellamy et al. 2021), or in the case of the Aichi Biodiversity Targets, by the 'restoration of at least 15% of degraded systems'. Yet, these might be considered proxies rather than direct measures of resilience. Lack of clarity and consistent understanding can lead to considerable confusion and shortcomings in policy and practice, as demonstrated in a similar manner with the term 'sustainability' (Donohue et al. 2016; Newton 2016; Mastrángelo et al. 2019; Xu et al. 2021). This ambiguity can hinder effective decision-making and implementation of strategies, with potentially detrimental consequences for ecosystems.

Part of this ambiguity lies in a lack of real-world, quantified examples of resilience. For example, a review by Prober *et al* (2019) showed that less than 10% of research papers recommending climate interventions demonstrated their effectiveness using field data, and this was most pronounced for options that aimed to enhance adaptive capacity or resilience (Prober et al. 2019). Thus, to understand and mitigation against the effects of climate change, clear, quantifiable measures based on monitoring data are essential (Angeler and Allen 2016; Pimm et al. 2019).

Another primary source of confusion around the use and meaning of resilience stems from its origins in the wider field of 'ecological stability' (Van Meerbeek et al. 2021). Here, 'stability' has been defined as '*one of the most nebulous terms in the whole of ecology*', with upwards of 163 different definitions, from 70 overarching concepts and more than 40 different measures (Grimm and Wissel 1997). These originate from, and apply to, a wide range of disciplines, including engineering, economics, psychology, and the social sciences. Meanwhile, many of the words associated with ecological stability and resilience are embedded within everyday public language.

As an umbrella term, ecological stability is often used interchangeably with ecological resilience, though two overarching and slightly diverging frameworks have developed for their conceptualisation and measurement (Van Meerbeek et al. 2021). The first (ecological stability) has traditional foundations where measures relate to dynamics around an equilibrium point. In empirical studies, the most frequently measured component in this regard is variability, typically quantified by the coefficient of variation, of quantities such as abundance or biomass (Donohue et al. 2016). Other measures include resistance (the ability to withstand change), persistence (the ability to maintain the same species assemblage over time, also a measure of turnover), engineering resilience (the rate of return to a pre-disturbed state), and network robustness (the range of disturbance a system can withstand before collapse, or tolerance to extinctions) (Pimm 1984; Dunne et al. 2002b; Donohue et al. 2013). Additionally, robustness can incorporate information on species interactions, e.g., predator-prey, that are commonly investigated in theoretical studies (May 1972; Harrison 1979; Pimm 1984; Ives and Carpenter 2007; Donohue et al. 2013).

The second conceptual framework (ecological resilience) tends to relate to non-equilibrium dynamics, and the ability of systems to ‘absorb’ change (Van Meerbeek et al. 2021). This concerns tipping points between multiple stable states, also referred to as critical thresholds, phase transitions, or regime shifts (Figure 2.1) (Holling 1996; Van Meerbeek et al. 2021). This definition, introduced by Holling in 1973, separated resilience from its traditional origins in engineering (Holling 1973; Pimm 1984; Holling 1996). However, in this framework, ecological resilience is notoriously difficult to quantify in natural systems, and remains a major source of confusion five decades later. For this chapter, ‘resilience’ will be used as a catch-all term to refer to both ecological resilience and ecological stability, quantifying concepts within these where appropriate. Disaggregating the constituent components is advantageous in a research context since this allows different facets to be investigated. Subsequent data chapters aimed at measuring resilience will adopt the ecological stability view for this purpose and in accordance with most scientific literature based on empirical studies.

For quantifying resilience, traditional measures such as temporal variability, resistance, and persistence have been favoured by empirical researchers, due to their longer history in ecology and ease of application to ecological data (McCann 2000; Allen et al. 2019). Meanwhile, far-from-equilibrium dynamics have largely been resigned to theory (May 1977; Donohue et al. 2016). However, advances in research aim to bridge the gap between theory and practice, using traditional measures to determine vulnerability to biodiversity and functional losses, or early warning signals prior to regime shifts in highly complex systems (Scheffer et al. 2009; Dakos et al. 2012; Donohue et al. 2013; Blonder et al. 2017; Kéfi et al. 2019).

Some common phenomena have been identified in nature, such as trade-offs between species resistance and recovery rates, and changes in the dynamics of systems as they near a threshold. For example, ‘critical slowing down’ describes a behaviour in which the characteristic rate of return (engineering resilience, *sensu* Pimm 1984) begins to slow towards a tipping point (Wissel 1984). Similarly, some studies have shown that systems become increasingly erratic or variable near thresholds (Scheffer et al. 2009; Kéfi et al. 2013; Chen et al. 2019; Clements et al. 2019). For instance, increased variability is a pattern seen in the abundances of exploited fish populations prior to collapse (Hsieh et al. 2006). Long-term biodiversity trends could also signify a loss of resilience, and concerningly, the rates of change seen in today's climate and biological systems have been likened to historical mass extinction events (perhaps the starkest example of a regime shift) (Danise et al. 2013; Dirzo et al. 2014; Ceballos et al. 2017; Slater et al. 2019;). Yet, regime shifts are not always catastrophic, and can be reversible, though this might require more energy than was initially needed for change. In any case, it is not always possible to predict the consequences until they occur (Scheffer et al. 2001; Kéfi et al. 2013).

In nature, other examples of regime shifts, or multiple stable states are relatively widespread. For example, marine systems, including fisheries and coral reefs are commonly studied in this context (Knowlton 1992; Sguotti and Cormon 2018). Catastrophic shifts have also been witnessed in terrestrial systems, as in the process of desertification (Scheffer et al. 2001; Herrmann et al. 2005; Mumby et al. 2007). For freshwater ecosystems, some lakes have been shown to switch between turbid and clear-water states (Scheffer et al. 1993; Hobbs et al. 2012). However, evidence of regime shifts in flowing waters has so far been limited to some microbial studies (Shang et al. 2021), and natural seasonal switching between heterotrophic and autotrophic production in temperate regions (Baxter et al. 2005). Instead, studies have indicated that riverine ecosystems are potentially highly resilient, with self-restoring mechanisms that enable recovery (Vaughan and Gotelli 2019; Gozzi et al. 2021).

Understanding the mechanisms that underpin ecosystem dynamics and resilience is a core topic in ecology (MacArthur 1955; May 1972; Holling 1973; Pimm 1984; Montoya et al. 2006; Ives and Carpenter 2007; Allesina and Tang 2012; Donohue et al. 2013). While poor definitions are a primary factor limiting consensus in this field, this is further compounded by the sheer complexity of ecosystems, and the multidimensional nature of disturbance regimes and ecosystem dynamics over both space and time. Moreover, the mechanisms that govern resilience are likely to vary and interact across hierarchical levels (Gunderson and Holling 2002; Allen et al. 2014). Thus, studies that differ in their focal system, the level of biological organisation, and timescales may be very difficult to compare (Donohue et al. 2016; Domínguez-García et al. 2019; Kéfi et al. 2019). This highlights the need for deeper exploration into multiple facets of ecological stability within systems to better understand the mechanisms involved, including linear and nonlinear dynamics across biological scales.

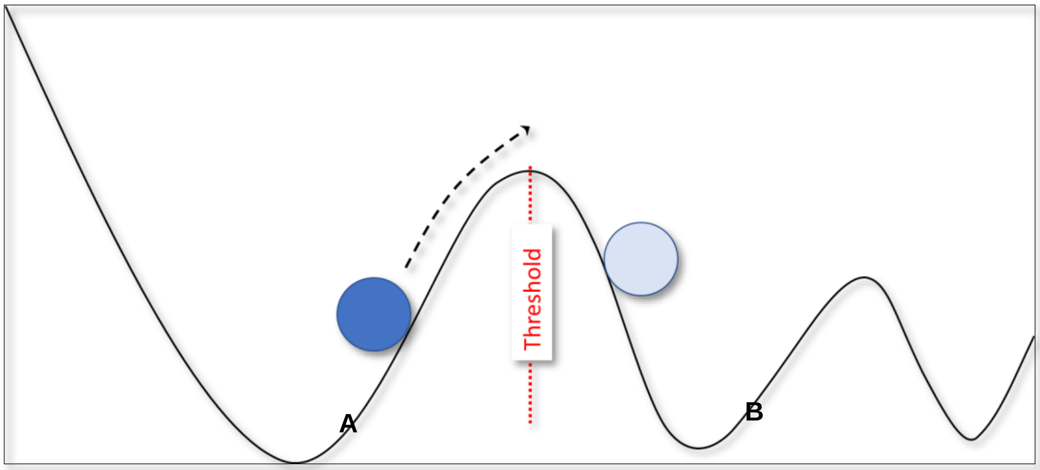


Figure 2.1 *The ball and cup model used to visualise concepts of ecological resilience. A) The dark blue ball represents the current state of the system within a stability domain (the cup). Here, variation can occur within the cup and internal relationships will still pull the system towards its basin of attraction (equilibrium). Alternatively, perturbations that are too large will push the system beyond its threshold and into a new stability domain and towards a new attractor (regime shift). B) The light blue ball represents a state for which new feedbacks govern dynamics and this state can be difficult to reverse. Traditional definitions denote that the rate at which a system returns to its former state after a perturbation determines its resilience ("engineering resilience" sensu Pimm 1984). This is measured regardless of the potential for alternate states, diverging from Holling's (1973) definition of resilience is defined in terms of thresholds or tipping points between states.*

2.3 The potential impacts of climate change on river ecosystems

Climate change is a complex threat of critical concern to all ecosystems, but especially for freshwaters where communities are highly dependent on hydrological and thermal conditions (Millennium Ecosystem Assessment 2005; Ormerod 2009; Reid et al. 2018). Under current climate projections, the UK is set to see warmer, wetter winters and hotter, drier summers as average temperatures rise, in addition to seasonal shifts and unpredictable extreme events (IPCC 2021). Since the pre-industrial baseline (1850–1900), average temperatures have risen by at least 1°C (Kendon et al. 2019), and the most recent decade comprised the warmest years since records began (NOAA NCEI 2022). Global warming of 2°C or higher is expected to exceed the critical thresholds for many socio-ecological systems worldwide, a reality that we are now likely to face (IPCC 2021).

Changes in precipitation and rainfall will impact freshwaters, with hydrological models suggesting increasing winter flows, decreasing summer flows, and greater frequency and magnitude of flood and drought events in some areas (Arnell 2011; Kay and Jones 2012; Prudhomme et al. 2012; Watts et al. 2015), potentially arriving in clusters (Kendon et al. 2023). However, these predictions are uncertain, with oceanic drivers such as the North Atlantic Oscillation (NAO) playing a significant and potentially exacerbatory role (Gerten and Adrian 2002; Durance and Ormerod 2007; Hannaford and Marsh 2008; Su et al. 2018; Brady et al. 2019). At local scale, factors that include urbanisation and agriculture also influence trends in temperature and discharge, and reduce prediction certainty further (Hannah and Garner 2015).

Already, however, river temperatures across England and Wales are estimated to have risen by 0.03°C each year between 1990 and 2006, with at least some of this trend thought to be directly related to climate change (Orr et al. 2015). In some upland streams, where smaller waterbodies have lower thermal inertia than large rivers (Caissie et al. 1998), temperatures are expected to track climate more closely, and rates of change may be even faster (Durance and Ormerod 2007). Some of the largest temperature increases are also projected for European rivers, where warming is exacerbated by declining discharge (van Vliet et al. 2013).

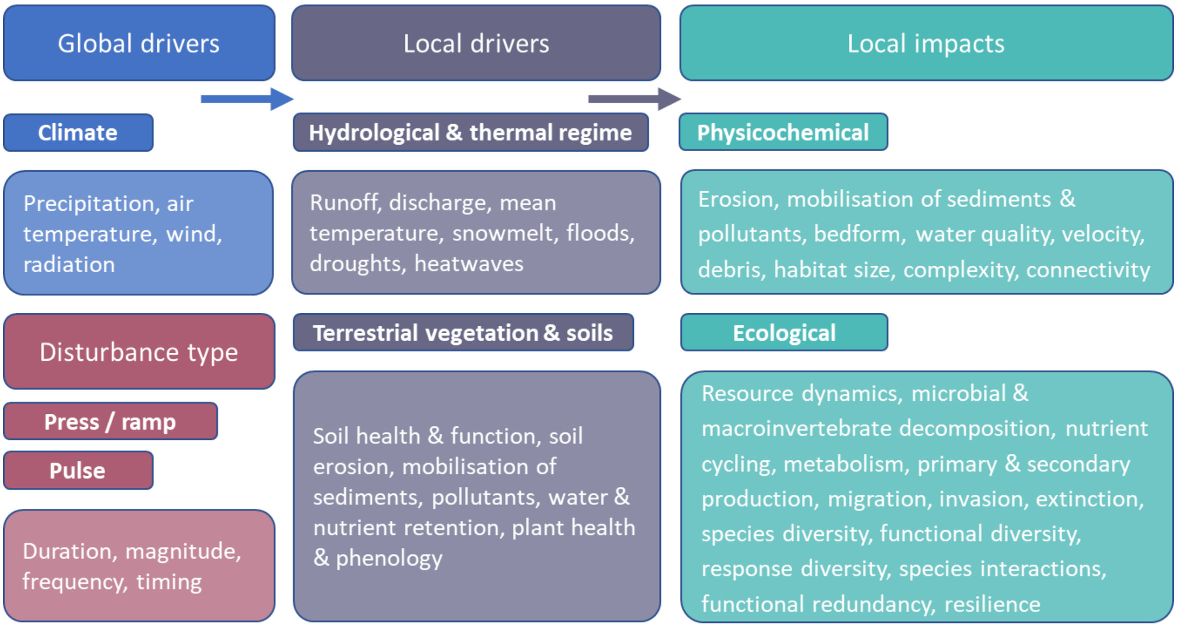
Although long-term trends in annual runoff and flow are consistent with increasing precipitation in temperate regions (Dai 2016), predictions of hydrological change are less accurate than for temperature and are seasonally dependent (Hannaford and Buys 2012). In higher latitude and altitude areas such as headwaters in upland Wales, particularly strong positive discharge trends have been shown for autumn and winter (Dixon et al. 2006; Biggs and Atkinson 2011; Hannaford and Buys 2012; Capell et al. 2013). Meanwhile, Hannaford and Buys (2012) found no compelling evidence that summer flows have decreased, contradictory to projections. Trends in spring flow are perhaps the most complex, often dependent on winter groundwater recharge and snowfall. Although initial increases in spring flow have been observed, a switch to decreasing flow after 1980 are indicative of an environmental regime shift (Hannaford and Buys 2012). Models also predict that changes in short-term (monthly and inter-annual) flow variation exceed the rate of long-term change (Arnell and Reynard 1996), highlighting potentially greater risks of extreme events.

2.3.1 *Response of ecosystems to pulse, press, and ramp disturbances*

Both temperature and hydrology are fundamental drivers of physicochemical and ecological processes in rivers, and thus are major factors affecting the ecological structure and functioning of riverine communities (Poff 1997; Lake 2000). Temperature affects many processes such as ecosystem metabolism, respiration, and decomposition rates, while ectothermic species such as invertebrates, fish, reptiles, and amphibians are particularly sensitive to thermal change (Broadmeadow et al. 2011; Forster et al. 2012; Jackson et al. 2017). Hydrology affects resource dynamics and the physical structure of the habitat, influencing habitat area, connectivity, and flow velocity. Both hydrology and temperature further alter water quality, oxygen availability, species interactions, locomotion, and mortality, often simultaneously.

Within expected ranges, disturbances are a vital component of ecosystems, shaping the habitat and regulating communities (Lake 2000; Lytle and Poff 2004). Intermediate levels of disturbance are hypothesised to enhance community diversity and build resilience by maintaining weak interactions, flexibility of diet, functional redundancy, and adaptations; the ‘intermediate disturbance hypothesis’ (Reynolds et al. 1993; Townsend et al. 1997; Bunn and Arthington 2002; Brown et al. 2006; Ledger and Milner 2015). Yet, outside these ‘normal’ or expected ranges, disturbances can negatively impact biodiversity. Effects depend on the type of disturbance (press/ramp or pulse), the timing, frequency, magnitude and duration of disturbances, and interactions with other stressors within the habitat (Table 2.1) (Ledger and Milner 2015; Harris et al. 2018; Sabater et al. 2022).

Table 2.1 *Climate-driven changes in upland stream ecosystems. Arrows highlight primary direction of influence; however, interactions occur within and between boxes, leading to indirect and complex effects. Modified from Orr et al (2008).*



Global drivers	Local drivers	Local impacts
Climate	**Hydrological & thermal regime**	**Physicochemical**
Precipitation, air temperature, wind, radiation	Runoff, discharge, mean temperature, snowmelt, floods, droughts, heatwaves	Erosion, mobilisation of sediments & pollutants, bedform, water quality, velocity, debris, habitat size, complexity, connectivity
Disturbance type	**Terrestrial vegetation & soils**	**Ecological**
Press / ramp **Pulse**	Soil health & function, soil erosion, mobilisation of sediments, pollutants, water & nutrient retention, plant health & phenology	Resource dynamics, microbial & macroinvertebrate decomposition, nutrient cycling, metabolism, primary & secondary production, migration, invasion, extinction, species diversity, functional diversity, response diversity, species interactions, functional redundancy, resilience
Duration, magnitude, frequency, timing		

Press and ramp disturbances are characterised by sustained or gradual changes in environmental conditions (Lake 2000). In a climate change context, these relate to rising average temperatures and rainfall or discharge trends. Pulse disturbances are defined as abrupt, temporary changes in temperature or discharge, characterised by differences in timing, frequency, duration, or magnitude (Jentsch and White 2019). Distinguishing between these disturbance types is important because of how they alter the environment and how biological response might differ. To date, most evidence concerning climate change impacts comes from incremental changes over time, or across environmental gradients using space-for-time substitutions. However, effects of pulse disturbances are likely to differ significantly compared to rising averages, and are thought to be a much larger threat to biodiversity and ecosystem functioning in rivers and other habitats (Harris et al. 2018; Sabater et al. 2022).

At a wide spatial scale, conspicuous signs of climatic ramp effects include shifts in species distributions. Warming either restricts or expands ranges as individuals migrate to suitable conditions. Models have shown that cold-adapted headwater species at the upper end of the river continuum are at considerable risk from warming, where obligate aquatic individuals cannot migrate to access cooler water conditions (Domisch et al. 2011). In Welsh upland streams, up to 12% of cool-water taxa could be at risk of extinction with a 3°C rise in winter temperatures (Durance and Ormerod 2007). In the same study, a 1°C rise in winter temperatures was associated with a 21% decline in macroinvertebrate abundance.

Temperature is a key driver of functional processes, which is predicted to increase decomposition rates with initial warming via stimulated microbial activity. At higher temperatures, shredder activity is predicted to be supressed, resulting in changes in the quality and form of carbon available to the food web (Bärlocher et al. 2008; Friberg et al. 2009). Moreover, warming impacts larger individuals disproportionately, favouring those with lower metabolic demands. This could result in skewed size distributions towards smaller-bodied individuals (Hassall et al. 2007; Woods et al. 2022), with further consequences to production and energy transfer through food webs.

Climate change has also been implicated in phenological changes, including increased growth rates and earlier adult emergence times. For example, a 1°C rise in winter temperatures was estimated to accelerate dragonfly emergence by 6-7 days (Richter et al. 2008), and positive phases of the NAO have been linked to increased growth rates of stream insect nymphs (Briers et al. 2004). With regards to resources, many UK plants now begin to flower a full month earlier than a 1752-1986 average (Büntgen et al. 2022). Earlier leaf emergence and later leaf senescence have also been predicted (Schwartz *et al.* 2006; Menzel *et al.* 2006), but more recent research estimates a reversal of this trend with increasing stress (Zani et al. 2020). Given the importance of terrestrial inputs to aquatic systems, this could have knock-on impacts to community structure and functioning, and contribute to phenological mismatch, e.g., a disruption to consumer-resource interactions (Larsen et al. 2016).

Altered average streamflow, including reduced and earlier snowmelt in spring is also expected to impact river systems. For example, streamflow changes are predicted to have major consequences on carbon fluxes, causing headwater streams to emit greater quantities of respiratory CO_2 and limiting the transport of autochthonous (in-stream) energy downstream to other ecosystems (Larson et al. 2018; Ulseth et al. 2018). Similarly, a 40-60% reduction in flow has been identified as a possible tipping point for cyanobacterial blooms in streams and rivers (Rosero-López et al. 2022), with similar thresholds seen for some benthic invertebrates (Rosero-López et al. 2020).

Knowledge of the effects of extreme events is limited, largely because of their rarity, and because differences in their timing, magnitude, frequency, and duration can alter response and recovery dynamics (Radchuk et al. 2019). A recent meta-analysis of 71 studies from mostly temperate regions showed that extreme events are likely to have disproportionate effects upon freshwater ecosystem communities compared to rising average conditions (Sabater et al. 2022). The meta-analysis revealed that the largest effects on macroinvertebrates were related to dryness from flow interruption. Observed negative impacts on primary production also highlighted risks of extreme events (including winter floods) to ecosystem functioning. Floods can increase the quantity of organic matter inputs to streams initially, but this is followed by rapid export downstream, alongside dislodged or drifting animals (Dawson et al. 2008; Tank et al. 2010; Larson et al. 2018; Pye et al. 2022). Sudden runoff can impact water quality and flash floods can also scour algae from the surface of rocks (Jones et al. 1995), thus altering basal resource availability.

Extreme events have been shown to cause compositional shifts, biodiversity loss, food web re-structuring and rewiring in stream communities (Lake 2003; Feeley et al. 2012; Woodward et al. 2012; Lu et al. 2016; Woodward et al. 2016; Aspin et al. 2018; Sarremejane et al. 2018; Aspin et al. 2019). Frequent disturbance from flood and drought events has also been linked to ecosystems with simplified food webs and weak interactions (McHugh *et al.,* 2010). Many of the most negative consequences have been associated with droughts, which often coincide with high temperatures and exacerbate other stressors, such as pollution (Zhang et al. 2022). Simultaneous oxygen reductions associated with warming (hypoxic conditions of 5 kPa) have also been shown to reduce the thermal tolerance of stream invertebrates by as much as 8.2°C for some widespread mayfly nymphs (Verberk et al. 2016).

Given the multiple stressors that can affect rivers, and the complexity of natural, dynamic systems more generally, identifying specific disturbance effects can be challenging. Moreover, relationships between climate and biological communities are often found to be nonlinear (Jourdan et al. 2018; Baranov et al. 2020), with many direct, indirect, and interacting local factors contributing to the state of an ecosystem in any given moment. These interacting stressors can make impacts difficult to predict (Figure 2.2). For example, pulse or ramp disturbances that trigger biodiversity loss or restructuring of communities could subsequently lower thresholds and alter relationships with climate, i.e., state dependency (Sugihara et al. 2012). This could also occur in the absence of clear structural and functional change, if past events have contributed to an ‘ecological memory’, i.e., the materials and information maintained within a system after a disturbance event, which can change future perturbation response in unexpected ways (Johnstone et al. 2016; Hughes et al. 2019; Jackson et al. 2021).

Theoretically, gradual changes could allow communities to adapt if these changes are slow enough not to exceed thresholds in the meantime (Chester et al. 2015). For example, a 1-2°C rise over several decades might have limited effects on river ecosystems, which are naturally adapted to environmental variation well within this range. Under a high emissions scenario, by 2070 the UK could see temperatures up to 6.8°C higher than the record for the hottest day (as of 2019) (Kendon et al. 2019). Events like this are much more likely to exceed thresholds and lead to structural and functional losses, particularly if they occur during sensitive life stages. Maintaining environments within intermediate levels of disturbance, or buffering the rate of environmental change, could therefore be vital for ensuring resilience.

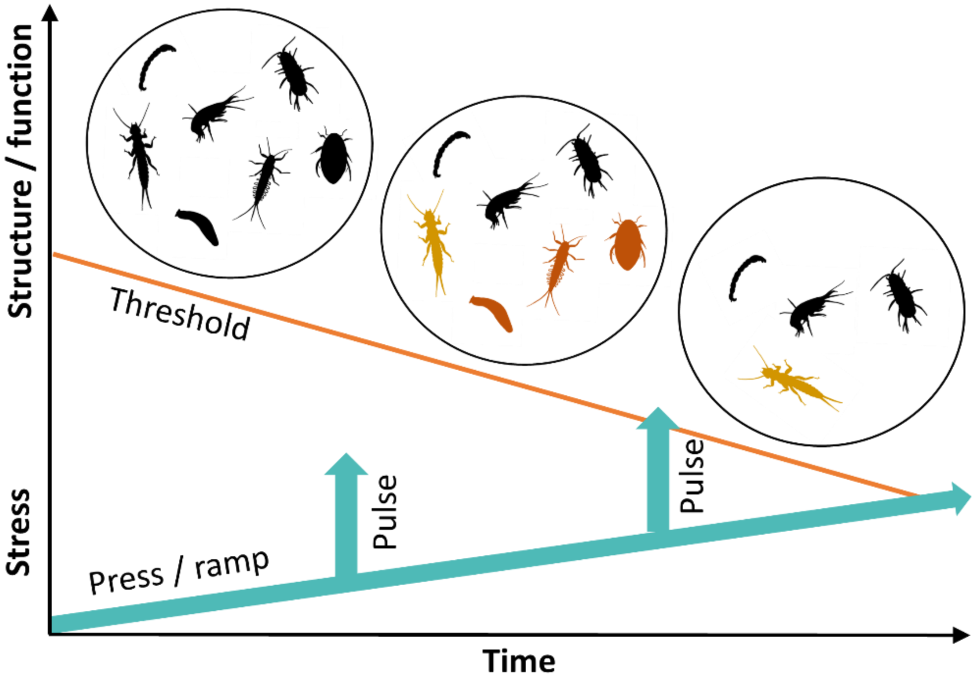


Figure 2.2 Conceptual diagram of potential interactive and state-dependent effects of press and pulse disturbances on community structure and function. As press or ramp disturbances intensify, e.g., temperature, ecological thresholds and tolerances could decrease (orange). Thus, response to pulse disturbances of the same type and magnitude could differ depending on the current system state. Consequently, relationships between biodiversity and stress can be nonlinear and changing over time.

2.4 Can broadleaf woodland enhance river resilience to climate change?

Rivers are inextricably linked to the surrounding landscape (Lindeman 1942; Likens and Bormann 1974). Land use in the riparian zone and wider catchment area affect many of the physical, chemical, and ecological properties of draining waters (Likens and Bormann 1974; Hynes 1975; Wallace et al. 1997). Many of these properties have been linked to resilience, either through thermal or hydrological buffering, or through influences on community composition and energy flows (Figure 2.3). Van Looy *et al* (2019) identified three groups of mechanisms contributing to the resilience of river communities; refugia, resources, and the recruitment of individuals from the wider, connected landscape. These are explored and adapted in the context of the possible ways that broadleaf woodland could enhance climate resilience.

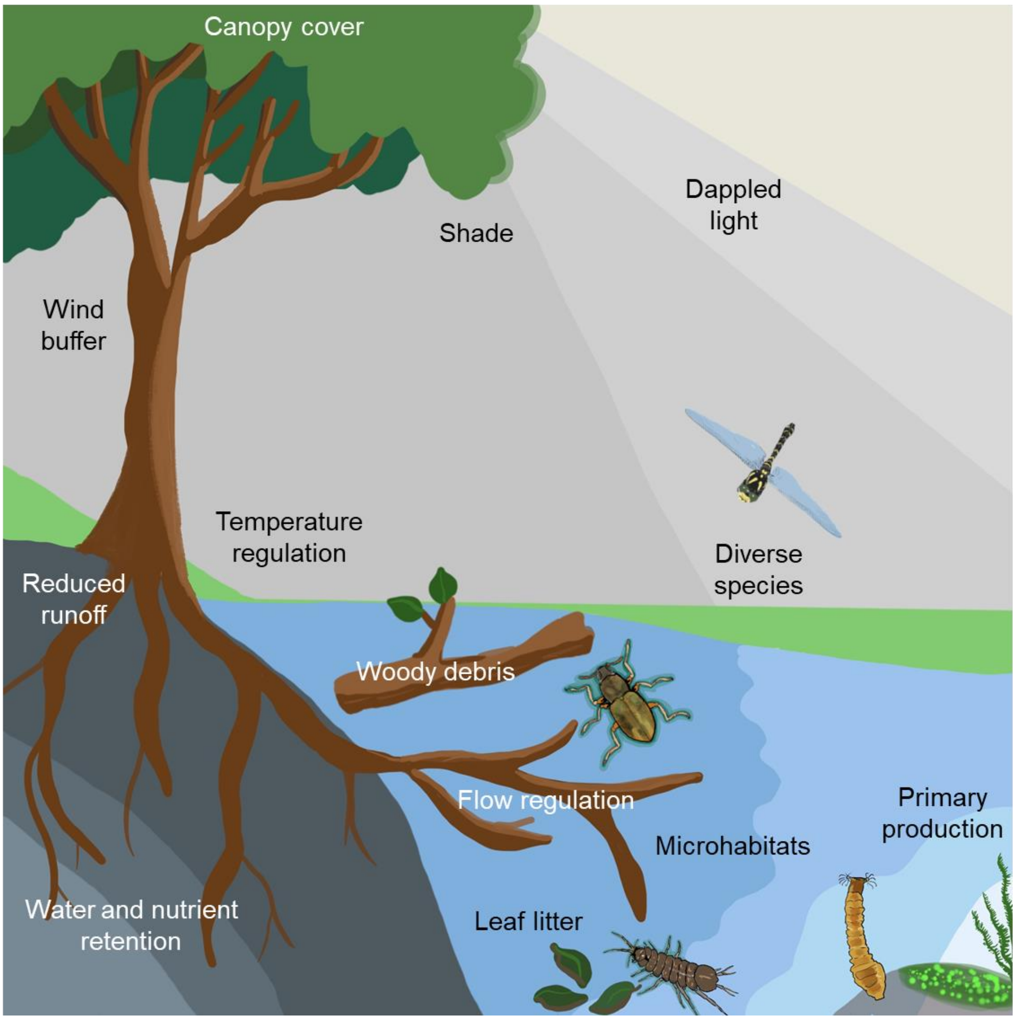


Figure 2.3 *The main pathways by which riparian woodland influences stream ecosystems.*

2.4.1 *Refugia*

Trees physically alter rivers in a variety of ways. The diversity of terrestrial subsidies inputted by riparian woodland, such as woody debris, leaf litter and flowers (Tank et al. 2010) contribute to habitat complexity, an important factor for maintaining benthic organism densities and diversity (Gurnell et al. 1995; Gurnell et al. 2002; Haapala et al. 2003; Gurnell et al. 2005; Schneider and Winemiller 2008; Frainer et al. 2018). Two major influences of woodlands include the effects of course woody debris on flow and retention of materials, and canopy cover as a regulator of thermal conditions and basal resource ratios. In addition to habitat heterogeneity, these factors contribute to the ability of organisms to evade stress, and have therefore been associated with increased community resilience (Mykrä et al. 2011; Van Looy et al. 2019).

As a regulator of temperature, riparian woodlands have first and foremost been promoted as a natural buffer against rising temperatures and climatic extremes (Ormerod 2009; Broadmeadow et al. 2011; Thomas et al. 2015; O'Briain et al. 2017). Shading can have multiple impacts on thermal processes. These include intercepting short-wave solar radiation and retaining outgoing longwave radiation, which are major sources of heat and a driver of energy fluxes at the air-water interface (Webb and Zhang 2004; O'Briain et al. 2017; Dugdale et al. 2018). Through evapotranspiration, buffering of wind, and increased water retention, riparian woodland can also create a microclimate effect, if the wooded area is extensive enough (Davies-Colley et al. 2000; Hannah et al. 2008; Garner et al. 2015).

Forests have been shown to reduce average temperatures during summer and spring, potentially buffer cold days during winter, and reduce inter-annual temperature variability (Weatherley and Ormerod 1990; Garner et al. 2015). Mean temperatures in semi-natural broadleaf woodland streams can be at least half a degree Celsius cooler during summer compared to open grassland streams, and similar or a further 0.5°C cooler in densely packed coniferous woodland (Hannah et al. 2008; Broadmeadow et al. 2011; Dugdale et al. 2018). Likewise, maximum temperatures in summer can be 2-5°C lower in forested compared to deforested and open moorland streams (Sweeney 1993; Malcolm et al. 2008; Bowler et al. 2012). These reductions have important implications for species' critical thermal maxima (Verberk et al. 2016), with as little as 20% riparian shade able to maintain summer high temperatures below lethal limits for temperature-sensitive species (Broadmeadow et al. 2011); the optimum dappled shade is suggested to be around 50% (Broadmeadow and Nisbet 2004). It is probable that climate change increases the need for denser canopy cover, and forest buffers of less than 40 m in width are already thought to provide insufficient shelter from environmental stressors (Davies-Colley et al. 2000). Moreover, evidence suggests that more than 30 m riparian buffers would be needed to support ecological functioning, e.g., energy transfer and processing (Lind et al. 2019), and this is greater than the current average recommended width. Many of these estimates vary, however, depending on factors such as stream size.

Shading may play a lesser role downstream as rivers widen and deepen (Vannote et al. 1980; O'Briain et al. 2017). However, trees are associated with many other benefits that extend beyond temperature buffering (Palmer et al. 2005; Broadmeadow and Nisbet 2004;

Broadmeadow et al. 2011). For example, through roots and woody debris, broadleaf woodlands can regulate flow, creating a range of riffles and pools that constitute microhabitats (Gurnell et al. 2005; Frainer et al. 2018). By slowing flow velocity through increased 'roughness', broadleaf woodlands can enhance the retention of water, sediments, nutrients, and organic matter within the system (Likens and Bormann 1974; O'Connor 1991; Muotka and Laasonen 2002; Gurnell 2014). Trees also contribute to stream bed and bank stability, reducing soil erosion, runoff, and improving water quality (Castelle et al. 1994; Broadmeadow and Nisbet 2004). Riparian buffers are frequently recommended for use in agricultural landscapes for these reasons.

In lowland areas, improvements in water quality have been shown to potentially offset ~1°C of climate warming (Vaughan and Gotelli 2019). Additionally, upland catchments forested with mature semi-natural broadleaf woodlands have been shown to reduce peak runoff and discharge rates by up to 60% compared to grazed pasture (Monger et al. 2022). In part, this was attributed to woodland soils being up to 20 times more permeable. Although conifer forest might also mediate flood and drought risk, tree harvest via standard clear-felling practices negates any of these benefits, and is a significant threat to water quality and benthic invertebrates (Gee and Smith 1997; Neal et al. 1998). Conifers are also widely understood to cause acidification that could contribute as a press disturbance or to multi-stressor effects (Malcolm et al. 2014).

The primary mechanisms by which increased resilience arises from habitat complexity are thought to be functional redundancy and response diversity (Mori et al. 2013; Van Looy et al. 2019; Biggs et al. 2020). Both of these can provide insurance to the network, acting as a buffer against disturbances. Functional redundancy occurs when taxa overlap in their functional roles, such that processes would be maintained if some, but not all, taxa were lost. Similarly, response diversity determines the range of ways that taxa respond to a given disturbance, and ensures that taxonomic or functional groups are maintained. Examples include the River Wye, UK, where models predicted decreasing response with increasing pollution (pH and nutrients), particularly in upper reaches where a higher diversity of sensitive specialists might occur (Bussi et al. 2018). In plant studies, land use intensification has also been shown to reduce functional redundancy and response diversity (Laliberte and Legendre 2010). Similarly, in a plant-pollinator study, response diversity decreased with agricultural intensification.

However, this was not found to correspond with resilience, suggesting alternative mechanisms (Cariveau et al. 2013). Moreover, there are some notable limitations to studies assessing these factors, which may confound relationships with resilience.

Suggestions of high functional redundancy of microbial and invertebrate communities have been made for both broadleaf and conifer streams (Riipinen et al. 2010; Ferreira et al. 2017), and even streams converted from tropical forest to agriculture (Espinoza-Toledo et al. 2021), suggesting that this property may be widespread. Links between resilience and response diversity are also limited, since response diversity is frequently inferred indirectly for a non-standardised set of traits rather than measured directly (Ross et al. 2023). Methods employing response traits were also initially developed for plants, meaning their applications to aquatic organisms are less advanced and require further research.

2.4.2 *Resources*

Resource quantity, quality, and temporal dynamics are key drivers of community structure and function, with important implications for resilience. Thus, factors that affect these aspects, such as the environment, play a key role. The main biological mechanisms thought to confer resilience in response to changing resources are competition and facilitation, i.e., species interactions that effectively partition and re-direct resources in times of stress, enabling community re-assembly (Connell and Ghedini 2015; Van Looy et al. 2019). Resource quantity, quality and timing are strongly determined by riparian vegetation (Webster and Meyer 1997). In rivers with high habitat heterogeneity multiple mechanisms, directly related to both invertebrate communities and their resources, are likely to occur simultaneously to drive community re-assembly processes.

Links with riparian zones also play a key role in resilience through facilitation by reciprocal subsidies. Allochthonous organic matter is a crucial resource for rivers, in structuring of networks and functions, and subsequently sustaining these networks (Lindeman 1942; Odum 1957; Odum 1968; Cummins and Klug 1979; Vannote et al. 1980). Through the combined influence of leaf litter inputs and retention by debris dams, riparian broadleaf woodlands have been shown to increase the standing stocks of course particulate organic matter (CPOM) significantly more than moorland or conifer buffers (Thomas et al. 2016). Higher CPOM stocks are also maintained even after high flow events, which could potentially offset some of the effects of increasingly wet winters (Hannaford and Marsh 2008; Pye et al. 2022).

Course particulate organic matter contributes to higher density and biomass of shredders (Thomas et al. 2016), a major functional feeding group for nutrient and carbon cycling, and the decomposition of CPOM into finer particulates for other feeding groups (Cummins et al. 1989). In rainforest streams, for example, terrestrial inputs account for 56-74% of the basal energy assimilated by primary consumers (Neres-Lima et al. 2017). In temperate headwaters where terrestrial biomass is lower, 50% of all macroinvertebrate production has been estimated to originate from terrestrial energy sources (Thomas et al. 2016). This importance decreases downstream as other food sources dominate (Rosi-Marshall and Wallace 2002; Collins et al. 2016). Perhaps surprisingly, however, riparian grasslands can provide a similar quantity and quality of organic matter as found in forested streams, indicating that mixed grasses and herbaceous plants are important allochthonous resources (Menninger and Palmer 2007).

Just as river food webs receive subsidies from land, aquatic-to-terrestrial transfers are also vital to the processing and distribution of energy across landscapes. These reciprocal subsidies have been estimated to contribute 25 to 100% of energy in the diets of birds, bats, reptiles, and predatory invertebrates such as spiders and beetles (Nakano and Murakami 2001; Baxter et al. 2005; Bartels et al. 2012; Thomas et al. 2016; Lafage et al. 2019). These mutual interactions also occur in compensatory ways. For example, when aquatic macroinvertebrate biomass is low, dependence on terrestrial subsidies increases. Likewise, low terrestrial invertebrate biomass in spring can be offset by peak emergence of freshwater species (Nakano and Murakami 2001). Thus, reciprocal subsidies may play a crucial role in sustaining energy flows during or after disturbance events, and contribute to resilience. Riparian vegetation that provides a refuge to terrestrial wildlife when aquatic biomass is lowest, most vulnerable, or degraded, could therefore prove to be an important conservation and biodiversity restoration tool.

In addition to litter dynamics, canopy cover strongly influences light intensity and the balance between autotrophic and heterotrophic production (Baxter et al. 2005). This balance between green and brown energy pathways has been hypothesised to contribute to the resilience of food webs (Canning et al. 2019). An imbalance could arise through disturbances to basal resource ratios (Zelnik et al. 2022) or alterations to canopy cover, that subsequently propagates through networks. However, trophic cascades may not necessarily occur in predictable ways. For example, despite shredders predominantly being associated with leaf litter (Cummins et al. 1989), studies have shown that autochthonous energy sources, such as algal biofilms on leaf litter, contribute to shredder diets, and are therefore more important to woodland stream communities than previously thought (Hax and Golladay 1993; Torres-Ruiz et al. 2007; Thomas et al. 2016). Likewise, some taxa actively select for the higher nutritional (nitrogen) content of algal resources (Leal et al. 2023), and this is a particularly important food source in all lotic systems. Given the high nutrient quality of algae, efficient assimilation and secondary biomass in open streams can actually be higher than forested streams (Canning et al. 2019). However, here too, fine particulates bound in epilithic biofilms contribute to grazer diets (Hamilton et al. 2005). Thus, there is evident overlap between green and brown energy pathways, i.e., taxa employing a breadth of feeding strategies, that may influence community resilience.

Although effects of riparian land cover to community composition are known, studies have not shown clear relationships with some facets of resilience. For example, differences in green:brown energy pathways in open versus forested streams were not associated with differences in food web robustness of mountainous stream communities (Canning et al. 2019). These results might suggest that in habitats exposed to frequent disturbance, species interactions may be a less important determinant of resilience than environmental filtering. As climatic disturbances increase in frequency and magnitude, other mechanisms are therefore likely to be required, including interventions that promote the stability of the environment and food resources.

2.4.3 *Recruitment*

Recruitment relates to the ways in which individuals repopulate a habitat following disturbances, which is strongly determined by species traits, habitat connectivity, and the metacommunity species pool (Van Looy et al. 2019). The complexity of resources and diversity of species and functional traits supported by woodland streams are likely to contribute to recovery processes. Evidence for recruitment mechanisms is mixed, and potentially more dependent on landscape-scale rather than local scale conditions. Nevertheless, each local patch contributes to the wider landscape, to habitat connectivity, and metacommunity dynamics, and increasing fragmentation may decrease diversity and resilience overall (Suurkuukka et al. 2014; Cote et al. 2017).

Species traits including generalism and diet flexibility are often shown to increase tolerance to environmental perturbations and resource variability (Lisi et al. 2018). Similarly, traits for resting stages and small body size confer greater resistance (Fritz and Dodds 2004; Bogan et al. 2015; Bogan et al. 2017). Specialist traits like aerial dispersal abilities, rapid reproduction, and multivoltinity contribute to repopulation and recovery rates (Nislow et al. 2002; Chester et al. 2015). Typically, selection for such traits is associated with environmental filtering by high stress habitats (Heino 2005; Heino et al. 2015). Thus, communities already adapted to stress could fare better in response to climate change. For example, Collier and Quinn (2003) showed that communities in pasture streams have higher initial resistance to a flood, likely because they were already adapted to the underlying press disturbance of historical forest loss (Collier and Quinn 2003). By buffering stress and regulating disturbance regimes, riparian broadleaf woodland communities could therefore be more sensitive to extreme climatic events (Ruijven and Berendse 2010).

Other, passive dispersal mechanisms might also contribute, however, and wetting of the riparian zones and terrestrial areas between sites can aid dispersal of flightless species, such as molluscs and some beetles (Bilton et al. 2001). The capacity for woodlands to retain water could contribute to this pathway of dispersal, though equally reduce surface water in the short-term through higher infiltration compared to moorland catchments. Moreover, the density of passive dispersers has been shown to increase in restored streams with reductions in flow, in addition to increasing numbers of sensitive taxa (Pilotto et al. 2018). The possibility that riparian woodland provides a physical barrier has also been investigated (French and McCauley 2019). However, this is unlikely to deter strong fliers such as Odonata (dragonflies), and evidence suggests that most emergent adults rarely fly more than 10 m from stream banks (Petersen et al. 2004).

Riparian vegetation is particularly important for invertebrates with emergent life stages (Chester et al. 2015) and increases the capacity of populations to recover where internal reserves are limited, thus promoting ecological resilience (Bengtsson et al. 2003; Allen et al. 2016). Fragmentation of old-growth riparian forest may lead to loss of persistence of freshwater species, similar to observed patterns in terrestrial species decline (Suurkuuka et al. 2014). Moreover, dispersal across open moorlands risks higher mortality through climatic stress (wind, high temperatures) and predation, and individuals may be reluctant to fly too far from high humidity (Petersen et al. 2004; Firmiano et al. 2021).

2.5 Knowledge gaps and management opportunities

On a global scale, the loss of forests and natural grasslands over the past millennia has been extensive, with the majority of the converted land now used for agriculture, particularly for grazing (Moore and Chater 1969; Williams 2003). In the UK specifically, agricultural land accounts for approximately 71% of the total land area, primarily for animal agriculture (DEFRA 2021), while only 2.5% remains as ancient woodland (Reid et al. 2021). This context presents a significant opportunity for transformation and restoration of woodlands to enhance biodiversity, sequester carbon, and potentially increase resilience. Broadleaf woodlands play a crucial role in supporting river ecosystems by regulating temperature, water flow, carbon cycling, and nutrient dynamics (Ellison et al. 2017). Moreover, there are several recognised pathways through which riparian woodlands can contribute to resilience. Direct evidence linking riparian management to enhanced resilience of aquatic communities to climate change, however, is limited, and highlights a pressing need to conduct research and evaluate their effectiveness, as well as to understand the underlying mechanisms involved.

Even in the absence of conclusive evidence of increased resilience, the established benefits of riparian broadleaf woodlands make their conservation and restoration a "low regrets" option (Prober et al. 2019) that contributes positively to biodiversity conservation and ecosystem functioning. A further consideration that may be crucial to resilience goals, is that degraded systems might demonstrate resilience, particularly if tipping points have already been surpassed or where environmental filtering constricts the community to generalist and stress-tolerant species (Gutiérrez-Cánovas et al. 2013; Canning et al. 2019). Thus, decision-makers must exercise caution when considering goals, and clearly specify desired outcomes to ensure that conservation and restoration efforts aim to achieve not just resilience but also the maintenance of biodiversity and ecological functioning. Moreover, resilience is a multidimensional concept – whether viewed from the ecological stability or ecological resilience perspective – which cannot be properly understood without quantifying the array of response and recovery dynamics that dictate community structure and function over time (Donohue et al. 2013). In rivers, very little is known about how these dynamics operate together, nor how climate change and local scale factors such as land use might interact to alter dynamics. An underestimation of the complexity of these systems could have detrimental consequences.

Given the uncertainties discussed, there is a clear gap in our understanding of how broadleaf woodland might enhance resilience compared to other land use types. This highlights several needs including the need to *i*) assess whether riparian woodland can increase the resilience of stream communities in the context of other land use types, and the need to *ii*) disaggregate resilience and investigate its constituent components to gain greater insights into underlying mechanisms (Donohue et al. 2013). Moreover, there is a general need to *iii*) assess the current state of rivers and their response to climate change, and particularly extreme events. These gaps form the basis of the next chapters in this thesis.

2.6 Conclusion

Freshwater ecosystems are at significant risk from climate change, alongside existing stressors that could exacerbate climate effects. Reducing stress at local scale through management of riparian zones has been suggested as a potential way to mitigate against climate change and enhance resilience. Broadleaf woodland could provide multiple benefits, including increased shading, regulated flow, and enhanced biodiversity and functioning, providing a possible natural solution to the pressing issues of climate change and biodiversity loss. However, resilience is a poorly defined concept that has so far limited understanding, and there have been few attempts to test the extent to which riparian woodlands could increase the resilience of aquatic ecosystems. Policy targets that include resilience need clear definitions and quantifiable measures for targets to be met. Thus, studies comprising multifaceted approaches that elucidate the response and recovery dynamics of river ecosystems in response to climate and local scale management, are urgently required. This is of utmost importance for riverine ecosystems that underpin the wellbeing and survival of billions of people worldwide.

Chapter 3: Long-term trends in upland stream macroinvertebrate communities and the effects of climate and land use

3.1 Summary

The long-term maintenance of stream ecosystem structure and function is crucial for numerous essential processes that support human well-being and broader biodiversity. Climate change poses a significant threat through rapidly rising temperatures, changes in precipitation, with many direct and indirect consequences to streams. Recent evidence of rapid global biodiversity declines has raised significant concern. However, multidecadal data from freshwaters are limited, and trends have been varied, particularly for river invertebrates.

In this study, trends in community structure and function were assessed using long-term macroinvertebrate monitoring data from 16 headwater streams in mid-Wales, UK. The primary objective was to determine the rate and direction of change in various taxonomic and functional community-level indices and examine differences in climate sensitivity between streams with contrasting riparian land use and acidity.

Results demonstrated the complex taxonomic and functional changes occurring in upland streams, which could partially be attributed to hydrological and thermal variation. Of the key findings, widespread and significant shifts in taxonomic and functional composition, and large declines in total abundance were seen, that corroborate trends seen in some terrestrial systems. Communities in streams draining conifer plantations were found to be at heightened risk, having experienced a 53% decline in total abundance in 37 years. However, changes were widespread, with evidence that shifts reflected declines in plecopteran detritivores. Moreover, local land use appeared to have little effect on the relative sensitivity of stream communities to climate. A 1°C rise in mean summer temperatures corresponded to an estimated 33% decline in abundance, with evidence of complex interactions and varied permutations among other climate variables.

Taken together, these results carry significant implications for biodiversity and functioning in upland streams, and suggest that local management strategies alone may be insufficient to mitigate the effects of climate change.

3.2 Introduction

The long-term functioning of freshwater ecosystems is critical to life on Earth. Such ecological functions, including organic matter processing and carbon storage, are underpinned by diverse communities of insects and other invertebrates (Cummins and Klug 1979; Wilson 1987; Poff 1997; Balian et al. 2008). Over the past century, however, agricultural intensification, pollution and climate change have become primary drivers of biodiversity loss (Raven and Wagner 2021), with rivers and other freshwaters among the most threatened of all ecosystems (Dudgeon et al. 2006; Reid et al. 2018). Consequently, freshwater vertebrate populations have declined by an estimated 83% since 1970 (WWF 2022), with concerns that unprecedented changes in climate (Kendon et al. 2019; Fischer et al. 2021; IPCC 2021) could further exacerbate many of the other drivers of loss (Reid et al. 2018).

Despite mounting evidence of widespread and rapid declines in vertebrates, trends in freshwater invertebrates are unclear (Durance and Ormerod 2007; Jourdan et al. 2018; Baranov et al. 2020; van Klink et al. 2020; Outhwaite et al. 2020). A few long-term studies have shown both decreases in diversity and abundance (Hallmann et al. 2017; Hallmann et al. 2020), increases (van Klink et al. 2020; Outhwaite et al. 2020), and significant nonlinearity (Jourdan et al. 2018; Baranov et al. 2020). In the UK and other countries, improvements in water quality following legislative action have been associated with biological recovery (Vaughan and Ormerod 2012; Outhwaite et al. 2020). These recovery dynamics, and the presence of a range of other stressors common to lowland areas, potentially mask effects of climate change and reduce the predictability of future impacts (Ormerod et al. 2010). Moreover, long-term trends in functional diversity are often overlooked, despite their potential to reveal important, and possibly more ecologically relevant, changes to communities (Suding et al. 2008; Floury et al. 2013; Larsen et al. 2018; Mouton et al. 2020). Understanding the extent to which climate change is linked to the long-term changes in freshwater macroinvertebrate community structure and function is therefore a research priority for informing policy and management.

Among the key stressors affecting rivers, climate change has already been associated with altered streamflow and temperatures, including increasing temperature and discharge and extreme events (Prudhomme et al. 2012; Hall et al. 2014; Madsen et al. 2014; Orr et al. 2015).

Knowledge mostly obtained from short-term studies or sampling across environmental gradients has revealed that temperature and hydrology exert major controls over the distribution, structure, and functioning of riverine macroinvertebrate communities (Poff 1997; Bunn and Arthington 2002; Lytle and Poff 2004; Woodward et al. 2016). Increasing discharge and temperatures can alter factors such as resource availability, metabolic processes, and species movement (Townsend et al. 1998; Young et al. 2008; Van Looy et al. 2019; Battin et al. 2023), but may offer some opportunity for adaptation if these changes occur within tolerance limits. Alternatively, extreme conditions that are sudden, frequent, or severe (i.e., pulse disturbances) could have unpredictable and more severe consequences (Jourdan et al. 2018; Sabater et al. 2022). Moreover, the combined effects of high temperature and low flow commonly associated with summer droughts are thought to be particularly detrimental to aquatic ectotherms, with potentially irreversible impacts to community abundance, diversity, food web structure and function (Harper and Peckarsky 2006; Ledger et al. 2013; Woodward et al. 2016; Aspin et al. 2019; Leigh et al. 2019). Such disturbances could accelerate long-term biodiversity trends (positive and negative). To date, linking climate variables to macroinvertebrate trends has proven particularly challenging, since effects can be complex and nonlinear (Jourdan et al. 2018; Baranov et al. 2020), and heavily influenced by local-scale variation.

Partly because they are embedded in terrestrial landscapes, communities in freshwater ecosystems are exposed to diverse physical and chemical stressors that interact across temporal and spatial scales (Ormerod et al. 2010; Waldock et al. 2018; Jackson et al. 2021). These interactions can be additive, synergistic or antagonistic (Piggott et al. 2015; Jackson et al. 2016; Bowler et al. 2017; Birk et al. 2020). Land use, for example, is one of the leading drivers of ecological degradation in both terrestrial and aquatic ecosystems (Reid et al. 2018; IPBES 2019). Yet, whilst these impacts may be exacerbated by climate change, this also provides a potential opportunity for natural management solutions. For example, riparian broadleaf woodland can buffer thermal and hydrological stress, improve water quality, (Chapter 2), all of which could potentially offset some of the effects of climate change and enhance ecological resilience (Broadmeadow and Nisbet 2004; Snyder and Johnson 2006; Marshall et al. 2014; Garner et al. 2015; Thomas et al. 2015; Van Looy et al. 2019; Vaughan and Gotelli 2019). Understanding the relationships between land use, climate and river ecosystems could therefore inform climate adaptation strategies based on riparian management.

Assessing the potentially interactive effects of climate change and land use is easier in systems where other human stressors are minimised. Upland streams are often affected by a smaller range of stressors than their lowland equivalents, whilst being especially vulnerable to climate change owing to their small thermal mass and sensitivity to changes in precipitation (Caissie et al. 1998). Besides the inherent importance of potential changes in headwaters, this may also provide an early warning signal to larger rivers, either where they are less sensitive to environmental change or where other stressors confound effects. It is also valuable for studies to have a sufficiently long-term perspective for climate change effects to be seen against a background of natural climatic and biological variability. This variability might include effects of nonlinear processes such as the NAO, or recovery from other widespread historical stressors such as acid deposition. For example, in upland Britain the acidifying effects of atmospheric deposition have left a legacy on communities, which could mask or exacerbate climate impacts (Durance and Ormerod 2009; Murphy et al. 2014). Likewise, there is a need to consider other sources of long-term change, such as ongoing forestry activities (Donald and Gee 1992; Helliwell et al. 2001; Briers and Gee 2004; Durance and Ormerod 2007), historical woodland clearing (Simmons 2003) and upland animal farming. So far, few such studies meet these requirements.

Here, a 40-year dataset of headwater stream macroinvertebrate abundances was used to address these gaps, i.e., to understand how upland freshwater communities have changed in relation to changes in climate, and how local catchment character (semi-natural broadleaf woodland *versus* more modified land use types) may mitigate effects. Thus, the aim of this study was to assess the long-term trends in community structure and functional diversity in relation to contrasting land use and acid-base status, and their interaction with climate variables. This extends analyses from 15 years ago (Durance and Ormerod 2007), with the addition of data from two broadleaf woodland streams, functional trait data, and continued changes in climate over this time. It was hypothesised that:

1. Taxonomic and functional diversity would decline, and composition would significantly change, but at rates that would be slower in catchments least modified by land management and acidification due to different climate sensitivities.
2. Loss of functional diversity would outpace declining taxonomic diversity, suggesting a loss of functional redundancy.
3. Local summer temperature and discharge, and climate extremes, would account for more variation in communities than winter or average annual conditions, or large-scale synoptic variables such as the NAO.

3.3 Methods

3.3.1 *Study sites and macroinvertebrate sampling*

Study sites used in this analysis comprised 16 perennial headwater streams situated in the Tywi catchment in upland Wales, UK, bordering the Llyn Brianne reservoir (5218°N 3145°W; Chapter 1, Figure 1.2). Each stream was of similar elevation, ca 200-400 metres above sea level, within a basin area of ca 180km^2 and < 35km inland. This meant that all were likely exposed to similar maritime and temperate climatic conditions, with previously recorded annual precipitation rates of around 1900 mm, and mean daily stream temperatures generally ranging from 0-20°C (Weatherley and Ormerod 1990; Durance and Ormerod 2007). Streams were characterised by four contrasting stream types, grouped by broad differences in land use and chemistry: semi-natural broadleaf woodland, managed as part of a nature reserve (BW: GI1 and GI2), actively managed and periodically clear-felled acidic coniferous woodland (AC: LI1 to LI4 and LI8), and intensively sheep-grazed moorlands that were either acid-sensitive (AM: CI1 to CI6 and LI5) or buffered by small calcite veins and therefore of circumneutral pH (CM: LI6 and LI7). From 1981 to 2020, macroinvertebrates were kick-sampled each spring and preserved, identified, and counted. Further details of study sites and sampling methods can be found in Chapter 1, Section 1.3. For the purpose of this study, macroinvertebrates were pooled to genus-level or higher for comparability with trait data.

3.3.2 *Community structure and function*

To assess changes in macroinvertebrate community composition and diversity, and taxonomic and functional properties, several community-level indices were calculated. These were total abundance, taxonomic richness, functional richness (FRic) and functional dispersion (FDis) as descriptors of taxonomic and functional diversity, while measures of composition were derived from non-metric multidimensional scaling (NMDS). Taxonomic diversity metrics used in this study were selected based on their ease of interpretation and comparability to recent evidence of invertebrate trends, as introduced in Section 3.2. Functional metrics were chosen to capture changes in the richness of and distribution of functional traits within communities, and FDis is closely related to other common measures such as Rao's quadratic entropy, functional divergence, and functional evenness (Laliberte and Legendre 2010; Mason et al. 2013; Swenson 2014). In addition to these, rarefied richness, and the standardised effect sizes (SES) of each functional diversity metric were calculated to assess whether changes were greater than could be accounted for by differences in species richness and/or abundance among samples. For example, lower than expected functional diversity could indicate low functional redundancy despite high taxonomic diversity, or *vice versa* (Chase 2007; Díaz et al. 2013; Kraft et al. 2015; Bruno et al. 2019).

To calculate functional diversity, a set of traits was selected from a publicly available database of European freshwater macroinvertebrate traits (Tachet et al. 2010). Despite a lack of scientific consensus on which traits should be used, here, functional traits were selected based on *a priori* hypotheses of their relationships with ecosystem functioning. These included traits that might affect the movement and transfer of nutrients and energy in the environment (Moretti et al. 2017; Mathers et al. 2018; Beck et al. 2022). Generally, these traits characterise the Eltonian niche, and are also loosely referred to as 'effect traits' (Suding et al. 2008). Trait grouping features were maximum body size, locomotive technique, food preference, and trophic guild, for which there were 7, 8, 9, and 7 individual traits, respectively (see Chapter 5, Table 5.1 for full list). For each trait and taxon, affinity scores of 0 to 3 or 5 were assigned based on a fuzzy-coding approach (Chevene et al. 1994), with dietary information supplemented with regional data from South Wales (Durance & Ormerod *unpublished*). In this way, taxa can be categorised, for example, as both shredders and grazers. Where taxa from study sample data were identified at coarser resolution than trait data, European freshwater taxa were filtered to UK-only species according to National Biodiversity Network Atlas records, and mean affinity scores across species were calculated. Affinity scores were then standardised so that the sum of traits within each grouping feature was 1.

FRic and FDis were derived from a Euclidean distance matrix of traits and abundances using R packages *ade4* (version 1.7.22) and *FD* (version 1.0.12.1) (Villéger et al. 2008; Laliberte and Legendre 2010; Laliberté et al. 2014; Thioulouse et al. 2018). FRic was calculated as the convex hull following reduction of the number of dimensions to 6 (Maire et al. 2015). FDis was calculated as the mean distance in multidimensional space of all taxa to their centroid. Subsequently, SES FRic and SES FDis were calculated using a standard null modelling approach with R's *picante* package, version 1.8.2 (Kembel et al. 2010). For SES FRic, randomisation was performed using "independentswap" within the *randomizeMatrix* function, reallocating taxa among samples whilst maintaining the observed richness. SES FDis was calculated using the null model "richness", which randomly reallocates abundances across taxa, whilst holding their identity constant (Mason et al. 2013).

To quantify community composition, non-metric multidimensional scaling (NMDS) in two dimensions using Bray-Curtis dissimilarities was used. Analyses were performed using the *metaMDS* function from the R package *vegan* (version 2.6.4) (Oksanen et al. 2022) separately for $\log_{10}(x+1)$-transformed taxon abundances and community-weighted mean (CWM) traits derived from *FD*. Transformation has been suggested to allow better comparison between taxon and trait composition (Schmera et al. 2014; White et al. 2017). From each NMDS analysis, both axes were extracted to assess long-term trajectories in community composition (Matthews et al. 2013).

3.3.3 *Climate data*

To relate community structure and function to climate-driven changes in stream environmental conditions, all available in-stream data were obtained. Discharge (Q m^3s^{-1}) data were only available for part of the study period (1996 to 2019) from a flume at LI1 (Nant Y Maen, SN8087052974). These were provided by Natural Resources Wales (NRW) and comprised 15-minute gauged records, subsequently averaged at monthly scale to reduce variability and uncertainty from stage-discharge equations. Values were standardised by dividing by catchment area (km^2) above the LI1 monitoring station. Similarly, in-stream temperatures were only available for a short period (2010-14), recorded every 15 minutes using Hobo temperature loggers in eight of the streams, two of each stream type; BW: GI1, GI2, AC: LI1, LI2, AM: CI1, CI4; and CM: LI6, LI7.

To generate a complete time series of discharge and water temperature, *in situ* datasets were calibrated against HadUK-Grid precipitation and air temperature data, and resulting models were used to provide estimates across the complete study period for each stream. Previous work has shown that in-stream conditions can be accurately predicted from local air temperatures and precipitation in these upland and predominantly rain-fed streams (Bradley and Ormerod 2001; Durance and Ormerod 2007). HadUK-grid data were downloaded from the Met Office Hadley Climate Programme online climate data repository at the highest available temporal resolution. In addition to the invertebrate sampling years, data were obtained for the past 100 years (1920 to 2019) to provide context of climatic changes for the area prior to study start. Daily precipitation and monthly mean air temperatures were obtained at 5 km spatial resolution, extracted and processed for each stream using *ncfd4* (version 1.2.1), *raster* (version 3.6.14) and *rgdal* (version 1.6.4) packages in R (Bivand et al. 2023; Hijmans 2023; Pierce 2023). To confirm that the data were representative of local conditions, HadUK-grid data were cross-checked against shorter runs of rain gauge and air temperature records within the catchment and nearby. These were found to be highly correlated (Pearson's $r > 0.9$) (Table A.1).

Estimations of discharge and water temperature for the full study period were obtained by constructing linear models between mean monthly climate and in-stream variables (Table 3.1). For each stream without water temperature data, linear models were constructed based on the mean slope and intercept from models of corresponding stream types. Although relationships have been shown to be largely linear, air temperatures below 0°C rarely drive freezing temperatures in streams at Llyn Brianne, and so estimated values were adjusted to a minimum of 0°C (Durance and Ormerod 2007). For discharge, although canopy interception and evapotranspiration from differences in land cover could affect discharge rates, vegetation has been shown to have little influence on flood flows in a similar upland catchment to the Tywi; Plynlimon (Kirby et al. 1991). Potential differences in discharge regime were therefore considered negligible and the same model was applied across all streams. Additional confirmation that hydrological trends were similar across all streams was made by comparing discharge at LI1 to two sites within 40 km of study streams, and these were found to be highly correlated (Pearson's $r = 0.9$; Table A.1).

Table 3.1 Linear relationships between climate data and in-stream conditions. Linear regression ($y = a + bx$) was used for measured mean monthly water temperature against mean monthly air temperature (Durance et al, in prep), and mean monthly discharge against mean monthly rainfall. p < 0.001 in all cases.

Variable	Site	Stream type	*a* (±SE)	*b* (±SE)	R^2 (%)	*F*	df
Temperature	CI1	AM	1.71 (0.168)	0.861 (0.0194)	97.7	1963	47
	CI4	AM	1.63 (0.162)	0.849 (0.0194)	97.9	1916	42
	GI1	BW	3.97 (0.17)	0.641 (0.0182)	97.3	1242	35
	GI2	BW	2.89 (0.229)	0.726 (0.0244)	96.9	883	29
	LI1	AC	3.27 (0.2)	0.659 (0.0224)	95.3	865	44
	LI2	AC	3.02 (0.2)	0.68 (0.0219)	96.3	961	38
	LI6	CM	3.44 (0.355)	0.722 (0.0371)	96.2	378	16
	LI7	CM	4.1 (0.191)	0.596 (0.0214)	95.8	774	35
Discharge	All	All	5.9 (2.1)	11.1 (0.3)	80.0	1090	265

From the climate-related stream variables, hereafter referred to as climate variables, a range of ecologically relevant statistics were calculated to assess effects on annual macroinvertebrate samples. These comprised variables considered to capture the effects of rising means, extremes, and differences in the timing of events that are predicted to drive different community responses (Sabater et al. 2022). For annual means and extremes, each year was defined as the 12 months prior to macroinvertebrate sampling in spring, thereby running from April to the following March. Seasonal (spring-summer and winter-autumn) variables were calculated in the same way for the antecedent April-September ("summer"), and October-March ("winter") separately, which typically reflect the warmer, drier and wetter, colder halves of the year. Climate data for the final three months prior to the last sampling occasion (2020) were not available at the time of this analysis, and so the final year was excluded.

Climate variables were compared using principal component analysis (PCA) with the *prcomp* function in R to determine general correlations, to reduce confounding effects in subsequent analyses, and to select those that best captured environmental variation in each of the ecologically relevant categories mentioned above. The final list of variables used in this study were annual mean and maximum temperature (°C), annual mean and minimum discharge ($m^3s^{-1}km^{-2}$, hereafter m^3s^{-1}), and seasonal mean temperature and discharge (see Table 3.2 for details). Due to the presence of some strong correlations between annual and seasonal scale variables (Table 3.2), these were separated in subsequent analyses. Within each temporal scale, only the pairwise relationship between Q.mean and Q.min (mean and minimum discharge) were correlated (r = 0.56) but this was considered low enough not to confound results.

In addition to local-scale variables, data for the winter NAO Index (December to March) were obtained as a comparison. Previous studies have shown macroinvertebrate communities to closely track changes in large-scale synoptic climate variables such as the NAO (e.g., Bradley and Ormerod 2002b). These data were obtained from the National Centre for Atmospheric Research, after Hurrell (2003). Pairwise comparisons with local-scale variables showed no correlation. However, for the purpose of comparing differences in explanatory power, these were analysed separately.

Table 3.2 *Hydrological and thermal ("climate") variables used, and their pairwise correlations. Pearson's correlation coefficients are provided for temperature (Tw) and discharge (Q) calculated at annual- (mean and monthly maximum, max) and seasonal- (summer, S and winter, W means) scale, and the North Atlantic Oscillation, NAO.*

Variable	Unit	Temporal scale	Statistic	Code
Water temperature	°C	Annual	Mean	Tw.mean
			Maximum	Tw.max
		Seasonal	Summer mean	Tw.S / summer Tw.mean
			Winter mean	Tw.W / winter Tw.mean
Discharge	m^3s^{-1}	Annual	Mean	Q.mean
			Minimum	Q.min
		Seasonal	Summer mean	Q.S / summer Q.mean
			Winter mean	Q.W / winter Q.mean

	Tw.max	Q.mean	Q.min	Tw.S	Tw.W	Q.S	Q.W	NAO
Tw.mean	0.38	-0.4	0.03	0.70	0.88	-0.25	0.10	-0.07
Tw.max		-0.17	-0.08	0.71	0.03	-0.40	0.03	0.19
Q.mean			0.56	-0.21	0.08	0.55	0.87	0.10
Q.min				-0.01	0.05	0.41	0.42	0.10
Tw.S					0.28	-0.18	-0.14	0.01
Tw.W						-0.22	0.22	-0.11
Q.S							0.06	0.02
O.W								0.11

3.3.4 *Statistical analyses*

Community composition

General differences in community composition between stream types were assessed using NMDS analyses, as detailed in Section 3.3.2. Statistical significance of differences was determined using PERMANOVA of Bray-Curtis distances, using the *adonis* function in the R package *vegan* (version 2.5.7) (Oksanen et al. 2020)*,* with 999 permutations. Since significance can be confounded by differences in within-group dispersion, multivariate homogeneity of group variances was assessed using the *betadisper* function*.* Some differences between stream types were detected, which were further tested using Tukey's *post-hoc* tests. For taxonomic data, significant differences (p < 0.05) in group dispersions were identified for all groups except between AC and BW, and CM and BW. For functional trait data, pairwise differences were significant for all except AC and AM, and CM and BW. However, based on visual inspection of plots, these differences were not thought to confound overall results.

Temporal trends

To determine the long-term trends in climate variables and invertebrate community indices, data were smoothed through time using generalised additive mixed models (GAMMs) using the *mgcv* (version 1.8.42) package in R (Wood 2017). This method allowed for both linear and nonlinear relationships, and is therefore less restrictive when analysing potentially complex data. For each community variable, an initial model just containing year and stream type as a smooth and fixed term, respectively, was fitted to provide a single mean trend across streams. An additional model was fitted by including stream type as a factor interacting with year. Where statistical significance was found from likelihood ratio tests (LRT, p < 0.05) between the two models, i.e., the interaction was significant, estimated trends were derived for individual stream types. All models were fitted using thin-plate smoothing splines for year, with the degree of smoothing selected using generalised cross-validation (GCV) (Wood 2000; Wood 2004). To account for differences in the intercept and site-level variation, stream type was also included as a fixed factor in each model, and individual stream was included as a random effect. Additionally, a temporal autocorrelation term with an autoregressive (AR) component of lag 1 was fitted to account for autocorrelation where evident (Pinheiro and Bates 2000). Dependent variables were log-transformed where necessary to meet the assumption of a Gaussian error distribution. Model fits were checked using plots of residuals, and final models were fitted with restricted maximum likelihood (REML).

Change over time was calculated by extracting the smoothed estimates for the second and penultimate year in each timeseries. This method has been recommended since first and last estimates from nonlinear models are considered less reliable (Hewson and Noble 2009). For macroinvertebrate models, long-term trends were therefore calculated from 1982 to 2019, while climate trends were calculated to 2018 based on the availability of data. Where data had been log-transformed, changes were calculated following back-transformation.

Climate effects

To assess the relationships between macroinvertebrate communities and climate variables, GAMMs were used, again enabling nonlinear and linear climate effects to be captured. Initial models included interaction terms between climate and stream type, and between climate variables where these were considered ecologically relevant. For example, the combined effects of low flow and high temperatures have been shown to be particularly detrimental (Aspin et al. 2018), which might occur suddenly (extreme drought), or over longer-time frames (means). Additionally, the impacts of predicted warmer wetter summers, and hotter drier summers on average (IPCC 2021) are largely unknown. Moreover, local stream type could further influence effects by providing environmental buffering, or enhancing the ecological resilience of communities. The models constructed here therefore aimed to disentangle some of these potentially complex and interactive effects. For each community variable, two global models were fitted with three-way interactions as follows:

1) y ~ te(Tw.mean, Q.mean, by = stream type) + te(Tw.max, Q.min, by = stream type)
2) y ~ te(Tw.W, Q.W, by = stream type) + te(Tw.S, Q.S, by = stream type)

where ‘te’ represents a two-way tensor product smooth, allowing for an interaction between two numerical variables (e.g., Tw.mean and Q.mean) and ‘by’ indicates an interaction between the te smooth and a factor, such that the smooth was refitted in each of the four stream types.

The primary aim in this study was to determine the best predictors of long-term macroinvertebrate community change, and so models were refined in a three-step process.

First, to test the significance of stream type interactions, global models were compared to those without the interaction using LRTs. Where the interaction was not found to be statistically significant ($p > 0.05$), it was removed. Secondly, climate interactions were assessed using a similar approach, refitting model terms using a tensor interaction (ti) to isolate the interaction from main climate variable effects (Wood 2017). Where this was not statistically significant following LRT, interaction terms were removed. In the final step, models were further refined using a process of backward elimination of non-significant terms from the model output, comparing the simplified and previous model, and selecting the model with the lowest AIC value. Final models were refitted with REML. In addition to the terms above, each model included stream type as a fixed factor to control for differences in the intercept, and site as a random term to account for repeated measures and unbalanced design. Where necessary, a first-order AR term was included, and dependent variables were log-transformed to meet the assumptions of a Gaussian distribution. Model checks were conducted via visual inspection of residual plots.

The ability of the GAMMs to account for temporal changes in the macroinvertebrate community was assessed in three ways: *i*) overall agreement between observed and predicted values (R^2), *ii*) comparing the magnitude of observed and predicted long-term trends, and *iii*) accuracy of predictions in different stream types, using root-mean squared error (RMSE) and normalised RMSE. For *i*, two additional GAMMs were fitted using either just the NAO Index and a fixed effect of stream type, or just a fixed effect of stream type to provide benchmarks to compare against models using local climate variables. For *ii*, predicted long-term trends were calculated in an equivalent manner to observed values detailed above (*Temporal Trends*), by smoothing model predictions and extracting values from the second (1982) and penultimate (2018) years to give an overall estimate of change (Hewson and Noble 2009). Estimates were temporally smoothed by stream type, where effects of climate were found to significantly differ, thereby deriving a separate trend for each stream type.

To visualise the relationships with climate, partial effects plots were obtained from each model by holding all other variables constant at their median whilst predicting across a gradient for the variable of interest. To aid interpretation of interactive effects, predictions were made under different climate scenarios, such as “warm” versus “cool”, and “wet” versus “dry” conditions, by holding respective terms in each interaction at their upper and lower quartiles (Harrell 2015). Estimated effect sizes over the interquartile range of each climate variable were obtained using the *emmeans* package (version 1.8.4.1) in R (Lenth et al. 2023), and standardised by the mean to provide a summary of overall effects. All analyses presented here, and for the remainder of this thesis, were conducted using R statistical software, (versions 3.5.1, 4.0.3, and 4.2.2, R Core Team 2018, 2021 and 2023), and plots were produced using the *ggplot2* package, (version 3.4.1) (Wickham 2016).

3.4 Results

3.4.1 *Climate trends*

In the context of the last ca. 100 years since 1920, marked climate changes have occurred at Llyn Brianne. Following a cold snap in the early 1960s air temperatures have risen rapidly, and particularly so during the study period (Figure 3.1a). In all but four years within the last three decades mean air temperatures surpassed the overall mean since 1920 (7.43°C), with eight of the ten hottest years on record during this time reaching the highest recorded temperature in the year 2006; > 1.5°C above the mean. Correspondingly, estimated mean annual water temperatures were also highest in this year at 9.3°C; ca. 1°C above the mean for the study period and reflecting an exceptionally warm summer (Figure 3.1b). Temporal trends fitted with GAMMs were highly statistically significant for all stream temperature variables ($p < 0.001$). Between 1981 and 2017 (corresponding to the 1982 and 2018 macroinvertebrate samples), mean annual temperature increased by an estimated 0.79°C (9.5% above the study mean), and maximum monthly temperatures rose by 0.61°C (+4.7%). At seasonal scale, summer mean temperatures rose by 0.67°C (+6.2%), while winter temperatures had the largest magnitude of change, increasing by 0.89°C (+14.7%).

Changes in precipitation and discharge appeared less pronounced than temperature, though a large amount of variability was apparent, including extreme wet and dry years during the study. Annual precipitation since 1920 reached the two highest peaks on record in the years 1998 and 2000 (Figure 3.1c). In the year commencing April 2000, annual precipitation was more than 700 mm above the overall mean since 1920 (1838 mm). Additionally, five of the ten wettest years on record since 1920 occurred within the last 30 years. Between 1981 and 2017, estimated mean annual discharge (Q.mean) declined by 1.9 m^3s^{-1} (2.9% below the study mean) (Figure 3.1d). Mean winter discharge (Q.W) declined by 6.3 m^3s^{-1} (-8.0%), contrasting with summer discharge (Q.S) which increased by 1.9 m^3s^{-1} (+3.9%). Lastly, the driest month of the year (Q.min) became an estimated 5.1% drier (-1.2 m^3s^{-1}). Discharge data running from 1920 onwards (estimated from precipitation) showed a slight shift during the 1970s in the frequency of the driest month of the year more often occurring in the summer half rather than the winter half of the year, and particularly in spring (Appendix, Figure A.1). Other notable climate trends were changes in maximum daily precipitation in each year. In this instance, there was a subtle but apparent reduction in that volume of rainfall, and year-to-year variability following the 2000 peak in total annual precipitation. From 2005 onwards, maximum daily precipitation remained below the overall mean (53 mm) for 13 consecutive years. This was followed, however, by the highest volume of daily rain on record, far exceeding any other event, and a pattern unlike any in the past century (Figure A.2).

3.4.2 *Macroinvertebrate composition and diversity trends*

Across streams at Llyn Brianne, community composition clearly differed in relation to stream type (Figure 3.2). Differences were statistically significant for both taxonomic ($F_{3,454}$ = 59, p = 0.001, R^2 = 0.28) and functional ($F_{3,454}$ = 80, p = 0.001, R^2 = 0.35) data. In taxonomic NMDS analysis, axis 1 largely separated the stream types, especially acidic from circumneutral streams, and also increasing abundances towards BW and CM streams (Figure 3.2a). Axis 2 reflected differences in communities characterised by the triclads (*Phagocata* and *Crenobia*), some of the dominant Plecoptera (*Amphinemura, Protonemura,* and *Nemoura*), and *Nemurella* and *Caenis,* among others. While this partly differentiated AM and AC stream communities, axis 2 also appeared to be associated with time. NMDS ordination of functional traits (Figure 3.2b) highlighted compositional differences related to body size and trophic position across axis 1, with AM communities dominated more by larger-bodied predatory taxa compared to other stream types. Axis 2 reflected differences relating to the dominance of shredders in AC streams, contrasting with grazers in the open moorlands and BW streams. AC streams also had fewer passive filterers, water-swimmers, organisms permanently attached to the substratum, and flying taxa, i.e., those that may be sensitive or more responsive to disturbance events.

All community composition and diversity indices changed significantly over time at Llyn Brianne, except for rarefied richness (Table 3.3 and 3.4). GAMM analyses showed that, after controlling for the effects of time, the fixed effect of stream type significantly influenced community diversity and composition, for all indices except SES FRic. In more than 50% of instances, temporal trends differed among stream types, particularly with regards to functional measures (LRT $p < 0.05$). However, trends were often complex and nonlinear, with no consistent evidence of decline (Figure 3.3). Overall, evidence suggested that the largest changes occurred in abundance, taxonomic composition (NMDS2), SES FRic, and functional composition (NMDS1). Nonlinearity was also particularly apparent for abundance, richness, and taxonomic composition. The greatest changes occurred during 1993-4, and 2004-5, across multiple indices, and a further decline in abundance was also seen in AM streams in 2009-11. Trends in abundance were among the most prominent, and an estimated decline of 52.5% occurred in AC streams between 1982 and 2019. In CM and BW streams, absolute losses in abundance were either similar (CM) or twice as large (BW) as in AC streams, though percentage losses were lower (BW = 46%, CM = 22%), and trends were not statistically significant (Table 3.3). For taxonomic richness, losses of 1–4 taxa were also observed. Although these were considered small, and only statistically significant for acid streams, this equated to 10.1 and 13.3% of taxa in BW and CM communities on average compared to 7.1 and 2.6% in AC and AM, respectively.

Trends in FRic (Figure 3.3f) and SES FRic (Figure 3.3h) showed some of the largest contrasts among streams, notably between AM and CM. Estimated change in FRic between 1982 and 2019 revealed a 23.7% loss in CM streams, compared to a 27.6% increase in AM. Moreover, when using SES FRic, trends were extenuated, suggesting faster rates of change than could be accounted for by taxonomic richness. However, despite apparent increases in FRic in AM streams, the rate of increase appeared to slow during the last two decades, with evidence of a reverse in the direction of the trend in recent years. Similar changes in the last decade of the study were seen in the functional composition of AC streams (NMDS1). Here, an initial increase across NMDS1 during the mid-2000s reflected a temporary shift towards greater detritivore and grazer prevalence and fewer predators, while dramatic changes thereafter reflected a large shift in the reverse direction. Besides these details, analysis of community composition revealed that all stream types experienced a progressive shift over time such that by the end of the study, taxonomic composition differed considerably from the start, most notably relating to a decline in plecopteran detritivores.

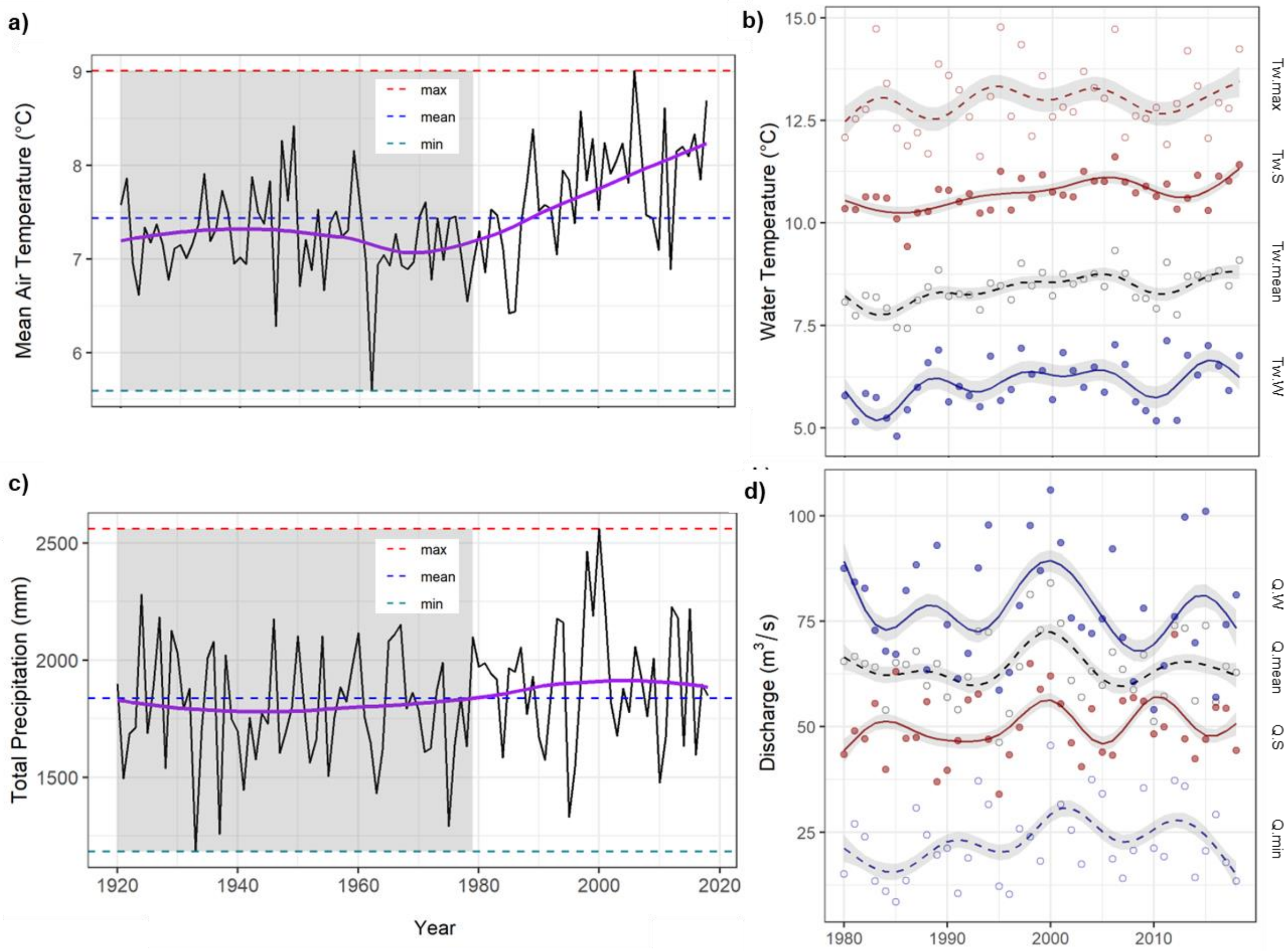


*Figure 3.1 Long-term trends in climate and corresponding in-stream conditions for the study area. Years correspond to macroinvertebrate samples in the following spring, and each year includes the first 3 months of the subsequent sample year. Plots show **a)** annual mean air temperatures from 1920**, b)** annual and seasonal stream temperatures from 1980, **c)** annual total precipitation from 1920, and **d)** annual and seasonal discharge from 1980. Purple trendline over the ca. 100-year timeseries fitted using a loess smoother, while trends for in-stream conditions were modelled using GAMMs.*

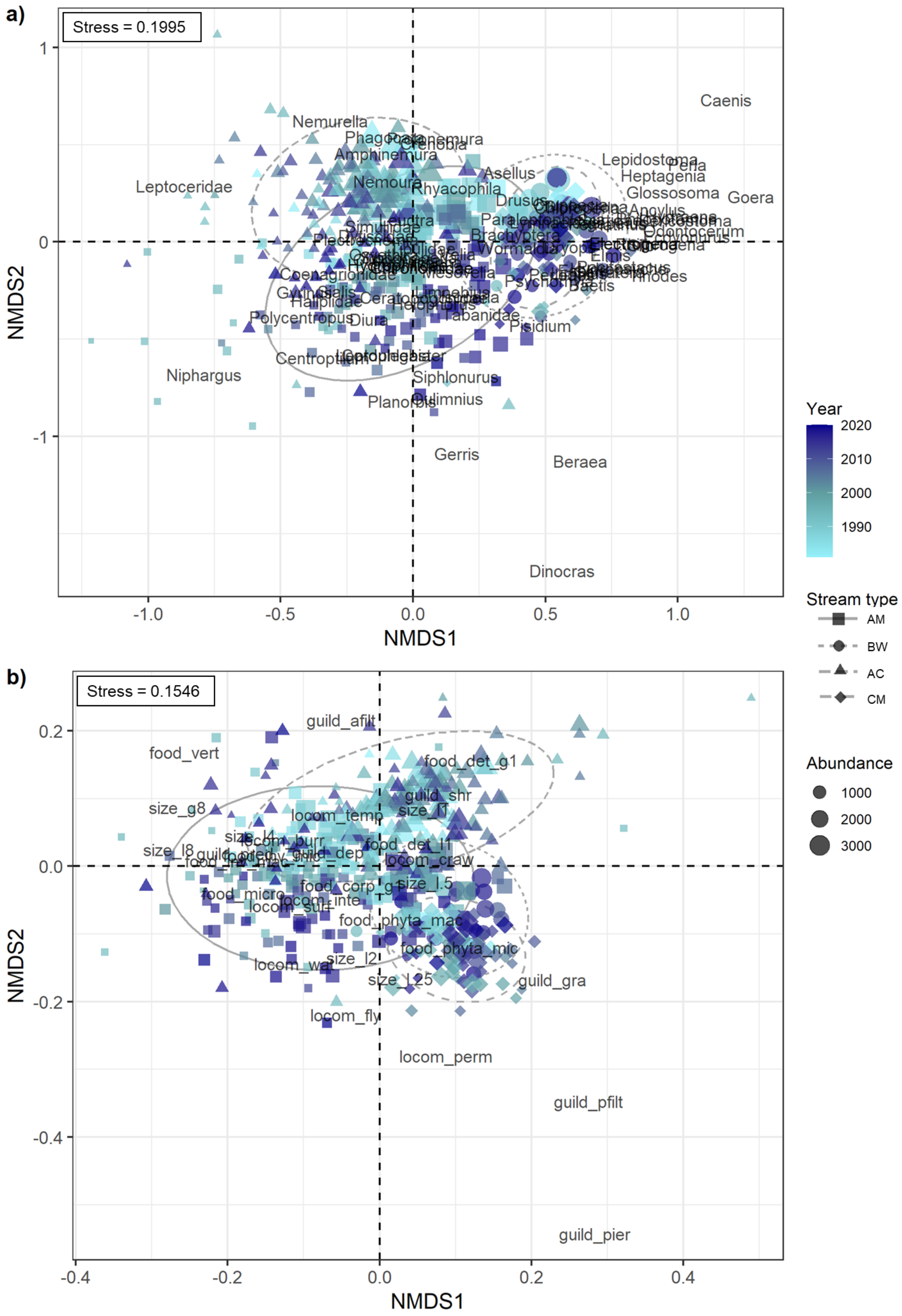


*Figure 3.2 Non-metric multidimensional scaling of taxonomic and functional composition for sample data. Plot **a)** shows taxonomic composition, and **b)** functional trait composition. Overlaying text represents species or trait scores.*

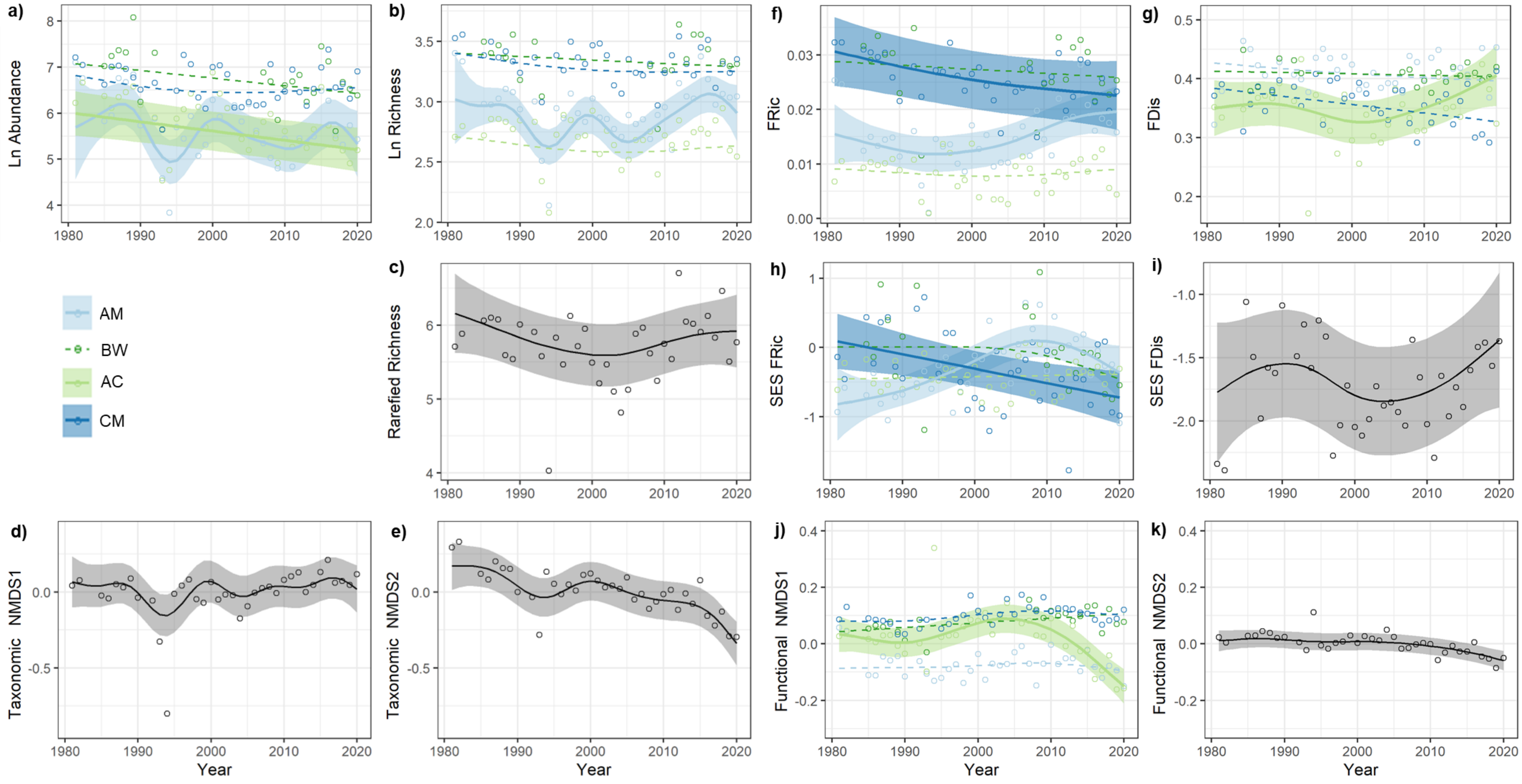


Figure 3.3 *Long-term trends in macroinvertebrate taxonomic and functional composition and diversity. Plots* ***a-e)*** *show trends in taxonomic indices, and plots* ***f-k)*** *show trends in functional indices. Trendlines were fitted using GAMMs. Where stream type was a significant interacting factor, results are shown for each stream type. Solid lines with 95% confidence intervals reflect statistically significant trends ($p < 0.05$). Points represent mean values across streams.*

Table 3.3 *Model outputs and estimated long-term trend in macroinvertebrate taxonomic composition and diversity. Results are shown for each level of stream type where this was found to significantly influence the trend (LRT = likelihood ratio test results showing the significance (LRT p) of year * stream type interaction).*

Response variable	LRT *p*	Term	Level	edf	*F*	*p*	R^2	Estimate		Change	%
								1982	2019		
Abundance	*0.0002*	Stream type			4.23	*0.006*	0.30				
		s(Year)	BW	1	1.39	0.2		1169	630	-540	-46.2
			CM	2	0.96	0.5		936	732	-204	-21.8
			AC	1	12.26	*0.0005*		426	202	-223	-52.5
			AM	7	4.35	*<0.0001*		348	275	-74	-21.2
Richness	*< 0.0001*	Stream type			16.32	*< 0.0001*	0.52				
		s(Year)	BW	1	0.44	0.5		30	27	-3	-10.1
			CM	2	1.98	0.3		30	26	-4	-13.3
			AC	2	1.98	0.1		15	14	-1	-7.07
			AM	7	6.19	*<0.0001*		20	20	-1	-2.63
Rarefied richness	0.6	Stream type			5.53	*0.001*	0.26				
		s(Year)		3	2.35	0.058		6.1	5.9	-0.2	-3.43
Composition NMDS1	0.6	Stream type			24.89	*< 0.0001*	0.65				
		s(Year)		8	3.87	*0.0003*		0.05	0.05	-0.001	-0.01
Composition NMDS2	0.8	Stream type			19.50	*< 0.0001*	0.49				
		s(Year)		2	24.14	*< 0.0001*		-0.01	-0.32	-0.30	2479

Table 3.4 *Model outputs and estimated long-term trend in macroinvertebrate functional composition and diversity. Results are shown for each level of stream type where this was found to significantly influence the trend (LRT = likelihood ratio test results showing the significance (LRT p) of year * stream type interaction).*

Response variable	LRT *p*	Term	Level	edf	F	*p*	R^2	Estimate		Change	%
								1982	2019		
FRic	*0.003*	Stream type			16.94	*< 0.0001*	0.55				
		s(Year)	BW	1	0.30	0.6		0.028	0.026	-0.002	7.55
			CM	3	6.67	*0.01*		0.030	0.023	-0.007	-23.7
			AC	3	0.66	0.6		0.009	0.008	-0.001	-8.45
			AM	3	9.00	*< 0.0001*		0.015	0.019	0.004	27.6
FDis	*0.01*	Stream type			3.57	*0.01*	0.22				
		s(Year)	BW	1	0.01	0.9		0.41	0.41	-0.003	-0.71
			CM	1	1.56	0.2		0.38	0.34	-0.032	-8.59
			AC	4	3.79	*0.004*		0.35	0.38	0.028	7.89
			AM	2	1.81	0.3		0.43	0.41	-0.023	-5.23
SES FRic	*0.0001*	Stream type			1.08	0.4	0.12				
		s(Year)	BW	2	0.69	0.3		-0.05	-0.42	-0.37	-681
			CM	1	10.45	*0.001*		0.08	-0.70	-0.78	-986
			AC	1	0.18	0.7		-0.46	-0.39	0.07	14.3
			AM	3	11.67	*<0.0001*		-0.81	-0.30	0.51	62.4
SES FDis	1.0	Stream type			10.68	*< 0.0001*	0.33				
		s(Year)		4	4.00	*0.009*		-1.78	-1.35	0.43	23.9
Composition NMDS1	*0.002*	Stream type			8.85	*< 0.0001*	0.47				
		s(Year)	BW	1	1.85	0.2		0.04	0.10	0.06	134
			CM	2	1.41	0.3		0.07	0.09	0.02	33.6
			AC	10	24.98	*< 0.0001*		0.06	-0.10	-0.16	-262
			AM	2	1.07	0.5		-0.06	-0.07	-0.005	-8.04
Composition NMDS2	0.3	Stream type			27.89	*< 0.0001*	0.67				
		s(Year)		4	14.55	*< 0.0001*		-0.003	0.005	0.008	282

3.4.3 *Effects of climate on upland stream communities*

Results of GAMMs with climate variables showed that temporal changes in all aspects of community composition and diversity were significantly correlated with climate variables in some way. However, the exact permutations of climate variables, and the proportion of variation explained varied considerably across community indices. Overall variance (R^2) was best explained by annual-scale variables, at 3-13% above the equivalent baseline models that only contained stream type (Table A.2). Of these, total abundance, taxonomic composition (NMDS2), and functional composition (NMDS1) had the highest R^2 values (≥ 10%). These indices were also among those with evidence of large temporal changes (Table 3.3 and 3.4). Seasonal-climate variables explained up to 10% of the variance in abundance, and the largest amount of the overall changes in taxonomic composition (NMDS1) and SES FRic, with 9% and 4%, respectively. These variables also explained only slightly less variation than annual-scale models in several cases, while local scale variables almost always explained more variance than the NAO.

At annual scale, most taxonomic indices were related to all climate variables, with evidence of interactions between temperature and discharge, and between these and stream type, particularly for composition (Table 3.5). Functional indices, however, were more commonly associated with Q.min, and permutations of other variables within each model varied (Table 3.6). Seasonal scale variables most commonly associated with change included both summer and winter conditions for taxonomic indices (Table 3.7), and more often just winter for functional indices (Table 3.8). Contrary to expectations (Hypothesis 3), in no instance were summer temperature and discharge found to have an interactive effect, unlike the equivalent winter variables and despite interactive effects of Tw.max and Q.min in annual scale models that might be expected to reflect summer droughts. Additionally, significant interactions between climate variables and stream type were less common when using seasonal scale variables than annual, and were most commonly associated with effects on composition. When such interactions were observed, acid streams typically responded differently from the other stream types.

Overall, relationships between macroinvertebrates and climate variables tended to be complex, particularly with regards to discharge. Effects on abundance were among the most pronounced, and generally representative of effects on other measures. The interactive effects of Q.mean and Tw.mean on abundance demonstrates this complexity (Figure 3.4a). Here, the largest differences appeared to occur across a gradient of mean temperature when mean discharge was high. When controlling for other variables in the model and predicting effects of Tw.mean under wet and dry climate scenarios (Figure 3.4b), abundance increased by an estimated 21% of the mean (CL: -0.5 –43%) per 1°C rise across the IQR for Tw.mean during wet years, and contrastingly declined by an estimated 7.5% (CL: -23 – 7.9%) in dry years. Effects of Q.mean were more complex. In cool conditions, i.e., the lower quantile for Tw.mean, abundance increased by an estimated 9% (CL: -58 – 24%) across the interquartile range (IQR; +10.4 m^3s^{-1}), and by as much as 28% (CL: 6.4 – 51%) when conditions were warm. Overall, these results highlight that abundance was highest in warm, wet years than any other combination of Q.mean and Tw.mean (Figure 3.4a). Whereas, at the highest discharge volumes (~ > 75 m^3s^{-1}), which were more likely to occur at cooler temperatures, abundance was at its lowest.

Across a gradient of Tw.max (Figure 3.4), abundance decreased by a similar amount to average warm, dry conditions; 8% (CL: 0.9 – 15%) of the mean for every 1°C rise across the IQR. Contrary to expectations, declines in abundance were also correlated with increasing Q.min, though this was the most complex of all relationships with an apparent bi- or tri-modal response. Higher discharge rates during the driest month of each year were related to a 10% decline (CL: -29 – 9%) across the IQR (+14 m^3s^{-1}). Although effects were less pronounced, rising Tw.max over the IQR (+1.3°C), and increasingly wet weather during the driest month of the year were estimated to corresponded to a loss of 1–2 taxa. However, similar increases to those seen for abundance were estimated for years with higher Tw.mean or higher Q.mean, and these effects were not interactive.

As perhaps the strongest observed impacts, rising summer temperatures across the IQR (+0.7°C) were associated with 23% (CL: 5 – 41%) loss of individuals with respect to the mean, or 33% per 1°C (Figure 3.5a). Diverging effects of summer temperatures on SES FRic were also evident (Figure 3.5b), highlighting functional losses in BW and CM streams, contrasting with increases in acid streams. However, these results were only individually significant for AM ($F = 17.6$, $p < 0.0001$), and the overall model R^2 was considerably low (0.05).

Evidence from GAMMs also revealed significant effects of climate to composition, and particularly to functional composition (NMDS2; $F = 37.9$, $p < 0.0001$) (Table 3.8). In this instance, linear declines in NMDS2 with rising summer temperatures reflected a compositional shift, with declines in detritivorous (generally the most abundant) taxa occurring across all types. Results from models including winter conditions revealed that rising winter temperatures were associated with an increase in most biodiversity measures (Figure 3.6). For example, effects on richness showed 1-2 additional taxa for 1°C of winter warming. Conversely, increasing discharge in both summer and winter correlated with declines, particularly when winters were cool. There was also evidence that warmer winters promoted predatory taxa in AC streams, similarly to warmer years on average. However, extreme temperatures, especially when conditions were dry, negatively impacted predatory taxa (according to NMDS1 scores) and instead favoured secondary consumers, and particularly grazers (Figure A.3).

In contrast to findings that annual scale variables explained more variance overall, results indicated that seasonal climate variables estimated long-term trends (% change over time) more accurately (Table A.3 and A.4). Of the taxonomic indices and stream types shown to have statistically significant and directional changes over time (abundance and composition NMDS2), seasonal variables explained an estimated 36-40% of the trend, though over-estimation was apparent for losses in AM abundance by almost 3.5 times. Additionally, although declines in abundance were not statistically significant for BW and CM streams, estimates from seasonal GAMMs corresponded to 41 and 93% of observed declines, respectively. For functional indices that showed the largest changes over time (SES FRic and NMDS1), seasonal GAMMs explained an estimated 40-92% of trends. However, measures of RMSE for each stream type revealed that mean error was almost always greater than the observed difference between the start (1982) and end (2018) of the study, highlighting that conclusions based on comparisons of individual time points such as this should be treated with caution.

In instances where long-term trends and/or climate effects differed with stream type, model goodness of fit (RMSE) for each stream type largely supported overall R^2 comparisons (Table A.2). That is, annual-scale climate variables often had lower estimation error compared to other model types, especially for SES FRic as per overall model R^2. Comparisons of RMSE between stream types revealed no consistent pattern of estimation error in any particular stream type. However, normalised values indicated greatest error (19% on average) in BW streams, compared to 17% in CM streams, and 13 and 14% in AC and AM, respectively. Similar results were found for mean error based on seasonal scale climate models, with 19, 17, 11, and 14% error for streams, respectively.

Table 3.5 *Summary of annual-scale climate models for stream macroinvertebrate taxonomic composition and diversity. Results of generalised additive mixed models are shown for each level of stream type where this was found to significantly influence effects (LRT p < 0.05).*

Response	Predictors	Level	edf	*F*	*p*	sig	R^2
Ln Abundance	Stream type			3.73	*0.01*	**	0.30
	Tw.mean * Q.mean		8	4.76	*< 0.0001*	***	
	Tw.max		1	9.48	*0.002*	**	
	Q.min		7	6.94	*< 0.0001*	***	
Richness	Stream type			18.34	*< 0.0001*	***	0.58
	Tw.mean		1	8.46	*0.005*	**	
	Q.mean		6	3.71	*0.002*	**	
	Tw.max * Q.min		8	4.84	*< 0.0001*	***	
Rarefied Richness	Stream type			4.02	*0.008*	**	0.27
	Tw.mean * Q.mean by stream type	BW	5	1.11	0.3		
		CM	3	3.00	*0.04*	*	
		AC	3	0.48	0.7		
		AM	4	0.19	1		
	Tw.max * Q.min by stream type	BW	3	0.34	0.8		
		CM	3	0.95	0.4		
		AC	5	3.37	*0.003*	**	
		AM	3	3.29	*0.01*	*	
Taxonomic NMDS1	Stream type			19.61	*< 0.0001*	***	0.63
	Tw.mean		1	4.67	*0.03*	*	
	Tw.max * Q.min by stream type	BW	4	0.51	0.6		
		CM	3	0.15	0.9		
		AC	6	1.72	0.1		
		AM	13	5.13	*< 0.0001*	***	
Taxonomic NMDS2	Stream type			10.48	*< 0.0001*	***	0.48
	Tw.mean * Q.mean		5	8.10	*< 0.0001*		
	Tw.max * Q.min by stream type	BW	6	2.52	*0.03*	*	
		CM	3	0.88	0.45		
		AC	12	5.27	*< 0.0001*	***	
		AM	11	1.56	0.10		

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

Table 3.6 *Summary of annual-scale climate models for stream macroinvertebrate functional composition and diversity. Results of generalised additive mixed models are shown for each level of stream type where this was found to significantly influence effects (LRT p < 0.05).*

Response	Predictors	Level	edf	*F*	*p*	sig	R^2
FRic	Stream type			15.63	*< 0.0001*	***	0.51
	Q.min		3	7.83	*< 0.0001*	***	
FDis	Stream type			3.32	*0.02*	*	0.22
	Q.mean		1	1.95	0.2		
	Tw.max * Q.min		11	4.61	*< 0.0001*	***	
SES FRic	Stream type			0.57	0.6		0.03
	Tw.mean		1	6.52	*0.01*	*	
	Q.min		1	1.76	0.2		
SES FDis	Stream type			10.28	*< 0.0001*	***	0.31
	Q.min		1	5.05	*0.03*	*	
Composition NMDS1	Stream type			10.21	*< 0.0001*	***	0.46
	Tw.mean * Q.mean		3	3.15	*0.03*	*	
	Tw.max * Q.min by stream type	BW	3	0.18	0.9		
		CM	3	0.03	1		
		AC	15	6.45	*< 0.0001*	***	
		AM	3	1.47	0.2		
Composition NMDS2	Stream type			19.21	*< 0.0001*	***	0.67
	Tw.mean * Q.mean by stream type	BW	3	0.43	0.7		
		CM	4	1.40	0.2		
		AC	5	1.73	0.1		
		AM	3	3.69	*0.01*	*	
	Tw.max * Q.min		10	1.62	0.1		

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

Table 3.7 *Summary of seasonal-scale climate models for stream macroinvertebrate taxonomic composition and diversity. Results of generalised additive mixed models are shown for each level of stream type where this was found to significantly influence effects (LRT p < 0.05).*

Response	Predictors	Level	edf	*F*	*p*	sig	R^2
Ln Abundance	Stream type			5.32	*0.001*	**	0.28
	Tw.S		1	19.22	*< 0.0001*	***	
	Q.S		1	12.85	*0.0005*	***	
Richness	Stream type			24.2	*< 0.0001*	***	0.57
	Tw.S		2	7.01	*0.001*	*	
	Q.S		3	2.87	*0.04*	*	
	Tw.W*Q		7	2.29	*0.03*	*	
Rarefied Richness	Stream type			5.05	*0.002*	**	0.25
	Tw.W*Q		8	2.10	*0.04*	*	
Composition NMDS1	Stream type			23.75	*< 0.0001*	***	0.69
	Tw.S		2	1.97	0.2		
	Q.S		2	2.26	0.09		
	Tw.W * Q by stream type	BW	5	0.38	0.8		
		CM	3	0.01	1		
		AC	3	0.25	0.9		
		AM	17	7.53	*< 0.0001*	***	
Composition NMDS2	Stream type			8.82	*< 0.0001*	***	0.45
	Tw.S		1	15.66	*< 0.0001*	***	
	Tw.W * Q		12	2.68	*0.002*	**	

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

Table 3.8 *Summary of seasonal-scale climate models for stream macroinvertebrate functional composition and diversity. Results of generalised additive mixed models are shown for each level of stream type where this was found to significantly influence effects (LRT p < 0.05).*

Response	Predictors	Level	edf	*F*	*p*	sig	R^2
FRic	Stream type			15.61	*< 0.0001*	***	0.51
	Tw.W		1	4.75	*0.03*	*	
FDis	Stream type			3.42	*0.02*	*	0.20
	Tw.W * Q		8	2.91	*0.004*	**	
SES FRic	Stream type			0.54	0.7		0.05
	Tw.S	BW	1	0.38	0.6		
	by stream type	CM	2	1.82	0.1		
		AC	1	0.67	0.4		
		AM	2	17.62	*< 0.0001*	***	
SES FDis	Stream type			10.29	*< 0.0001*	***	0.31
	Q.W		4	1.52	0.1		
Composition NMDS1	Stream type			8.34	*< 0.0001*	***	0.40
	Tw.W*Q	BW	3	0.29	0.8		
	by stream type	CM	3	0.29	0.8		
		AC	5	9.27	*< 0.0001*	***	
		AM	3	1.02	0.2		
Composition NMDS2	Stream type			18.93	*< 0.0001*	***	0.66
	Tw.S		1	37.90	*< 0.0001*	***	
	Q.S		3	3.12	*0.03*	*	

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$

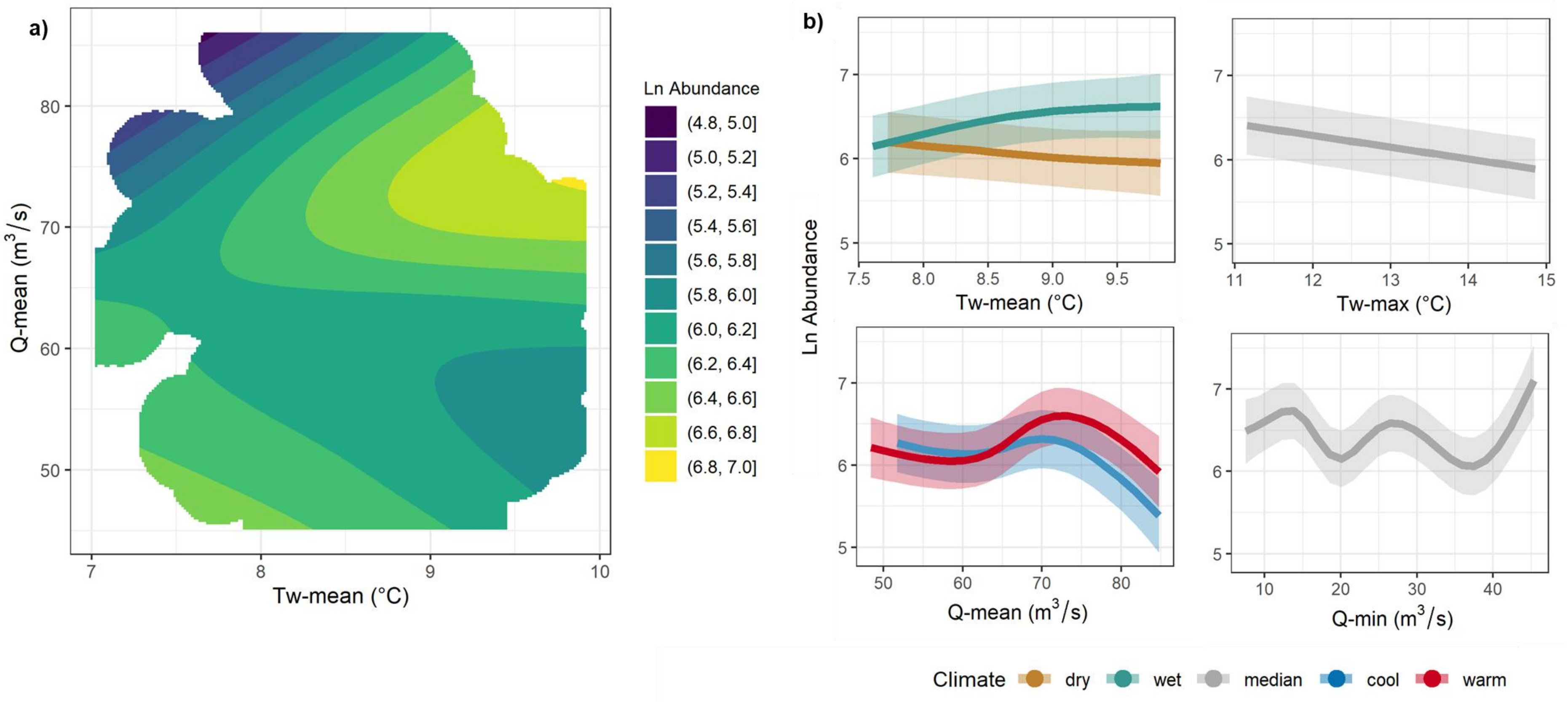


*Figure 3.4 Predicted partial effects of climate variables on macroinvertebrate abundance. In all plots, abundance was log-transformed. The contour plot in **a)** shows interactive effects of Tw.mean and Q.mean, while **b)** shows partial effects of all model terms, including effects of Tw.mean and Q.mean under different climate scenarios, holding other model terms constant. Grey/median line used where there was no interaction with other climate variables.*

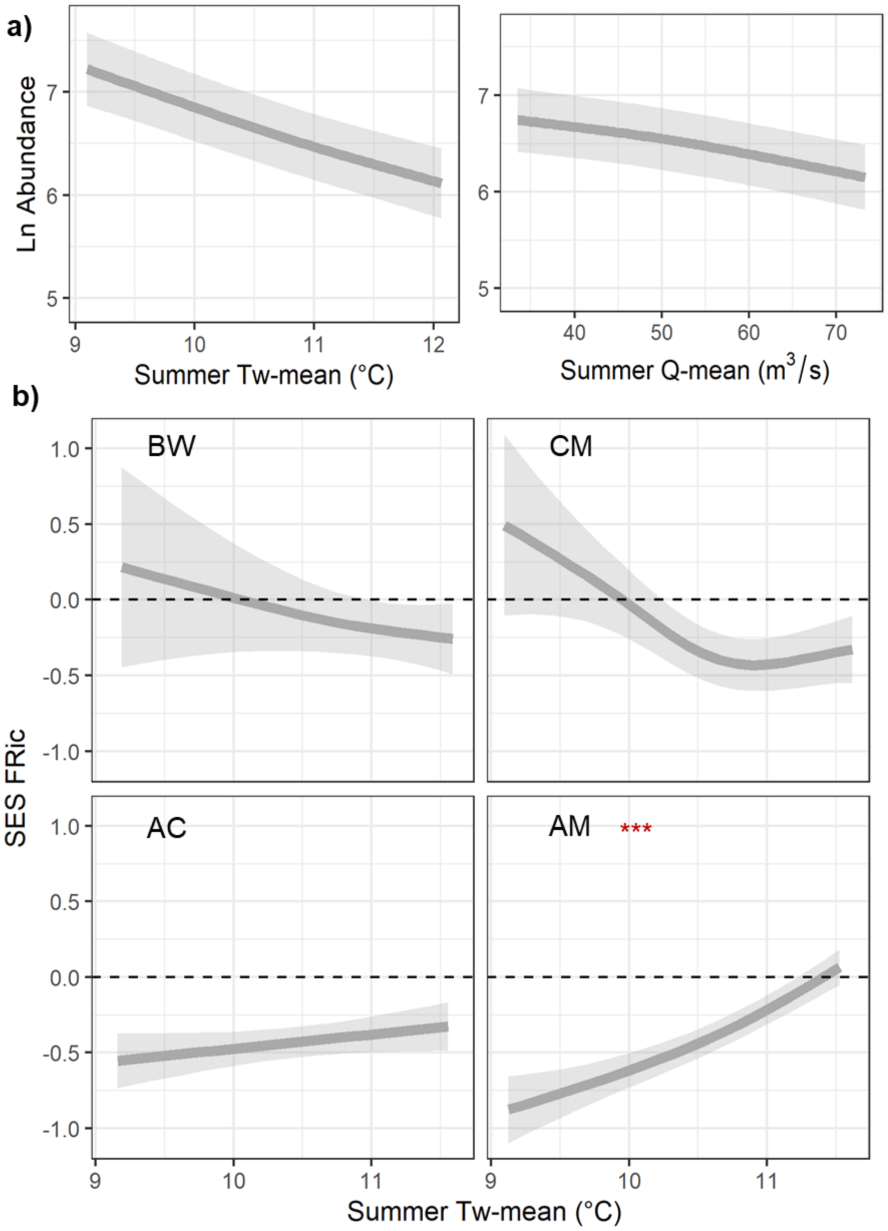


*Figure 3.5 Predicted partial effects summer conditions on abundance and SES FRic. Plot **a)** shows effects of summer Tw.mean (Tw.S) on abundance (log transformed), and **b)** shows effects of summer temperatures on SES FRic within each level of stream type; only the effect for AM was individually significant ($p < 0.001$).*

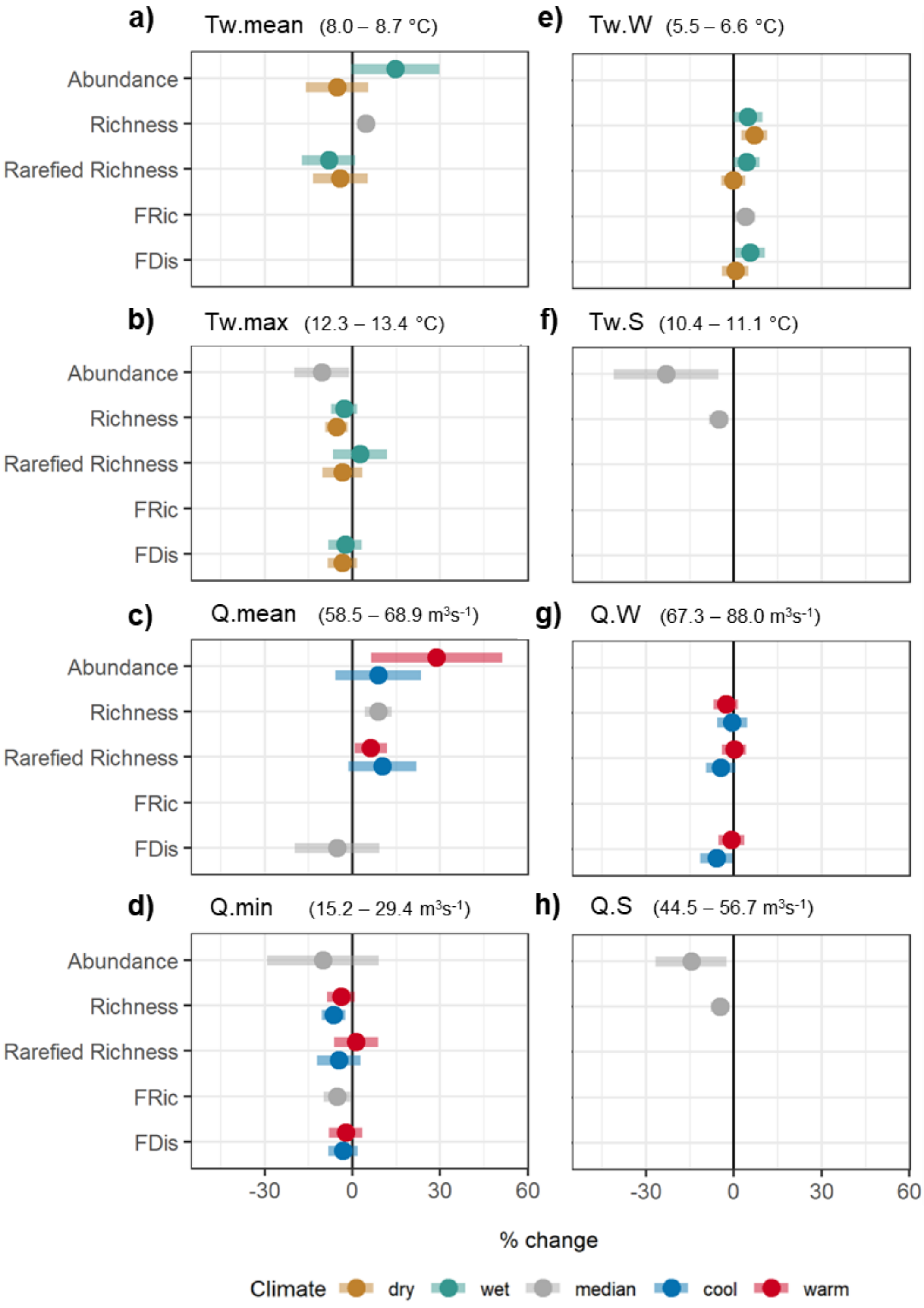


Figure 3.6 Mean percentage change in biodiversity across the interquartile ranges of annual and seasonal climate variables, and under different climate scenarios. Plots show percentage biodiversity changes estimated when ***a)*** *Tw.mean,* ***b)*** *Tw.max,* ***c)*** *Q.mean,* ***d)*** *Q.min,* ***e)*** *Tw.W,* ***f)*** *Tw.S,* ***g)*** *Q.W, and* ***h)*** *Q.S increase across the interquartile range, from lower (cool or dry) to upper (warm or wet) quartiles. For each estimate, all other model variables were held constant at their median. Note: measures of SES and NMDS are not included since mean values were close to zero.*

3.5 Discussion

Recent evidence of rapid global biodiversity declines and climate change has sparked major concerns over the long-term resilience of ecosystems (Hallmann et al. 2017; Sánchez-Bayo and Wyckhuys 2019; WWF 2020). However, trends in freshwaters, and particularly those relating to macroinvertebrate communities, have been contrasting (Vaughan and Ormerod 2012; van Klink et al. 2020; Outhwaite et al. 2020; Pilotto et al. 2020). So far, few long-term datasets spanning multiple decades have been available from relatively unpolluted and unmodified systems to adequately assess trends. Such datasets are required to disentangle climate-related effects from the array of stressors impacting freshwaters at local scales. In this study, a range of taxonomic and functional diversity measures, and measures of composition, derived from a 40-year macroinvertebrate dataset from upland streams were analysed in relation to hydrological and thermal conditions. Results corroborated the contrasting trends seen among community indices in the literature. The most striking changes were a decline in invertebrate abundance and compositional shifts away from shredding plecopterans (Hypothesis 1), while evidence suggested that functional losses also outpaced those of taxonomic change in some stream types and not others (Hypothesis 2). All climate variables were related to biological changes, though effects of summer and extreme conditions contrasted with the effects of winter and mean conditions (Hypothesis 3), highlighting the complexity of relationships between climate and riverine macroinvertebrate trends.

The results of this study provide sought-after evidence of structural and functional changes in freshwaters in response to climate, which has so far been elusive in many lowland systems. However, there are a number of caveats, meaning results should be treated with caution. Firstly, the low spatial replication of streams in this study is a key limitation, particularly for those characterised by broadleaf woodlands. Some differences in the temporal extent of data may also have impacted results. For example, BW streams often showed large effect sizes, but relationships were not statistically significant, which may reflect the smaller sample size. The use of nonlinear modelling techniques to derive relationships also requires careful interpretation as smoothing terms may sometimes be too sensitive to idiosyncrasies in the data (Wood 2017), and endpoints such as percentage changes could be sensitive to selection of the baseline years. Despite this, GAMMs are a well-recognised technique for use with ecological data such as these, and allow for more realistic relationships to be captured while controlling for random effects at site-level and the unbalanced replication described above. Despite the limitations, this study is among the first to provide evidence of multidecadal changes in upland systems, and to directly relate these to local, climate-driven variation in water temperature and streamflow (Durance and Ormerod 2007). Many of these issues outlined here are to be expected when using field data from highly complex, variable systems such as rivers, further highlighting the value of long-term analyses such as this.

Over the course of the study, mean water temperatures increased by around 0.8°C (1982-2018) with evidence of an acceleration in recent years, echoing global and European trends (IPCC 2021). Temperature changes were coupled with highly nonlinear but subtle changes in discharge. One of the most striking patterns in the climate data reflected the reduction in maximum daily precipitation and year-to-year variability. This result contradicts evidence that rainfall events are intensifying in the uplands (Burt and Ferranti 2012; Cotterill et al. 2021), but might partly be explained by a reduction in thunderstorms (Burt 2021). This could also be indicative of critical slowing down, a phenomenon which can occur prior to phase transitions (Scheffer et al. 2009; Dakos et al. 2012). Indeed, this period of quietening was subsequently broken by the heaviest daily rainfall event on record, coinciding with Storm Callum on 12th October 2018 (National Climate Information Centre 2019).

Changes in climate corresponded with progressive shifts in the structure and function of macroinvertebrate communities at Llyn Brianne. In the first hypothesis, measures of taxonomic and functional diversity were predicted to decline, alongside predicted shifts in community composition. Results of this study partially supported this. However, only abundance, FRic (and SES FRic), and measures of composition showed strong evidence of directional change, while trends in richness were highly nonlinear. Additionally, weak to no evidence supported the hypothesis that the rate of change would be slower in catchments least modified by land management and acidification. Instead, changes occurred in all streams, with evidence that total abundance in BW streams declined at rates more than twice as fast (46% loss between 1982 and 2019; 37 years) as moorlands (ca. 20%), and at a similar rate to AC (53%). Moreover, absolute abundance losses in BW were at least twice as high as any other stream type. However, BW trends were not statistically significant, and the greatest nonlinear trends were seen for AM stream communities. As discussed, a lack of significance could be due to low replication, and results should not be disregarded.

The declines in abundance seen here are in line with those reported for terrestrial insect communities (Dirzo et al. 2014; Hallmann et al. 2017; Hallmann et al. 2020; van Klink et al. 2020), though contradict the increases seen in other UK-based analyses where multiple stressors are likely to confound results (Vaughan and Gotelli 2019; van Klink et al. 2020; Outhwaite et al. 2020). An increasing number of studies from other countries, however, have shown similar declines, by 81.6% (42 years) and 23.3% (27 years) (Baranov et al. 2020; Rumschlag et al. 2023). This includes data collected from a German nature reserve (Baranov et al. 2020), corroborating that even in streams largely free from anthropogenic stressors, similar to the BW streams at Llyn Brianne, communities may not be protected from the far-reaching impacts of climate change. While warm, wet years were correlated with increasing abundance in this study, declines correlated with both cold, wet, and warm, dry years on average, in addition to extreme temperatures, and especially with hot summers. Moreover, predicted declines based on summer conditions were at least 36% as large as those observed over the study period, and up to 93% as large for CM streams.

The similar rates of decline in abundance seen for the two woodland stream types (BW and AC) in contrast with the two moorland types (CM and AM), in addition to changes seen among detritivores, could suggest links with terrestrial organic matter inputs. For example, climate change is thought to alter carbon:nitrogen ratios causing a decrease in the nutritional quality of organic matter received by streams, with potential impacts on detritivores and the wider food web (Fenoy et al. 2020; Fenoy et al. 2021). This is further supported by results of compositional shifts away from such functional groups that were seen in all streams. Additionally, declines in abundance might be explained by earlier spring emergence resulting from warm or dry weather (Harper and Peckarsky 2006; Baranov et al. 2020), as previously considered by Durance and Ormerod (2007) from analyses of this dataset 15 years prior. Given that warmer winters were associated with an increase in several biodiversity indices, this theory might not be supported. However, such phenological patterns can also be difficult to isolate, since early emergence can depend on the interaction between climate variables (Baranov et al. 2020), or might only be detected within short windows. For example, it could also coincide with early egg-laying, increased rate of egg development and hatching, thus rapid replacement of emerged adults within a matter of weeks (Brittain 1977; Gray 1981; Bonacina et al. 2023). A record of nymphal instars at the point of sample identification and counting, in addition to seasonal or year-round sampling might help to address this question, i.e., whether individuals are overwintering late instars or their offspring.

Trends in richness generally contradicted increases seen in recent freshwater studies (Baranov et al. 2020; Pilotto et al. 2020; Rumschlag et al. 2023), though there was clear nonlinearity in AM streams. Of the estimated losses, CM communities were worst affected, with a mean decline of 4 taxa in 37 years. This was not a substantial nor statistically significant decline, and overall changes in rarefied richness were negligible across streams suggesting a primary loss of abundance or sampling effect. However, results support previous findings that CM streams at Llyn Brianne are most at risk of species loss (Durance and Ormerod 2007). Beneath the subtle changes in overall taxon number, large shifts in taxonomic composition indicated that both losses and gains also occurred, supporting findings from other fast running, cold water systems (Floury et al. 2013). Losses seemingly corresponded to plecopteran genera, declines in which have been associated with warmer years in another long-term study (Jourdan et al. 2018), as seen here. Additionally, apparent losses in *Phagocata* within these compositional shifts contribute to previous evidence of the local extinction of another cool water triclad, *Crenobia,* from these streams (Durance and Ormerod 2010).

Although long-term changes to functional diversity were apparent, results were generally contrasting across stream types. In CM streams, an estimated decline of 24% FRic contrasted with the 28% increase in AM. These trends intensified when controlling for taxonomic richness (SES FRic), and highlighted a clear divide across an acid-base gradient. While this partially supports the second hypothesis that losses in functional diversity would outpace taxonomic decline, this clearly highlights a dependence upon local conditions. A decrease in SES FRic indicates a possible heightened sensitivity and erosion of functional redundancy in CM communities (Brown et al. 2018), which could have consequences upon key ecological processes involving energy processing, storage, and transfer. Moreover, declines could undermine ecological resilience, for which functional redundancy is considered a crucial property (Biggs et al. 2020). Meanwhile, the increase seen in acid streams suggests these communities may have been recovering from acidification (Helliwell et al. 2001; Malcolm et al. 2014; Murphy et al. 2014). If this is the case, then the positive correlation with warmer summers is most likely to be a confounding effect of improving water quality (Durance and Ormerod 2009; Baker et al. 2021). Yet, shifts in functional composition indicate that acid streams remain functionally distinct, if not further diverging from that of BW and CM streams, despite observed trait space expansion (Mouton et al. 2020). Particularly rapid changes in AC streams in recent decades suggest that local events, either acid episodes or forestry activities, could be responsible for this shift (Helliwell et al. 2001), and this was strongly related to hot, dry conditions.

The final hypothesis was partially supported, in that local conditions explained more variation than large-scale synoptic variables such as the NAO. However, effects were complex and often interactive such that identifying the best predictors of change was challenging. However, the weight of evidence suggested that warming, particularly in summer had the strongest effects. As detailed above, warmer summers, extreme temperatures, and the combination of warm and dry years were often correlated with biodiversity declines, while warmer mean conditions, winter warming, and the combination of wet and warm years appeared to promote biodiversity. This contrasts with previous studies at Llyn Brianne, where warmer winters were associated with lower diversity (Bradley and Ormerod 2001; Durance and Ormerod 2007), and highlights the importance of including multiple climate variables in analyses. Moreover, the effects of discharge were strongly nonlinear, with initial negative impacts of increased discharge in the driest months of the year, the most common predictor of functional variation. These effects could demonstrate the complex interplay between drought and re-wetting, which can mobilise sediments and a range of determinants including heavy metals and dissolved organic carbon (DOC) (Dawson et al. 2008; Mosley 2015), which is known to impact acid-sensitive organisms (Laudon and Buffam 2008).

Although this analysis attempted to capture some of the complex and interactive effects of climate and local conditions, the large amount of unexplained variation remaining highlights the challenges of analysing highly variable data through time, particularly at site level (McCain et al. 2016; Baranov et al. 2020). Despite the large changes in climate over the study period, stream type (as chemistry and land cover) remained the most effective predictor of community structure and function. Yet, there was little evidence that stream type affected climate sensitivity or temporal change, suggesting many other factors are likely to be involved, including local stressor interactions and indirect effects of climate change. Future research might focus on further characterisation of climate stressors, for example, by exploring temporal interactions such as the cumulative effects of consecutive dry months or years followed by a wet period (if these have occurred), and the short-term response and recovery dynamics (ecological stability; Chapters 4 and 5) that may underpin progressive shifts over time. Additionally, indirect effects of greenhouse gas emissions through changes to carbon:nitrogen ratios and nutritional inputs, changes in metacommunity dynamics and dispersal of flying insects over the landscape, reductions in genetic diversity, and phenological mismatch could all play a role (Taylor 1963; Service 1980; Bálint et al. 2011; Van Houtven et al. 2019; Baranov et al. 2020), presenting routes for further study.

Environmental managers should pay particular attention to the widespread nature of macroinvertebrate change, which suggests that local-scale solutions may be insufficient to maintain important ecological processes provided by upland stream communities. Additionally, the current positive trajectories seen in some streams and biodiversity metrics and in response to warm winters are unlikely to be sustained with accelerating climate change. Moreover, such changes could be associated with replacement of rare and specialist taxa with generalist species, which may disrupt the intricate feedback mechanisms necessary for maintaining community-level stability (see Chapter 5). Either way, the urgency of action required to ensure resilience of upland streams should not be underestimated.

3.6 Conclusion

The results of this study indicate that upland stream communities have undergone significant structural and functional changes in the past four decades, particularly with regards to invertebrate abundance. Diverging results across indices highlight the importance of considering functional diversity, since changes might otherwise be overlooked where only traditional measures such as species richness are used. While a substantial proportion of temporal variation in macroinvertebrates could be attributed to changes in climate-driven hydrological and thermal conditions, large uncertainty highlights the complexity of linking these two highly variable datasets. Moreover, local scale habitat conditions, including stream chemistry and land cover, influenced temporal dynamics and climate effects in unexpected ways that might exacerbate or mask the effects, particularly in acid streams. Although results were not statistically significant, broadleaf streams demonstrated some of most rapid declines in abundance alongside conifer streams, while circumneutral moorland streams were considered most at risk of functional diversity loss. Although greater replication is required to improve the statistical power of results, overall, these results contribute to the sought after evidence for macroinvertebrate trends in freshwaters. Moreover, results emphasise the need for prioritising conservation efforts of freshwaters at both local and larger scales.

Chapter 4: The ecological stability of upland stream macroinvertebrate communities

4.1 Summary

Climate change threatens the stability of all ecosystems, and particularly freshwaters. Management could enhance community and functional stability, but the many facets of long-term ecological stability in the face of climatic pulse disturbances are poorly understood, especially under different local conditions.

In this study, stability was defined multidimensionally to comprise resistance, engineering resilience, persistence, robustness, and temporal invariability. These measures were calculated to assess stability in 16 headwater streams of contrasting land use and chemistry (stream type) using 40 years of macroinvertebrate data and associated functional traits. The aims were to determine differences in taxonomic and functional stability under potentially interactive effects between stream type and climate change as measured using water temperature and discharge.

Ecological stability comprised at least two dimensions in these streams, the first relating to the volatility of communities or magnitude of change following disturbance (resistance, persistence, invariability, and negative robustness), and the second to resilience or speed of recovery. In general, headwater streams were more stable functionally than taxonomically, indicating functional redundancy among taxa. Across stream types, communities in broadleaf woodland streams were the most taxonomically and functionally stable, closely followed by circumneutral moorland streams. Coniferous woodland stream communities were the most volatile, with evidence of greater dimensional volume for stability and the greatest sensitivity to increased discharge in what were otherwise the driest months of the year, suggesting a heightened state of stress. Climate and local land use had complex and interacting effects through time through which pulse disturbances at unexpected times could disproportionately reduce stability. In particular, dry winters and wetter summers had significant effects on communities through extremes rather than mean conditions.

Overall, these results have important implications, indicating that natural woodlands could offer the best options for enhancing ecological stability, while conifers are the least effective.

4.2 Introduction

Ecosystems are increasingly exposed to novel and interacting disturbances, for example where climate change intensifies, and habitats are modified through land use (Millennium Ecosystem Assessment 2005; IPBES 2019). These disturbances imperil biodiversity and their functions and could alter multiple components of ecological stability, such as resistance (the ability to withstand disturbances) and engineering resilience (the ability to rapidly recover), among others (Table 4.1) (Pimm 1984; Ives et al. 1999; Ives and Carpenter 2007; Donohue et al. 2013). Understanding these effects is challenging, however, and recent research suggests that relying solely on single components of stability (the norm in most empirical studies; (Donohue et al. 2016) may be insufficient to determine the overall stability of a community (Donohue et al. 2013). Advances in our understanding of stability emphasise the importance of considering multiple components and their interrelationships to obtain reliable evidence for management interventions (Donohue et al. 2013; Hillebrand et al. 2018; Radchuk et al. 2019; Polazzo and Rico 2021; Urrutia-Cordero et al. 2022; Allen et al. 2023).

The dimensionality of ecological stability (DS) is an emerging concept that highlights the importance of considering multiple dimensions or components of stability when studying ecosystems (Donohue et al. 2013). It is increasingly recognised as a crucial property that may help to determine the overall vulnerability of ecosystems to disturbances or biodiversity loss (Urrutia-Cordero et al. 2022), which might otherwise be overlooked using traditional, single measures such as temporal variability (Donohue et al. 2016). Studies have shown that stability in undisturbed sites may be characterised by stronger relationships between components, thereby reducing the effective DS (Donohue et al. 2013). Conversely, high DS could suggest that relationships between components are decoupled, and that the processes governing stability are complex or disrupted by stress (Donohue et al. 2013). This has important implications for the ways in which stability might be understood and managed for. For example, if there are negative relationships between properties such as resistance and resilience (Harrison 1979; Webster et al. 1983; Donohue et al. 2013; Hillebrand et al. 2018; Cabrerizo et al. 2019), or if more comprehensive assessments are needed to capture complex dynamics, this would call for a more nuanced approach to management interventions and monitoring.

Among the ecosystems most threatened by climate change, rivers are recognised as being particularly at risk. Recent reports indicate large-scale declines in freshwater vertebrates (WWF 2020), and the presence of diverse stressors such as pollution and habitat loss at local scales (Reid et al. 2018; Chapter 2). The ecological significance of rivers, their rate of degradation, and sensitivity to land use and environmental changes, underscores the urgent need for management interventions and research in order to enhance their ecological resilience - the ability to maintain their current ecological structure and function in spite of disturbance (Holling 1973).

In running waters, thermal and hydrological conditions play crucial roles in shaping community structure and function and their temporal dynamics (Poff 1997; Brown et al. 2006). Hydrological regimes determine flow dynamics and habitat characteristics, while temperature influences oxygen concentrations, decomposition rates, and metabolic processes (Ferreira and Canhoto 2014; Verberk et al. 2016). These factors impact resource dynamics, water quality, species survival, interactions, and overall ecosystem function (Lake 2003; Griswold et al. 2008; Woodward et al. 2010; Woodward et al. 2016; Aspin et al. 2018; Aspin et al. 2019). The combined effects of low flow and high temperature, such as during droughts, may be particularly harmful, and have been shown in short-term studies to disrupt food webs and push communities beyond functional thresholds (Lake 2003; Ledger et al. 2013; Lu et al. 2016; Aspin et al. 2019). The emergence of increasing temperatures and altered flow regimes (Hannaford and Marsh 2008; Hannaford and Buys 2012), along with an increase in record-breaking climate events (Prudhomme et al. 2012; Fischer et al. 2021), therefore raises significant concerns about the future of freshwater ecosystems and their vital ecological processes.

Given their intricate links to terrestrial ecosystems, one management strategy that has been increasingly promoted for river ecosystem resilience is the maintenance and expansion of riparian broadleaf woodland (Ormerod 2009; Nisbet et al. 2011; Thomas et al. 2015; Thomas et al. 2016). Trees, and especially woodlands, are well known to reduce water temperatures and regulate flow, and could provide important buffering against extreme climate events (Broadmeadow et al. 2011). Provision of refugia in the form of woody debris, high stocks of organic matter, increased habitat heterogeneity, and greater diversity of species and functions that broadleaf woodlands afford, have all been linked to stability of communities and of their environment (Collier and Quinn 2003; Ives and Carpenter 2007; Mykrä et al. 2011; Downing et al. 2014; Thomas et al. 2016; Van Looy et al. 2019; Pye et al. 2022). Riparian zones also have important effects on the adult stages of aquatic insects, which seldom move more than 10 m from stream banks (Petersen et al. 2004). Moreover, potential improvements in water quality and the ecological benefits could alleviate local pulse and press disturbances, enhance community resilience, and offset some of the effects of warming (Scheffer et al. 2015; Vaughan and Gotelli 2019).

Despite their vulnerability and a wealth of studies supporting concerns about climate change, there remains a paucity of studies that have adopted the multidimensional perspective necessary to assess the stability of rivers in a more comprehensive manner (Eagle et al. 2021; Allen et al. 2023), and the long-term perspective necessary to capture response and recovery dynamics in relation to climate change. Mounting evidence indicates that extreme weather events, including floods, droughts, and heatwaves, pose a particular threat to riverine biodiversity and ecosystem functions, especially when compounded by local stressors (Ormerod et al. 2010; Harris et al. 2018; Comte et al. 2021; Dinh et al. 2022; Sabater et al. 2022). Moreover, taxonomic and functional properties of communities may respond in different ways, particularly given local stressor interactions (Hillebrand et al. 2018; Hillebrand and Kunze 2020; Polazzo and Rico 2021). However, current knowledge has predominantly been based on incremental gradients of environmental change, or space-for-time substitutions (i.e., press or ramp effects (*sensu* Lake 2000). Such analyses may underestimate the impacts of extreme pulse events, the rapid onset, rarity, potential severity, and unexpected timings of which could undermine stability (Woodward et al. 2015; Harris et al. 2018; Sabater et al. 2022). Moreover, few studies consider variations across taxonomic and functional properties (Hillebrand et al. 2018), their response to different types of disturbances (Radchuk et al. 2019) such as pulse or press disturbances (Lake 2000), and their interactions in natural systems (Kéfi et al. 2019; Polazzo and Rico 2021).

This highlights a clear need for long-term studies using natural freshwater systems to bridge the gap between theory, experiments, and real-world scenarios, and to provide more reliable evidence for management (Kéfi et al. 2013; Kéfi et al. 2019; Birk et al. 2020; Stelzer et al. 2021). While there are a few recognised examples of such assessments (Eagle et al. 2021; Allen et al. 2023), there are none, so far as currently known, that incorporate analyses from different possible management options, such as broadleaf woodlands. Where studies have investigated combined impacts of local land use with hydrology and temperature (Bradley and Ormerod 2001; Collier and Quinn 2003; Collier 2008; Canning et al. 2018; Canning et al. 2019), these are often based on single measures of stability, and evidence is often mixed. Moreover, few analyses combine assessments of taxonomic and functional stability, despite potential differences in response and subsequent conservation needs.

Here, a 40-year dataset of upland macroinvertebrates from 16 streams of contrasting land use and chemistry was used to address these gaps in knowledge. These comprised catchments characterised by semi-natural broadleaf woodland, intensively grazed moorland, and conifer forestry. The primary objective of this study was to determine the ecological stability of communities in relation to contrasting management regimes. It was hypothesised that:

1. Stability would not differ between taxonomic and functional indices, and overall stability could therefore be reduced to a single dimension, suggesting that relationships governing the stability of taxa and their traits, and individual components of stability are largely the same.
2. Variations in stability over time would be explained by climatic disturbances, and particularly extreme conditions (high temperatures and low summer discharge) as opposed to average or winter conditions.
3. Ecological stability and its relationship with climate would differ relative to local catchment conditions. In particular, broadleaf woodland streams would be more stable (resistant, resilient, persistent, robust, invariable, and lower DS) compared to other more modified stream types (grazed moorlands and conifer plantation).

4.3 Methods

4.3.1 *Study sites and macroinvertebrate data*

Study sites comprised 16 perennial headwater streams in upland Wales that were sampled for macroinvertebrates from 1981 to 2020 each spring - noting that the number of streams sampled reflected access difficulties and resources in some years. Streams were characterised by varying catchment-scale chemistry and vegetation types, comprising four distinct groups (= stream type): semi-natural broadleaf woodland (BW: GI1 and GI2), coniferous woodland (AC: LI1 to LI4 and LI8), circumneutral moorland (CM: LI6 and LI7), and acid moorland (AM: CI1 to CI6 and LI5). A detailed description of sites and sampling technique can be found in Chapter 1, Section 1.3.

For each sample, eight common community-level variables describing taxonomic and functional properties were calculated: total community abundance, taxonomic richness, rarefied richness, and Simpson's evenness as taxonomic variables, while functional variables were functional richness (FRic), functional dispersion (FDis) (as used in Chapter 3), functional evenness (FEve), and functional divergence (FDiv), calculated using a species functional traits and corresponding abundances in the R packages *ade4* (version 1.7.22) and *FD* (version 1.0.12.1) (Villéger et al. 2008; Laliberte and Legendre 2010; Laliberté et al. 2014; Thioulouse et al. 2018). Although FEve (how evenly individuals are distributed in trait space) and FDiv (the extent to which taxon abundances are distributed towards the extremities of occupied trait space) provide information that can largely be captured by other functional variables (Laliberte and Legendre 2010; Mason et al. 2013; Swenson 2014), by including a wide suite of indices this ensured that some of the complexities and nuances of communities were elucidated, while insuring that limitations of individual indices were minimised (Kosman et al. 2021). Subsequently, primary analyses focused on the mean stability among these indices to reduce variation (see Section 4.3.2). Functional traits used to calculate these indices were maximum body size, locomotive technique, food preference, and trophic guild, for which there were 7, 8, 9, and 7 individual traits, respectively. A matrix of community-weighted-mean (CWM) traits for each sample was derived from functional trait and $\log_{10}(x + 1)$-transformed taxon abundance data (Schmera et al. 2014; White et al. 2017) to summarise functional composition (see Chapter 3, Section 3.3.2 for further details, and Chapter 5, Table 5.1 for full list of traits).

4.3.2 *Stability measures*

Measures of stability commonly applied in empirical studies include temporal variability, resistance, persistence, resilience, and robustness (Donohue et al. 2016). Each of these was calculated for macroinvertebrate taxonomic and functional data detailed above (Section 4.3.1). A summary of definitions and interpretation of measures is presented in Table 4.1. The primary analysis in this study was based on decadal values of stability; 1981-1990 (T1), 1991-2000 (T2), 2001-2010 (T3), 2011-2020 (T4). This allowed effects of stream type and trends through time to be assessed simultaneously, and increased the available data needed for calculations of dimensionality. To minimise the influence of unequal sampling effort between streams, stability was calculated for each stream and decade where data were available for at least five years. As a validation step, stability was also calculated only for streams with near-complete data (10 streams, ≥five sampling occasions in all four decades), which excluded both broadleaf woodland streams (GI1 and GI2), and CI3, CI6, LI3 and LI5. Comparisons were made between these two datasets and no substantial differences were found.

Variability was measured as the coefficient of variation (CV) for each community-level variable (see Table 4.1). To remove possible temporal trends that might impact the variance, data were first detrended using linear models applied to each time series (Ives 1995). CV was calculated using the standard deviation of model residuals divided by the mean (Tilman et al. 2006; Donohue et al. 2013): $CV = standard\ deviation^{detrended}/mean.$ For primary analysis, an average CV was taken from all measures calculated (taxonomic and functional separately), giving equal importance to each overarching stability variable used in subsequent analysis. This was also considered to provide a general overview of community variability and the many qualities they comprise.

Resilience (λ) was also calculated using detrended data, creating a stationary series where data were not time-dependent i.e., the mean, variance and covariance were not a function of time (Ives et al. 2010). For each community variable (Table 4.1), resilience was defined as the characteristic return time, $||\lambda||$, to a stationary point, derived from autoregressive moving-average (ARMA) models fitted with linear-mixed effects. Models were constructed using the *lme4* package in R (version 1.1.31) (Bates et al. 2015). Following Ives *et al.* (2010), the autoregressive (AR, p = 1 to 2) and moving average (MA, q = 0 to 2) components for each model were selected by minimising Akaike's Information Criterion adjusted for small samples sizes (AICc). The characteristic return time, $||\lambda||$, was the absolute value of the real part of the dominant eigenvalue of the matrix containing the estimated MA and/or AR coefficients. Values ranged from 0 to 1, where values close to 0 indicated short return times and therefore high resilience, and values approaching 1 indicated low resilience (long return times).

Resistance (BC) was measured as Bray-Curtis dissimilarity in community composition between consecutive years, using either abundance or CWM trait data (Donohue et al. 2013). Persistence (J) was calculated in the same way, but with Jaccard's dissimilarity index based on presence/absence values for taxa and traits (Bradley and Ormerod 2001). This gave inter-annual values that could be assessed over time and relative to climate variables. Values ranged from 0 to 1, where 0 indicates complete resistance or persistence, while 1 indicates complete dissimilarity. To aid interpretation, inter-annual gains and losses of taxa and traits were derived using the R package *codyn,* version 2.0.5 (Hallett et al. 2020).

Robustness (Rb) was measured as the number of primary species extinctions required for 50% loss of all taxa in the network (primary plus secondary extinctions) (Dunne et al. 2002b). For this, topological food webs were constructed for each sample by matching macroinvertebrate data to a publicly available database of aquatic trophic links using the *WebBuilder* function in R (Gray et al. 2015). These links were either observed from dietary analyses or inferred from the literature, primarily from the UK. Both macroinvertebrate-only and full webs were constructed, with the latter including four broad-scale groupings of basal food resources: course particulate matter (CPOM), fine particulate matter (FPOM), diatoms and algae (primary producers). For each web, mean sample robustness was derived from 100 simulated random node removals using R package *NetworkExtinction* (version 0.1.1) (Corcoran et al. 2019). Values ranged from 0 (not robust, i.e., fragile) to 0.5 (maximum robustness), representing the proportion of taxa required to be removed (primary extinctions) that would cause 50% loss of taxa (primary plus secondary extinctions). No large differences were seen between the two web types, so mean Rb values were calculated for each sample.

Three food web descriptors that are expected to be positively associated with robustness – connectance, modularity, and diet generality (May 1972; Dunne et al. 2002b) – were also calculated using R packages *cheddar* (version 0.1.636) (Hudson et al. 2013; Hudson et al. 2020) and *bipartite* (version 2.16) (Dormann et al. 2008; Dormann et al. 2009). Connectance describes the number of realised links within a network, while modularity refers to the degree of trophic interaction between subgroups of organisms. Generality provides a mean diet breadth score for taxa in the web. For visual purposes, aggregate webs for each stream type were constructed by averaging taxa across sites and samples (Figure A.4-7).

So that annual and inter-annual measures of stability (BC, J, and Rb) could be compared against CV and λ, their mean values were calculated for each stream and decade.

Table 4.1 Calculation and interpretation of community stability variables used in this study. Primary analyses were conducted using mean values where multiple aspects were calculated within each Group e.g., resilience, variability, robustness. Values for persistence, resistance, and robustness were also averaged over time.

Stability variable	Quantification	Interpretation	Community variables assessed in this study	Code
Resistance	Inter-annual Bray-Curtis dissimilarity Index (Donohue et al. 2013)	Values ranging from 0 = no change / complete resistance to 1 = full compositional turnover / no resistance	Taxonomic composition based on $\log_{10} x+1$ abundances	BC.T
			Functional trait composition determined by community weighted means (CWM)	BC.F
Persistence	Inter-annual Jaccard's dissimilarity Index (Bradley and Ormerod 2001)	Values ranging from 0 = no change / complete persistence to 1 = full turnover / no persistence	Taxon presence/absence	J.T
			Trait presence/absence	J.F
Variability	Coefficient of variation over time CV = σ / μ, where σ = standard deviation of residuals from detrended data μ = mean (Tilman et al. 2006)	Increasing values = higher variability and reduced stability	Taxonomic mean of CV for abundance, richness, rarefied richness, and Simpson's evenness	CV.T
			Functional mean of CV for FRic, FDis, FDiv, and FEve	CV.F
Resilience	Characteristic return time, Lambda $\lVert\lambda\rVert$ derived from ARMA models (Ives et al. 2010)	Values ranging from 0 = high resilience to 1 = low resilience (slow return / non-stationary, random-walk behaviour)	Taxonomic mean of return time for abundance ($\log_{10}$), richness, rarefied richness, and Simpson's evenness	λ.T
			Functional mean of return time for FRic, FDis, FDiv, and FEve	λ.F
Robustness	Proportion extinctions causing 50% loss of taxa (primary + secondary extinctions) (Dunne et al. 2002b)	Values range from 0 = fragile network to 0.5 = maximum robustness. This was considered in both taxonomic and functional analysis	Mean for trophic networks constructed with and without basal resources	Rb

4.3.3 *Environmental variables*

To assess the relationship between stability and environmental disturbances, climate variables were derived from HadUK-Grid data at 5 km resolution. These were mean monthly air temperature and daily precipitation from which stream-level variables were calculated, as detailed in Chapter 3, Section 3.3.3. Variables were calculated at annual scale and seasonal scale (April-September, ‘summer’, and October-March, ‘winter’) for each year prior to sampling. Annual-scale variables used in this analysis were mean stream temperatures (Tw.mean °C), maximum monthly mean stream temperatures (Tw.max °C), mean catchment area-standardised discharge (Q.mean m^3s^{-1}), and minimum monthly mean discharge (Q.min m^3s^{-1}). This allowed separation of average and extreme conditions that were predicted impact communities differently (Harris et al. 2018; Sabater et al. 2022). Maximum monthly mean discharge was not included as this was strongly correlated with Q.mean (Pearson’s $r = 0.81$). Similarly, cold months were correlated with Tw.mean ($r = 0.79$), and were therefore not included.

In addition to annual-scale variables, seasonal-scale variables were also calculated. Those selected for analysis were summer maximum monthly mean discharge (Q.maxS m^3s^{-1} and winter minimum monthly mean discharge (Q.minW m^3s^{-1}). These were the only two variables that were not highly correlated with annual-scale measures. For example, rising summer and winter mean and minimum temperatures were correlated with Tw.mean, ($r > 0.75$) . Annual Q.mean represented extreme and mean winter discharge ($r > 0.8$), while Q.min reflected the driest months of summer ($r = 0.83$). Similarly, Tw.max was a direct reflection of the hottest month of summer ($r = 1$). The strongest correlation among the final set of variables was between Q.mean and Q.min ($r = 0.57$), which was considered acceptable for subsequent use in models. A summary of trends and variation over the study period for all variables used in this chapter are presented in Figure 4.1.

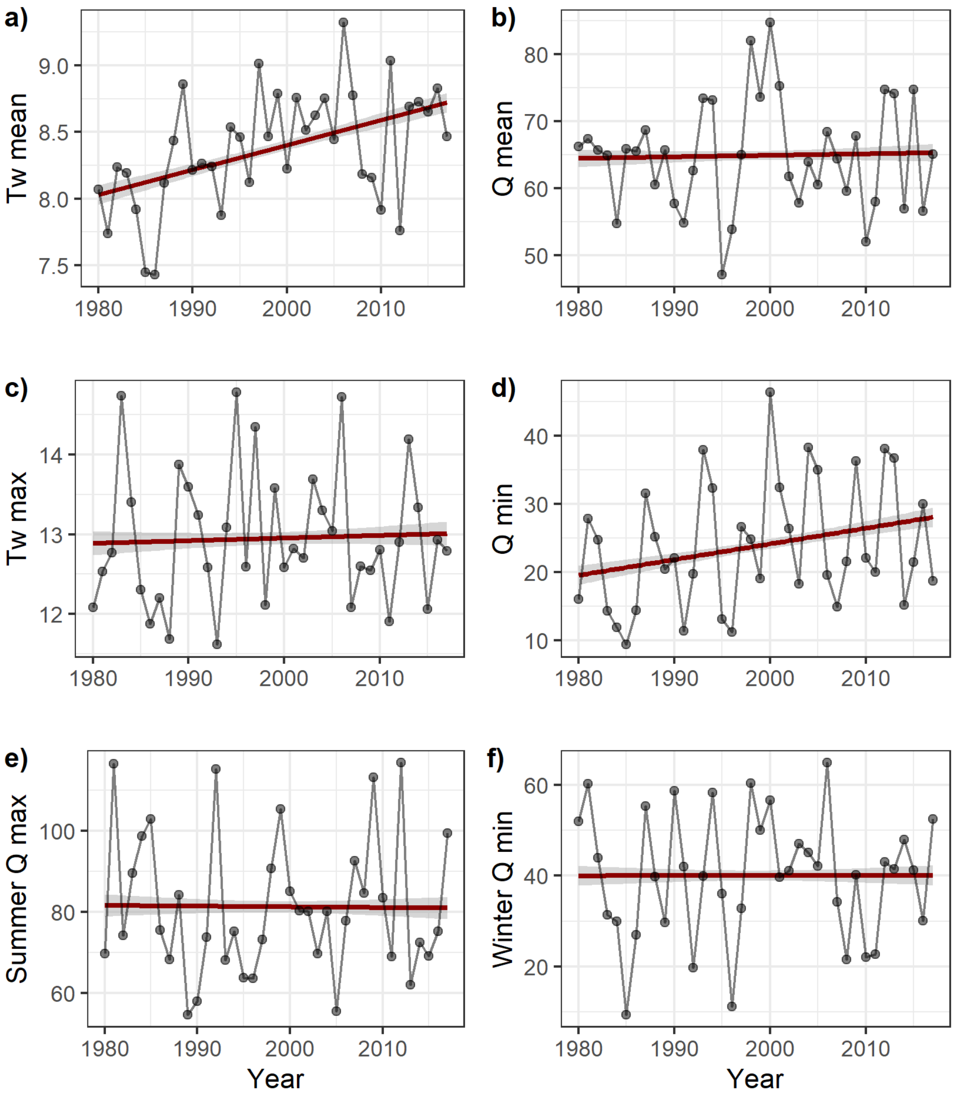


Figure 4.1 Summary of the mean disturbance regime across streams. Linear models show general trend over time while points represent mean values over streams for ***a)*** *annual mean stream temperature (°C),* ***b)*** *annual mean discharge (m^3s^{-1}),* ***c)*** *annual maximum monthly mean temperature (°C),* ***d)*** *annual minimum monthly mean discharge (m^3s^{-1}),* ***e)*** *summer maximum monthly mean discharge (m^3s^{-1}), and* ***f)*** *winter minimum monthly mean discharge (m^3s^{-1}).*

4.3.4 *Statistical analyses*

Taxonomic and functional stability

To address Hypothesis 1, that ecological stability can be simplified to a single dimension, and that taxonomic and functional stability would not differ from one another, analyses were conducted in two steps using principal component analysis (PCA). PCA was conducted using the R package *vegan* (version 2.5.7) (Oksanen et al. 2020), ensuring that the scales for all variables were standardised by subtracting their means and dividing by the standard deviation (Donohue et al. 2013).

Firstly, data for all stability variables (taxonomic and functional; n = 9), and for all streams and decades, where available (n = 53), were combined. In this step, PCA allowed relationships between measures of stability to be assessed, and the number of dimensions deemed sufficient to explain overall stability (Donohue et al. 2013) was selected according to Kaiser criterion (eigenvalues were >1). Pairwise relationships between variables were further analysed using Pearson's correlation coefficient (36 pairs in total).

Next, separate PCAs were conducted for taxonomic and functional stability measures (with Rb present in both) to enable a comparison of the dimensionality of stability, DS (Figure 4.2). For each PCA, the number of dimensions were selected, and relationships were compared using Pearson's correlation, as detailed above. To measure DS, the ellipsoid volume was calculated for each covariance matrix using the *ellipse.volume* function from the R package *dispRity* (version 1.7.0) (Guillerme 2018). Volumes were standardised by dividing by the maximum possible volume for an ellipsoid of the same number of dimensions (5) and equal relative axes lengths (1). Values close to 1 would therefore correspond to high DS and a more spherical shape, while values close to 0 represented a 'cigar' shape with low DS (Donohue et al. 2013). Following Donohue *et al* (2013), relative semi-axes lengths were calculated as the square-root of each principal component eigenvalue and dividing by the maximum axis value for each matrix.

Differences in stability properties among streams

To test for differences in each of the components of stability derived from taxonomic and functional PCAs, linear mixed-effect models were constructed using the R package *lme4* (version 1.1.26) (Bates et al. 2015). The effects of stream type and decade were tested simultaneously for each dimension of stability (PC), with a random effect of sample site to control for repeated (decadal) measures. Due to small sample sizes, particularly for CM and BW streams, streams were also grouped by pH (acid/neutral) and canopy type (wooded/open) to elucidate their effects and maximise the available information. The effects of these were tested as per stream type, i.e., simultaneously controlling for decade. Standard model validation checks were applied via visual assessment of residual plots assuming Gaussian error distribution. Effects were visualised using the *effects* (version 4.2.2) package and *ggplot2* (version 3.3.3) in R. Where significant, Tukey's *post-hoc* tests of pairwise comparisons were performed using the *multcomp* (version 1.4-16) package in R. Although data limitations are acknowledged, analyses were also conducted to provide some information about the DS within groups, using PCA and covariance matrices run separately for each group, as described in the steps above.

Long-term trends in stability components

To assess the more detailed changes in stability over time, smoothed temporal trends for stability measures that could be calculated annually or inter-annually (J, BC, Rb) were assessed using generalised additive mixed models (GAMMs) fitted with the *mgcv* (version 1.8.42) package in R (Wood 2017). Year was modelled using a smoothing spline, with the degree of smoothing selected using generalised cross-validation (GCV) (Wood 2004). An autoregressive (AR) structure for the residuals with lag 1 was included where this reduced model AIC, and stream was fitted as a random effect to control for repeated measures over time. To test whether temporal trends were mediated by stream type, equivalent models containing an interaction between year and stream type (via a 'by' argument within the smooth term for year) and no interaction term were compared using likelihood ratio tests (LRT). Final models were fitted with restricted maximum likelihood (REML).

Effects of climate

GAMMs were also used to determine if climate could explain year-to-year variation in stability, and whether stream type mediated these effects. In using GAMMs, this allowed for potential nonlinear relationships, while controlling for temporal autocorrelation (AR lag 1) and repeated measures over time within sites, as per temporal models detailed above.

Models were fitted with all climate variables as smooth terms, with the degree of smoothing selected via GCV (Wood 2004), and with stream type as a fixed effect to control for differences in the intercept. Models included both average and extreme conditions for discharge and temperature, as detailed in Section 4.3.3 and presented in Figure 4.1. Models were therefore constructed as follows for each aspect of annual or inter-annual stability, S_a:

S_a ~ Stream type + s(Tw.mean) + s(Tw.max) + s(Q.mean) + s(Q.min) + s(Q.maxS) + s(Q.minW)

To test whether stream type mediated effects of climate, stream type was fitted using the ‘by’ argument for each smooth term in the model. To minimise issues of over-fitting, a forward addition rather than backward deletion approach was taken. Each model with the added interaction term was compared to the base model above using LRT to determine significance (Lewis et al. 2011).

Similarly, to test for interactions between climate variables, and specifically, the combination of low flow and high temperature conditions (Tw.max*Q.min and Tw.mean*Q.mean), the same forward selection approach was taken, comparing the significance of each to the base model using LRT. In this instance, the base model was refitted using tensor interaction (ti) terms to allow appropriate separation of interaction and fixed effects (Wood 2017).

Final effects were estimated with REML, and residual plots were checked to ensure model assumptions were met based on Gaussian error. Response variables were transformed where necessary, which included a square-root transformation of functional persistence (J.T) to achieve normality of residuals. Significance of each term was derived from model outputs, based on Wald tests, and relationships for each term were visualised over gradients by holding all others at their median value.

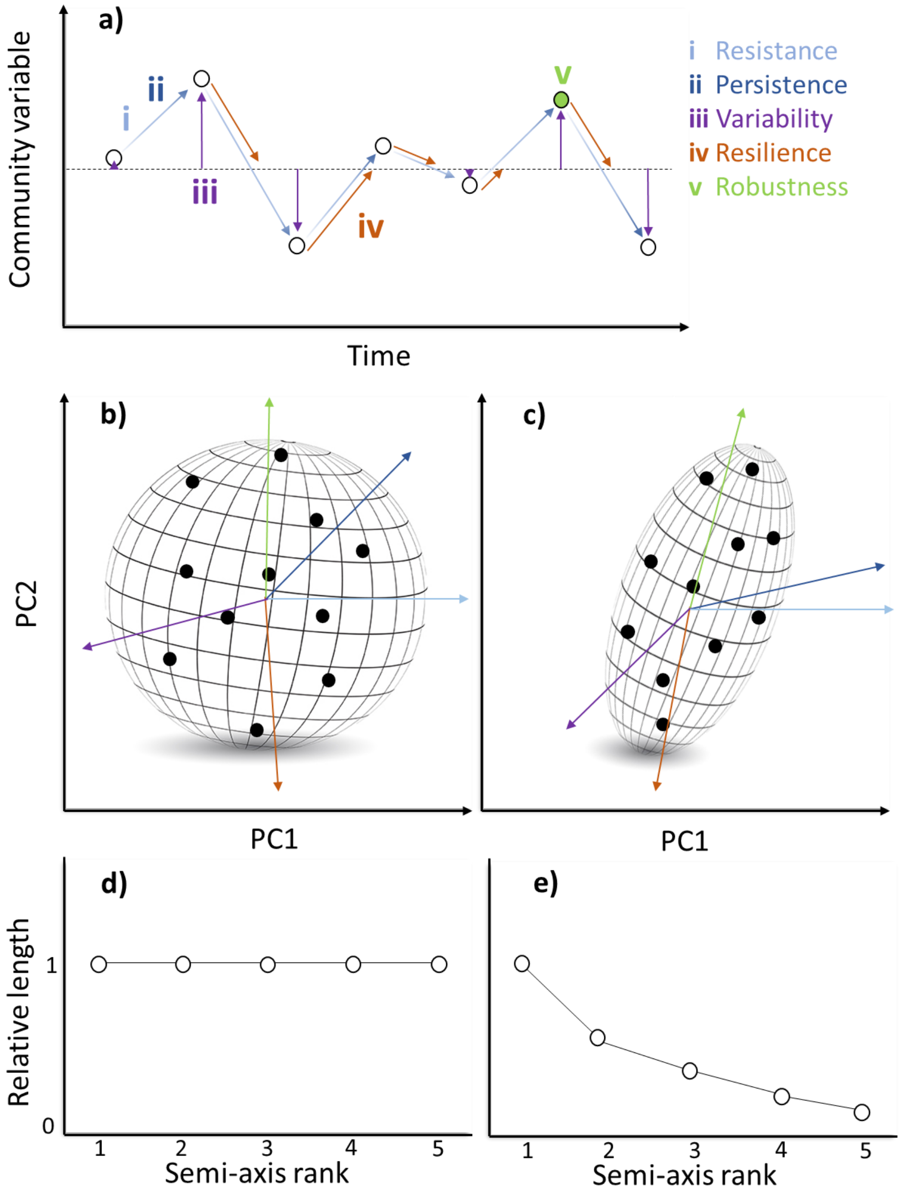


Figure 4.2 Conceptual diagram of dimensionality of stability analysis. Plot ***a)*** *represents the derivation of multiple properties that describe community dynamics over time,* ***b-c)*** *shows separate PCAs and construction of ellipsoids for two hypothetical datasets where relationships are weak and DS is high (a), or relationships are strong and DS is low (b), and* ***d-e)*** *show relative semi-axes lengths that derived from covariance matrices from each dataset, respectively. These indicate ellipsoid shape, either as spheroidal where DS is high (d) or 'cigar-shaped' where DS is low (e).*

4.4 Results

4.4.1 *Taxonomic and functional stability*

Overall, the stability of Llyn Brianne stream communities was considered high, particularly for functional traits (Table 4.1). Averaged across streams and decades, functional stability was found to be greater than taxonomic for every variable. This difference was especially prominent for BC and J, where mean inter-annual changes in functional traits were exceptionally low (6% versus 39% for J, and 8% versus 30% for BC). The margin of difference between respective measures of λ, however, was small (0.03), though the range of values was larger than for other stability measure. Moreover, there was evidence that measures of λ and CV calculated from the original range of community indices (Table 4.1), rather than the averages presented here, varied. This was particularly apparent for aspects of λ. Moreover, measures based on abundance were the least stable (CV = 0.59, λ = 0.44) (see Appendix, Figure A.8). Robustness (Rb) of networks was found to be extremely high, with a mean of 0.48, close to the 0.5 maximum. Higher mean values reflected webs with fewer taxa (Pearson's $r = -0.88$), higher connectance ($r = 0.88$), lower modularity ($r = -0.83$), and lower trophic generality ($r = -0.77$) on average.

Pairwise comparisons between stability measures averaged for each stream and decade revealed that 20 of the 36 combinations were significantly correlated ($p < 0.05$; Figure 4.3), suggesting a high amount of redundancy among components. The strongest correlations were among measures of BC and J.T ($|r| > 0.7$). Although still significant, correlations with this group of variables and functional J were much weaker (≤ 0.5). Robustness (Rb) was more strongly correlated with functional stability variables, particularly for functional CV ($r = -0.61$), though this was negatively so. The only significant correlation found for λ was with itself (taxonomic versus functional) ($r = 0.37$, $P < 0.01$). Excluding Rb, which was neither considered taxonomic nor functional at this stage, overall mean absolute correlations among taxonomic and among functional measures were comparable ($|r| = 0.35$). However, when Rb was included, mean correlation increased for functional ($|r| = 0.36$) but decreased for taxonomic stability ($|r| = 0.32$), reflecting the stronger relationships with functional measures. Mean absolute correlation increased further yet when direct comparisons between respective functional and taxonomic stability measures e.g., taxonomic BC versus functional BC ($|r|$ = 0.58), further highlighting similarities.

These interrelationships were made visible in PCA, where the number of dimensions could be reduced from 9 (all variables) to just 2 (Table 4.3). PC1 described changes in both taxonomic and functional CV, BC, J, which loaded positively along this axis (less stable with increasing PC1 scores), and Rb, which loaded negatively (more stable). Thus, with the exception of Rb, this axis encompassed patterns in the year-year variation, or 'volatility' of communities. Conversely, PC2 reflected changes in λ, i.e., the speed of recovery from perturbations, which also loaded positively along this axis (less stable with increasing PC2 scores). There was also evidence that Rb varied along PC2, highlighting its potential links to multiple dimensions despite only a weak correlation with λ.T (r = -0.22), and no correlation with λ.F (r = -0.02). Together, the first two dimensions explained 64% of the variation in stability among streams and decades. PCA of stability variables based on original community indices (n = 21) rather than the means, however, indicated some increased complexity, but partitioning of variables along each axis remained largely the same, i.e., most measures of CV and λ were correlated along PC1 and PC2, respectively (Figure A.8).

When PCA was conducted separately for taxonomic and functional stability variables (with Rb grouped into both), results reflected those detailed above (Table 4.4). In each case, the number of dimensions could be reduced from 5 to 2, explaining 73% and 74% of the variation for taxonomic and functional stability, respectively, and patterns along each axis related to the volatility (but greater robustness) and speed of recovery in each case. However, unlike for the full PCA, J.F also loaded heavily on to PC3 (-0.82), highlighting some independence from other measures of stability. Calculations of the standardised ellipsoid volumes for each of the covariance matrices from taxonomic and functional PCA revealed differences in dimensionality, despite a comparable number of dimensions and variance explained. Although the values of functional stability properties were greater than for respective taxonomic properties, functional ellipsoid volume was larger (46% of the possible maximum area) than taxonomic (35%). This also contrasts with the stronger correlations seen among functional compared to taxonomic stability variables (Figure 4.3), but might reflect the contribution of J.F to PC3.

Table 4.2 *Summary statistics for each facet of community stability. Values are based on variables calculated at decadal scale for each stream. Lower values reflect greater stability for all variables except robustness.*

Stability variable	Group	Code	Mean (se)	Min	Max
Variability	T	CV.T	0.31 (0.01)	0.13	0.49
	F	CV.F	0.20 (0.01)	0.08	0.35
Resistance	T	BC.T	0.31 (0.01)	0.19	0.46
	F	BC.F	0.08 (0.003)	0.04	0.14
Persistence	T	J.T	0.39 (0.01)	0.25	0.55
	F	J.F	0.06 (0.004)	0.02	0.14
Resilience	T	λ.T	0.37 (0.02)	0.12	0.98
	F	λ.F	0.34 (0.02)	0.11	0.73
Robustness	T/F	Rb	0.48 (0.002)	0.44	0.49

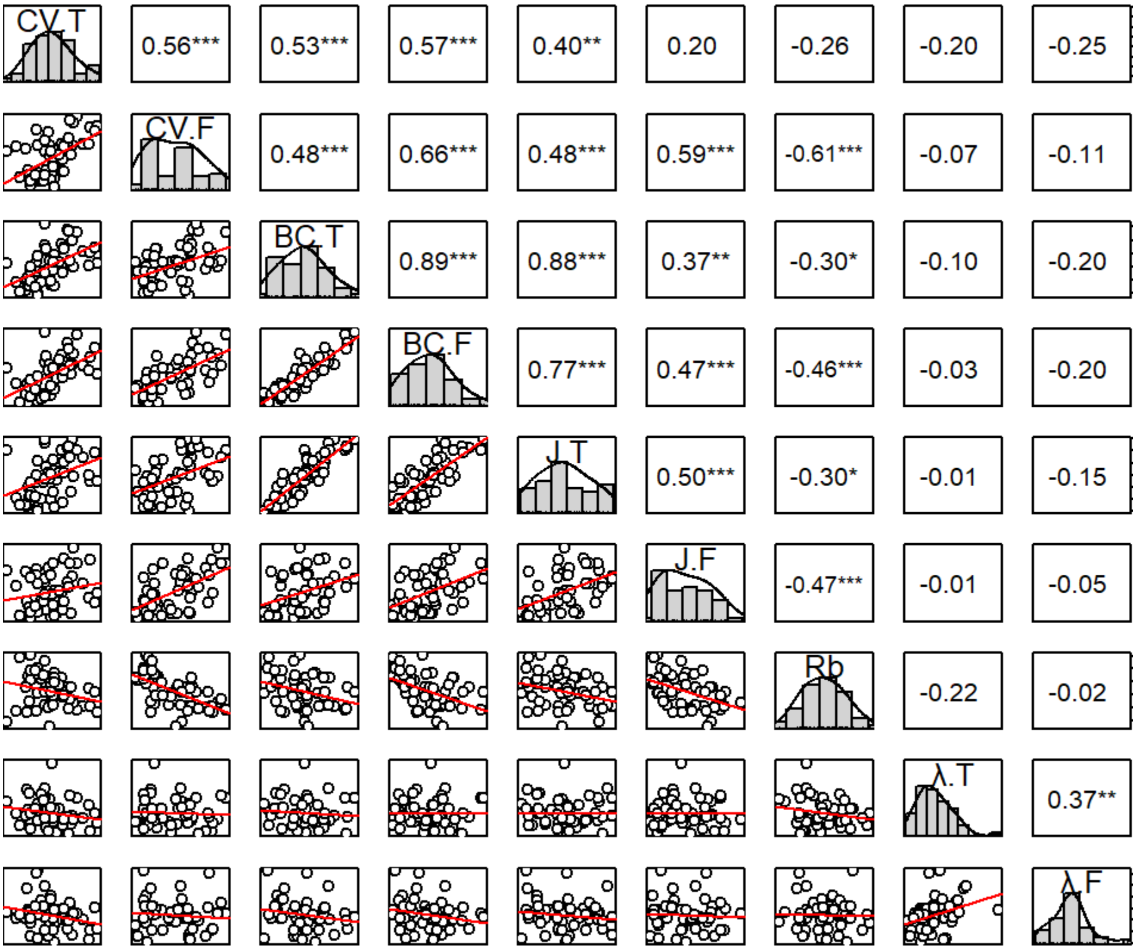


Figure 4.3 *Pairwise relationships between facets of stability. Upper right panels show Pearson's correlation coefficients and significance between variables (row versus column), and lower left panels indicate their linear relationships. *p < 0.05, **p < 0.01, ***p < 0.001.*

Table 4.3 *Results of principal components analysis of with taxonomic and functional stability variables combined. * = components selected for further statistical analysis. Eigenvector loadings are shown for the first 2 PCs where eigenvalues were > 1. Degree of shading highlights weight of loading on each eigenvector, with darker colour indicating variables with heavier loadings.*

Principal component	Eigenvalue	% Variation	Cumulative % Variation
1 *	4.20	46.6	46.6
2 *	1.54	17.1	63.7
3	0.98	10.9	74.6
4	0.74	8.2	82.8
5	0.66	7.4	90.2
6	0.42	4.6	94.8
7	0.25	2.8	97.6
8	0.17	1.9	99.5
9	0.05	0.5	100.0

Eigenvectors		
Code	PC1	PC2
BC.T	0.42	-0.12
J.T	0.41	-0.01
CV.T	0.32	-0.23
λ.T	-0.04	0.63
BC.F	0.45	-0.01
J.F	0.32	0.22
CV.F	0.39	0.12
λ.F	-0.12	0.56
Rb	-0.29	-0.4

Table 4.4 *Results of separate principal components analyses of taxonomic and functional stability variables. * = components selected for further statistical analysis. Degree of shading highlights weight of loading on each eigenvector, with darker colour indicating variables with heavier loadings.*

Principal component	Eigenvalue	% Variation	Cumulative % Variation
Taxonomic PCA			
1 *	2.42	48.4	48.4
2 *	1.21	24.1	72.5
3	0.74	14.7	87.2
4	0.54	10.7	97.9
5	0.10	2.1	100.0
Functional PCA			
1 *	2.65	53.1	53.1
2 *	1.03	20.7	73.7
3	0.53	10.6	84.4
4	0.49	9.8	94.2
5	0.29	5.8	100.0

Eigenvectors		
Code	PC1	PC2
BC.T	0.6	-0.06
J.T	0.57	0.04
CV.T	0.45	-0.23
λ.T	-0.06	0.81
Rb	-0.32	-0.53

BC.F	0.5	-0.17
J.F	0.47	0.1
CV.F	0.55	0.03
λ.F	-0.1	0.95
Rb	-0.47	-0.26

4.4.2 *Differences in stability properties among streams*

Ordination of the first two dimensions of taxonomic and functional stability from separate PCAs (Section 4.4.1) revealed some divergence in stability properties among stream types and decades (Figure 4.4). Across stream types, differences were more apparent for functional stability, where acid stream communities were more volatile (higher PC1 scores, more variable, less resistant, and less persistent) compared to CM and particularly BW stream communities, which were subsequently less robust. The mean volatility of communities was also lower in the first decade of the study (T1), while T4 appeared to be associated faster speeds of recovery (lower PC2 scores).

Results of linear mixed-effect models revealed significant effects of both decade and stream type (Figure 4.5). Functional PC1 differed significantly among stream types ($F_{3,6} = 6.2$, $p = 0.0078$), and *post-hoc* test results showed that AC communities were significantly more volatile in terms of functional properties than BW ($z = 3.54$, $p = 0.0024$) and CM ($z = 3.26$, $p = 0.006$) (Figure 4.5a). These effects were further supported by grouping streams based on pH, where neutral stream communities (BW + CM) were significantly less volatile than acid ones ($F_{1,15} = 13.5$, $p = 0.0023$). In grouping streams this way, effects were also seen for taxonomic PC1 where, again, communities in neutral streams were significantly less volatile ($F_{1,15} = 6.4$, $p = 0.023$). In no instance did the first two PCs differ between wooded and moorland streams (all $p > 0.05$), highlighting the potentially greater importance of an acid-base gradient compared to canopy cover. Moreover, there was no statistically significant effect of stream type nor pH on PC2.

Effects of decade were particularly evident for PC1 (taxonomic: $F_{3,34} = 24.6$, $p < 0.0001$; functional: $F_{3,34} = 25.5$, $p < 0.0001$). As seen from ordination plots (Figure 4.4), communities were the least volatile in T1, reducing significantly (higher PC1 scores) by T2 (taxonomic: $z = 7.83$, $p < 0.001$; functional: $z = 8.03$, $p < 0.001$). Although volatility decreased thereafter, communities remained less stable in this regard until the end of the study (T1-T3 taxonomic: $z = 4.1$, $p < 0.001$, functional: $z = 6.71$, $p < 0.001$; T1-T4 taxonomic: $z = 6.56$, $p < 0.001$, functional: $z = 4.73$, $p < 0.001$). To a lesser extent, changes in PC2 were also evident for both taxonomy ($F_{3,35} = 3.4$, $p < 0.02$) and function ($F_{3,44} = 5.6$, $p < 0.002$). In contrast to PC1, observed changes in PC2 across decades indicated that communities were significantly more functionally resilient in T4 compared to T1 ($z = 3.01$, $p = 0.014$), and also least resilient in T3.

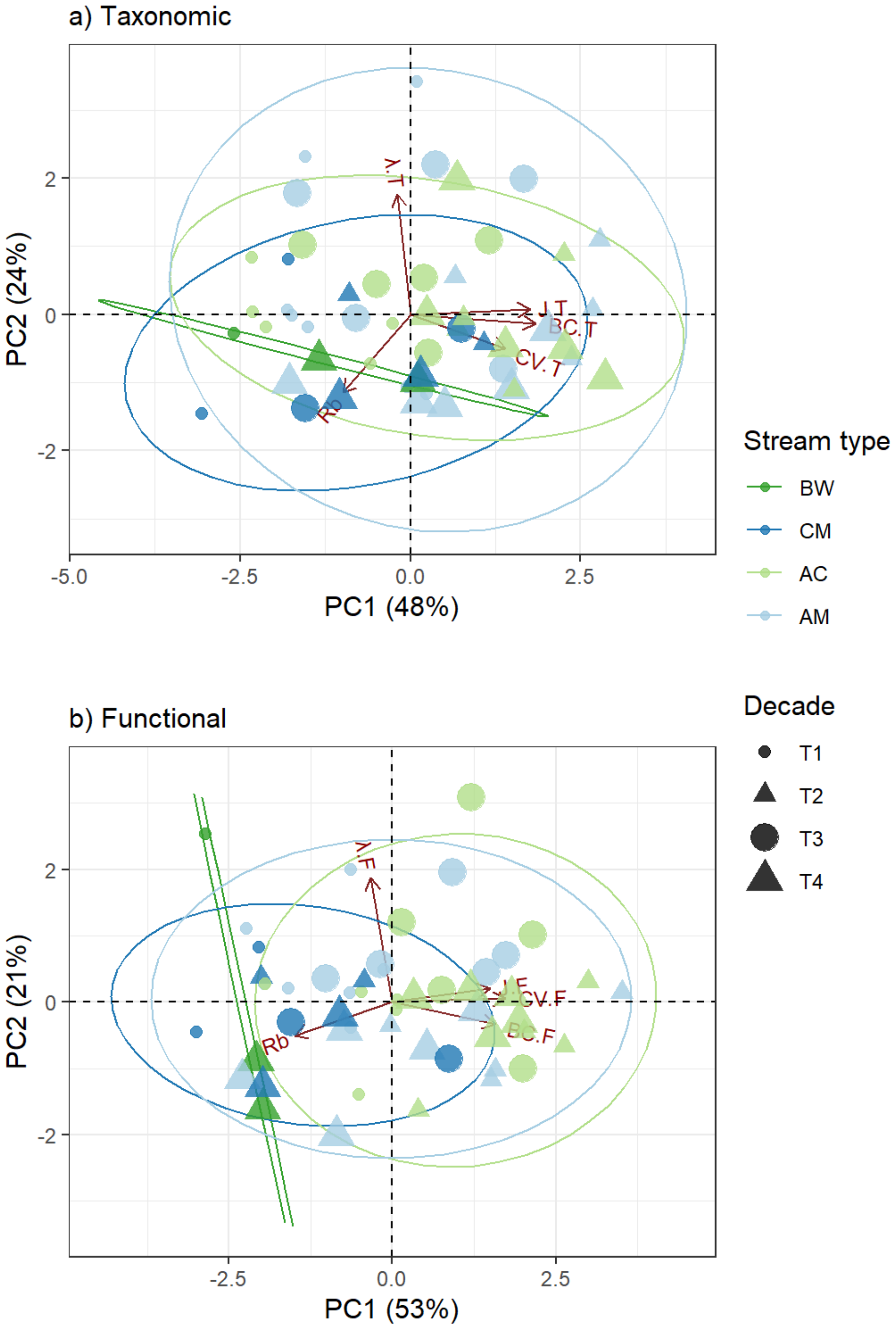


Figure 4.4 *Ordination of the first two components of taxonomic and functional stability. Plot* ***a)*** *shows taxonomic stability and* ***b)*** *shows functional stability, using values calculated for each stream and decade. Direction of arrows indicates lower stability, and ellipses highlight 95% confidence of the mean for each stream type. Note ellipse for BW is inaccurate due to limited data. However, these remain for visual aid.*

Covariance matrices constructed for separate stream groups (each stream type, wooded versus open, acid versus neutral, and each decade) revealed some differences in the shape and volume of ellipsoids (Figure 4.6). The most prominent differences were seen across stream types, where AC communities had the largest volume, particularly with regards to functional stability. In AC, ellipsoid volume was 65% of the maximum possible volume if no stability components were correlated, suggesting a more spheroidal shape and high dimensionality. Given the small sample sizes for CM and particularly BW streams, caution is warranted when interpreting their much lower volumes. However, when grouped into acid and neutral streams, similar differences were seen, increasing the confidence in this result. No clear differences in volume nor semi-axis lengths were seen for wooded compared to open streams, further supporting the potential importance of an acid-base divide. A review of eigenvector loadings for PCAs of acid and neutral streams provided some tentative evidence that relationships seen for full PCA (Section 4.4.1) were maintained. That is, resilience (and to some extent robustness) varied independently to other measures of stability (Table A.5).

Across decades, a reduction in ellipsoid volume could be seen during T2, coinciding with changes in the relative levels of stability properties (increasing volatility, increasing speed of recovery). There was also tentative evidence that relationships between stability variables changed, with λ.T loading more heavily, and positively, along PC1 of taxonomic analysis (0.46), alongside BC.T (0.52) and J.T (0.58), with CV loading negatively (-0.42) and Rb being unrelated (Table A.5). However, the variations in ellipsoid volume across decades were small in comparison to the effects seen for AC streams, noting also that less data were available during T2 (n streams = 10).

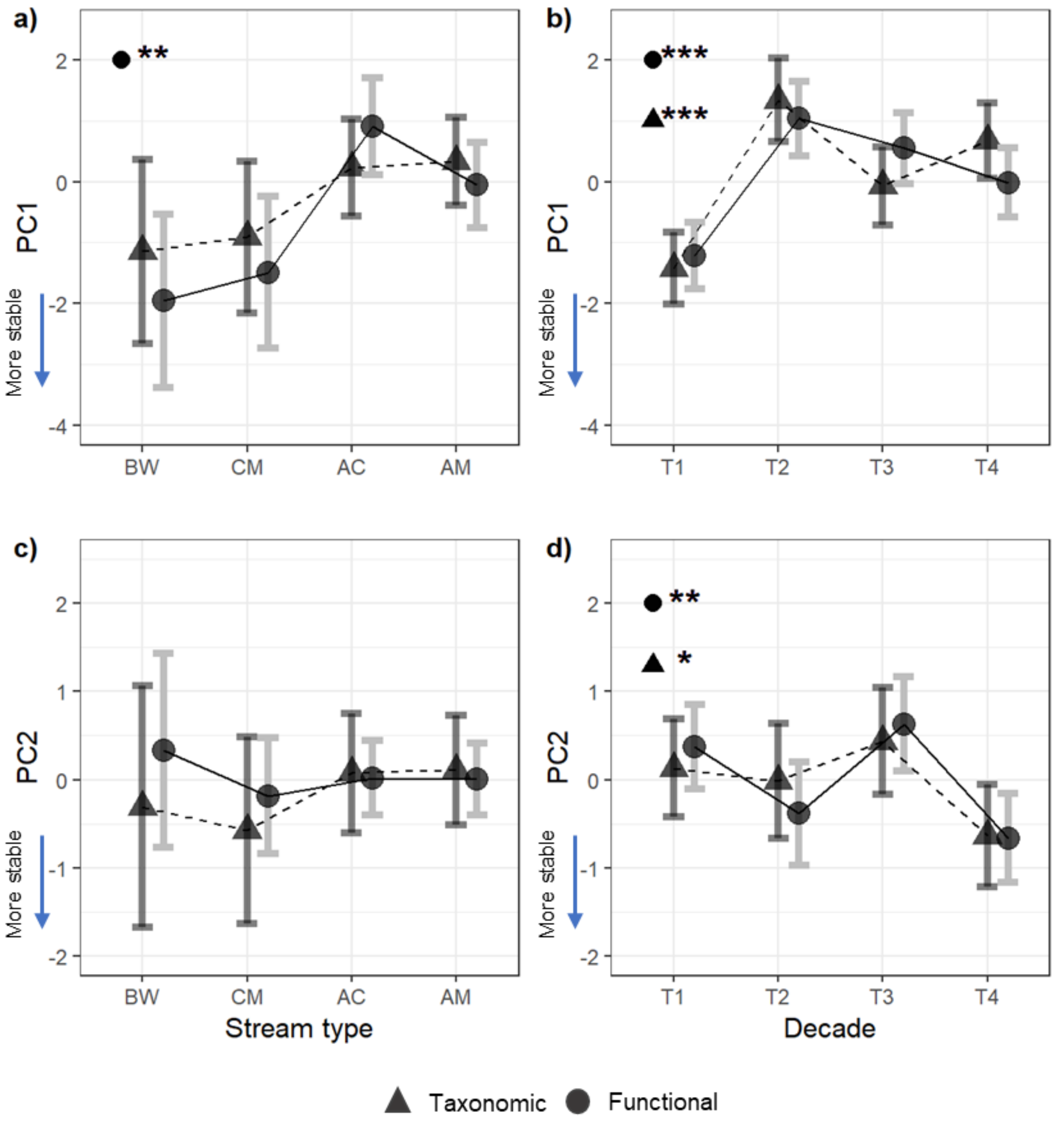


Figure 4.5 Effects of stream type and decade on the first two components of taxonomic and functional stability. Plots show differences in taxonomic and functional PC1 between ***a)*** stream types, and ***b)*** decades, and differences in taxonomic and functional PC2 between ***c)*** stream types, and ***d)*** decades. Where overall statistical significance was found, this is shown for taxonomic and functional data, respectively. *$^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.*

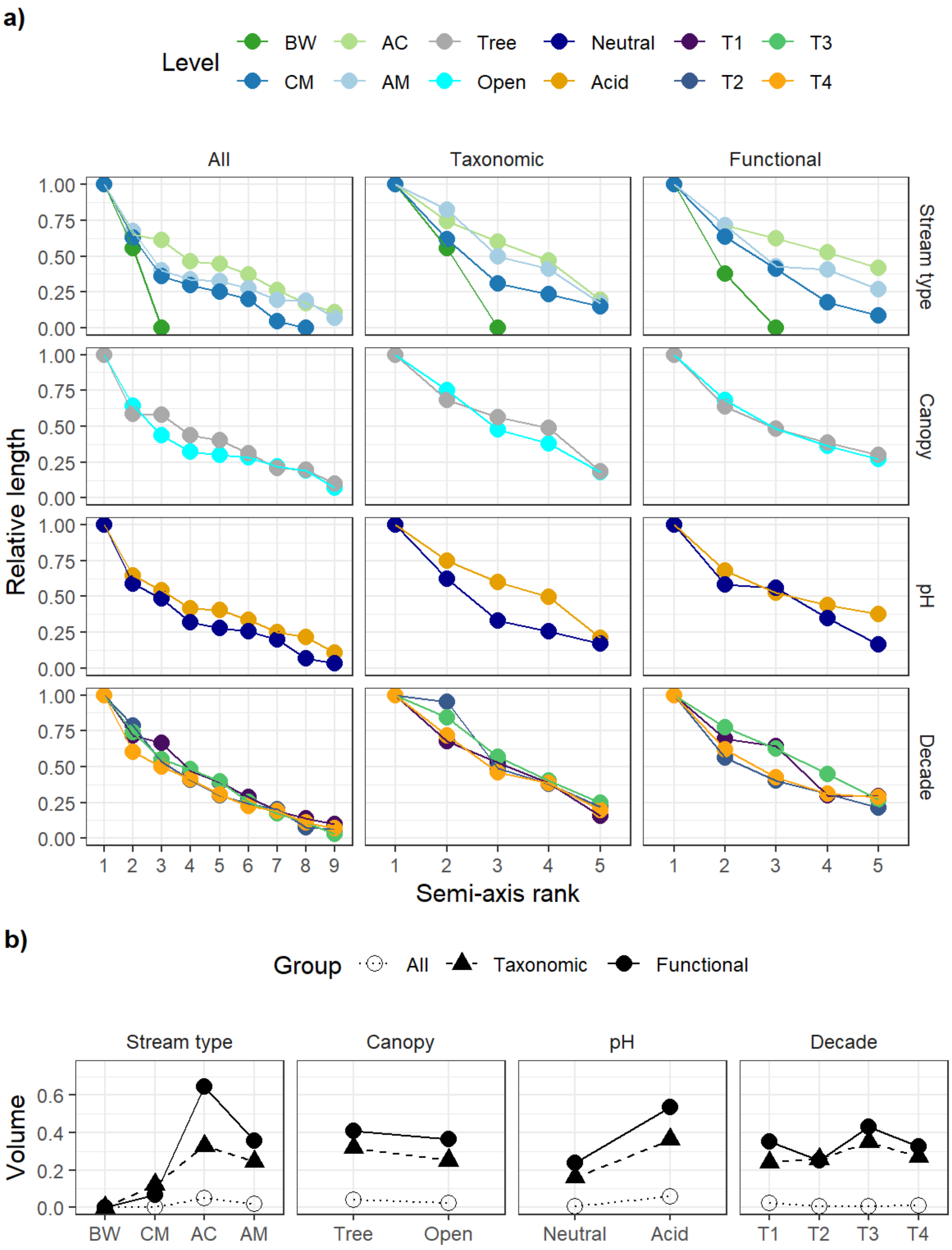


Figure 4.6 *Results of dimensionality of stability within stream groups. Plot **a)** shows relative semi-axes lengths and **b)** shows standardised ellipsoid volumes for each group. Analyses were conducted for all stability variables together (n = 9), and for taxonomic (n = 5) and functional (n = 5) stability variables separately. Note that BW was restricted to 3 dimensions due to limited data.*

4.4.3 *Temporal trends in stability*

Changes in stability over time were assessed for persistence (J.T and J.F) and Rb. Resistance was not included in further analyses since it was highly correlated with J.T (Section 4.4.1). Results showed that stability significantly varied through time, but that trends differed between stability components and stream types (Figure 4.7). J.T increased over time in all stream types, indicating a magnification in taxonomic turnover (reducing persistence). However, results were only statistically significant within CM ($F = 4.2$, $p = 0.0042$), AC ($F = 5.4$, $p < 0.0001$), and AM streams ($F = 5.4$, $p < 0.001$) (Table 4.5). Likewise, changes in J.F were statistically significant ($F = 7.1$, $p = 0.001$), but stream type was not found to be an interacting factor, despite some evidence of differences (Figure 4.7). In acid streams, an initial rise in J.F (reducing functional persistence) occurred until 2000-2005, and declined again thereafter, while there were apparent linear declines in CM over the study highlighting potential heightened vulnerability in these streams, both in terms of taxonomic and functional changes. Conversely, communities remained more persistent in BW than in any other stream type, despite a lack of statistical distinction determined in this analysis.

Changes in Rb also differed with stream type, and were only statistically significant within acid streams (AC $F = 8.6$, $p = 0.004$; AM $F = 5.8$, $p = 0.03$), as observed for J.T. In these instances, robustness increased linearly in AC streams, but followed similar patterns seen for J.F in AM streams, i.e., increasing until the early 2000s, with subsequent decline – noting that robustness was the most strongly negatively correlated with measures relating to functional volatility (including J.F) (Section 4.4.1). Moreover, changes in Rb were subtle, ranging from a minimum mean annual robustness of 0.42 in BW in 2012, to the highest possible maximum (0.5) in AM in 1994. This also coincided with the lowest observed taxonomic persistence (highest J.T values) over the study, where data were available (acid streams).

Changes in J.T reflected a simultaneous increase in taxonomic losses and gains, which appeared to oscillate in a lagged manner consistent with recovery, or multi-year resilience (Figure 4.8a). For example, large increases in J.T (reduced persistence) in the early 1990s (1993-4) were weighted towards taxonomic losses (> 50 %), but subsequently followed by gains in 1995 (based on available data). Overall, the number of years in which taxonomic losses outweighed gains was greater than years when gains outweighed losses by 13 – 42%, with the exception of BW and AC which were 1:1. Mean inter-annual losses (20.8%) were also marginally higher than gains (19.7%). Changes in J.F were similarly underpinned by simultaneous trait losses and gains (Figure 4.8b). Like J.T, greater functional trait loss years were 29 – 60% more frequent than greater gain years, and mean functional losses (3.5%) were slightly higher compared to gains (3.2%). Increasing Rb could be explained by higher web connectance (r = 0.64-0.75 across stream types). However, despite similar temporal trends in modularity to those for robustness, and a strong correlation between mean values (Section 4.4.1), the relationship between annual Rb and modularity was weak (r = -0.3).

Table 4.5 *Generalised additive mixed model outputs for temporal trends in key facets of community stability. Models are presented for taxonomic and functional persistence (J.T and J.F) and robustness (Rb). The significance of stream type as an interacting factor was assessed using likelihood ratio tests (LRT). Outputs are reported based on regional or stream type results depending on the significance of LRT.*

Stability variable	LRT *p*	Stream type	Parametric			Smooth		R^2 (adj)
			F	*p*	edf	*F*	*p*	
J.T	< 0.0001	BW	1.3	0.27	1	0.46	0.5	0.24
		CM			1	4.2	*0.004*	
		AC			7	5.4	*< 0.0001*	
		AM			7	5.4	*< 0.0001*	
J.F	0.97	Regional	2.7	*0.047*	3	7.1	*0.0001*	0.11
Rb	0.048	BW	5.1	*0.0017*	1	1.1	0.3	0.16
		CM			2	1.5	0.2	
		AC			1	8.6	*0.004*	
		AM			2	5.8	*0.003*	

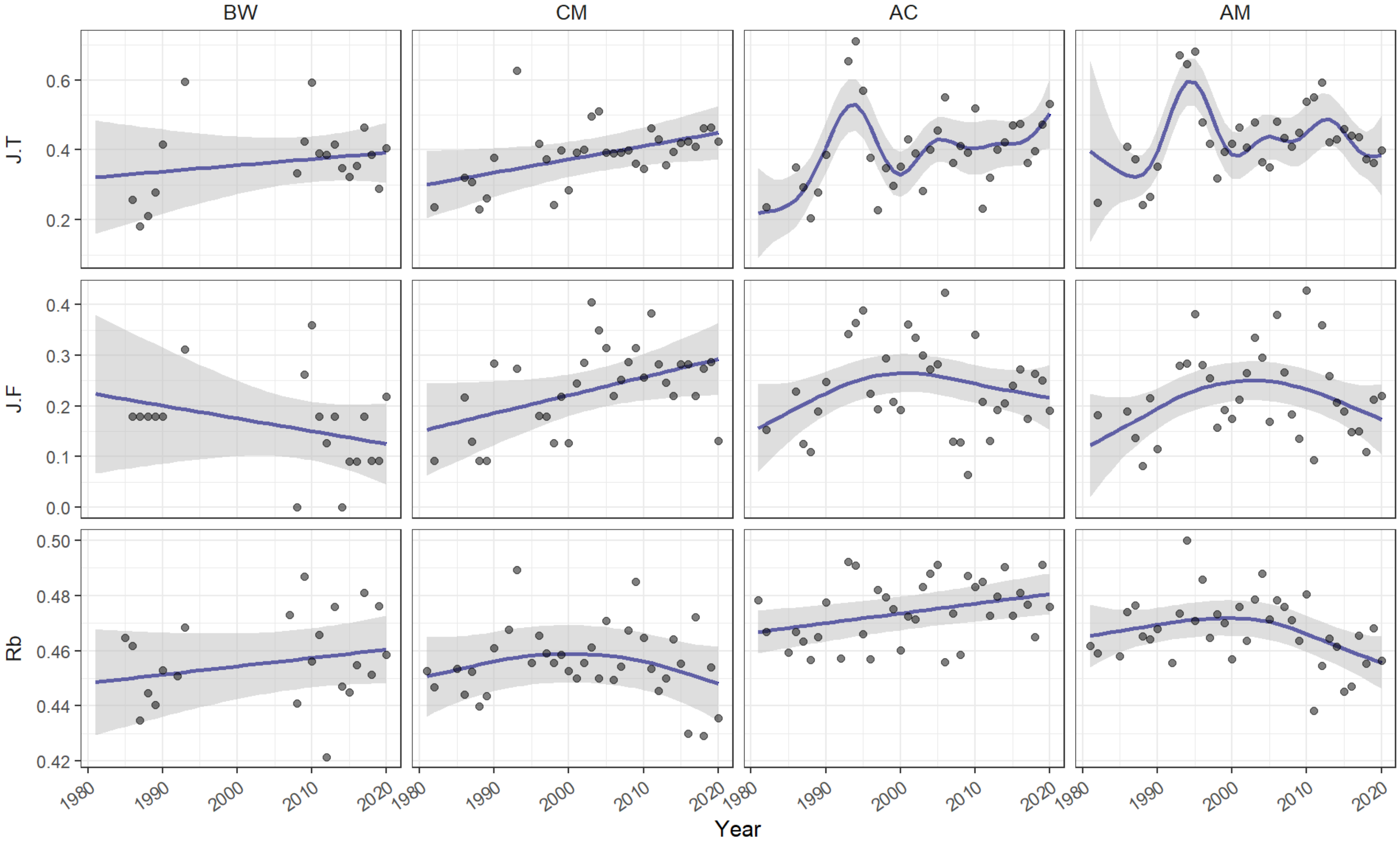


Figure 4.7 *Trends in key facets of community stability over time. Trends are shown for taxonomic and functional persistence (J.T and J.F), and robustness (Rb) in each stream type. Smoothed trendlines were fitted using GAMMs. Points represent mean values across streams. Note: year * stream type interaction for J.F was not statistically significant (LRT p > 0.05).*

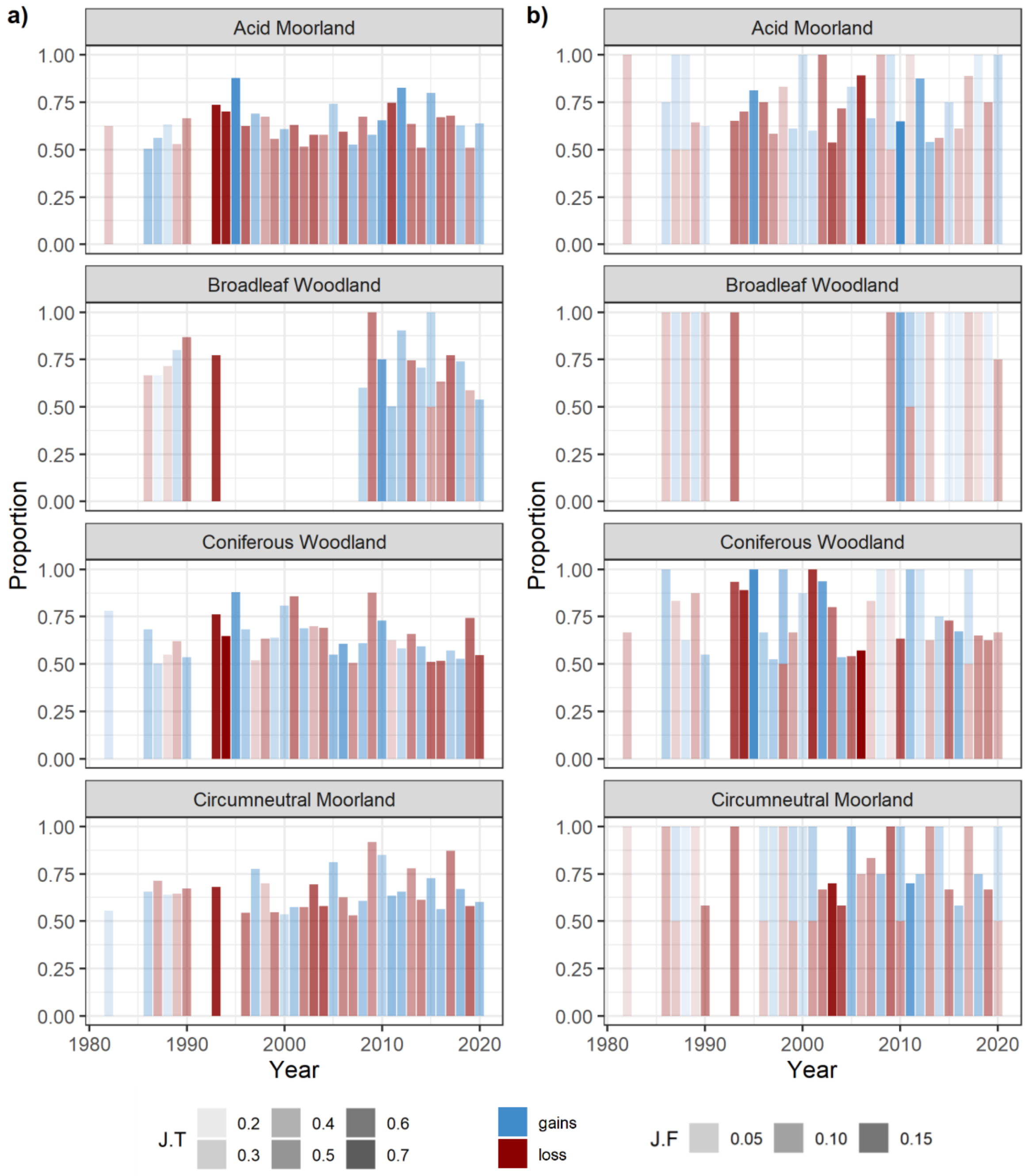


Figure 4.8 *Inter-annual losses and gains of taxa and traits in each stream type as a proportion of persistence/turnover. Plot* ***a)*** *shows taxonomic gains and losses as a proportion of J.T. Plot* ***b)*** *shows functional trait losses and gains as a proportion of J.F. Only losses and/or gains are shown in each year where these represented ≥50% of the turnover (J). Darker colours correspond to higher Jaccard's values and thus lower persistence.*

4.4.4 *Linking stability to climate change*

Over the 40 years of observations, stream communities were exposed to rising water temperatures of more than 0.5°C, increasing discharge in the driest months of the year, and large variations in high flows, low flows, and temperature (Figure 4.1; see Chapter 3 for further details). Climate variables summarising these annual and seasonal conditions were correlated with changes in annual stability (J.T, J.F, and Rb), explaining 4 to 16% of variation across streams and years (Table 4.6). Despite large changes in mean conditions over the study period, it was extremes that were significantly associated with stability, and particularly mean minimum discharge (Q.min) (Figure 4.9). There was little evidence of mediatory effects of stream type, except for the relationship between Q.min and J.T (LRT $p = 0.026$). In this instance, effects within each stream type were only significant in AC streams ($p < 0.05$).

All three stability measures were significantly correlated with Q.min ($p < 0.05$). However, the relationship with J.T was complex (edf = 5) and bimodal. This reflected a peak in both gains and losses at each peak in J.T. Across a gradient of increasing Q.min, J.T and J.F both generally increased (lower persistence), while robustness also increased. This was reflective of negative correlations between Rb, and other measures averaged over decades, though correlations at annual scale were weak (J.T $r = 0.19$, J.F $r = 0.22$). Similar destabilising effects of summer high flows were found for J.T. During winter, however, increasing Q.minW was correlated with lower J.T and higher Rb, reflecting potentially negative impacts of dry winters. Compared to median Q.minW, around 8% more taxa differed (turned over) in the community on average when Q.minW was at its lowest.

Unexpectedly, the only instance where significant effects of temperatures were found was for Rb, which increased with higher Tw.max. There was, however, evidence to support an interaction between Tw.max and Q.min for J.T (LRT $p = 0.0003$) and Rb ($p = 0.04$). For J.T, there was evidence that the greatest shifts in year-to-year composition were in the coldest and wettest of Tw.max and Q.min, and in the warmest and driest (Figure 4.10). Similarly, the years with the highest robustness were warmest and driest. Moreover, effects of Tw.max appeared unimodal for J.T, which could be explained by a peak in both losses and gains around median conditions (12.9°C).

Table 4.6 *Generalised additive mixed model outputs for the effects of temperature and discharge on key facets of community stability.*

Stability variable	Parametric term		Smooth terms				R^2 (adj)
	F	*p*		edf	*F*	*p*	
J.T	2.2	0.093	Tw.mean	1	1.7	0.20	0.13
			Q.mean	2	2.6	0.069	
			Q.min	5	3.3	*0.0055*	
			Tw.max	2	3.3	0.057	
			Q.maxS	1	7.9	*0.0052*	
			Q.minW	1	13.7	*0.00025*	
J.F	2.7	*0.043*	Tw.mean	1	0.4	0.54	0.04
			Q.mean	1	0.1	0.73	
			Q.min	1	7.1	*0.0079*	
			Tw.max	1	0.1	0.70	
			Q.maxS	1	1.4	0.24	
			Q.minW	1	2.3	0.13	
Rb	5.2	*0.0016*	Tw.mean	1	0.9	0.34	0.16
			Q.mean	1	1.0	0.31	
			Q.min	1	14.1	*0.00020*	
			Tw.max	1	8.9	*0.0030*	
			Q.maxS	1	0.0	0.84	
			Q.minW	1	15.4	*0.00010*	

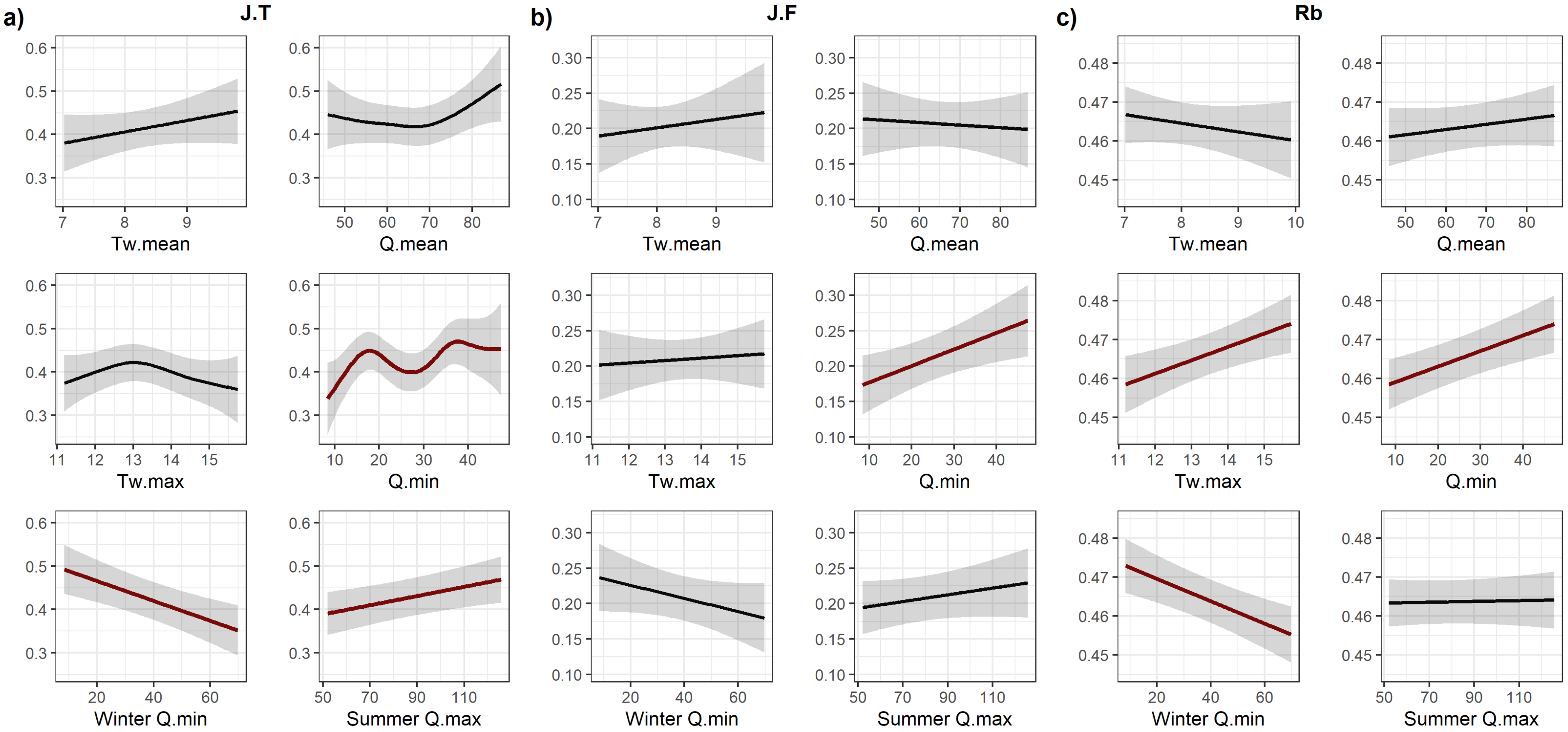


Figure 4.9 *Estimated partial effects of climate-driven stream conditions on key facets of community stability. Effects were estimated using GAMMs for* ***a)*** *taxonomic persistence (J.T),* ***b)*** *functional persistence (J.F), and* ***c)*** *robustness (Rb). Red lines indicate significant effects ($p < 0.05$).*

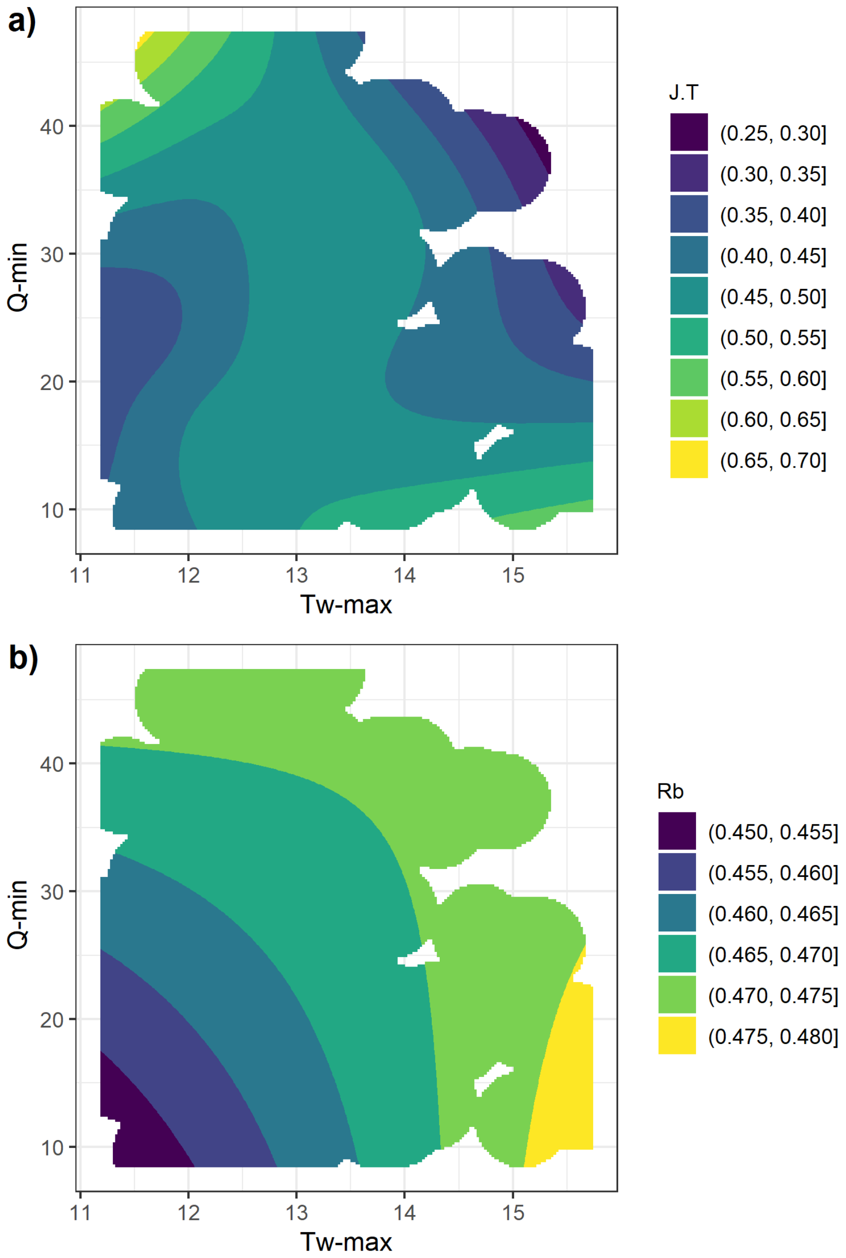


Figure 4.10 *Estimated partial effects of the interaction between extreme minimum monthly discharge (Q.min) and maximum monthly temperature (Tw.max) on community stability. Contour plot* ***a)*** *shows response of taxonomic persistence, J.T and plot* ***b)*** *shows response of robustness, Rb.*

4.5 Discussion

Freshwater ecosystems are facing increasing threats from global climate change and land use, resulting in disturbances of both pulse and press nature that impact the structure and function of invertebrate communities in rivers (Reid et al. 2018; Sabater et al. 2022). However, there is a lack of long-term empirical evidence demonstrating the effects of these disturbances on multiple aspects of ecological stability and their interrelationships (Donohue et al. 2013). Such assessments are crucial to enhance our understanding of stability and provide reliable evidence to inform management interventions aimed at promoting climate resilience in river systems. In this study, a 40-year dataset of macroinvertebrates in headwater streams was used to investigate ecological stability in relation to local catchment characteristics and climatic conditions. Results revealed that at least two dimensions were necessary to evaluate overall stability in these systems, one relating to community invariability, persistence, resistance, and negative robustness, and the other to resilience. Relationships were largely conserved across taxonomic and functional features with the exception of functional persistence, and to some extent, robustness which was more strongly negatively correlated with taxonomic resilience than functional resilience (Hypothesis 1). Variations in stability through time were most commonly associated with extreme conditions (Hypothesis 2). However, despite differences in temporal trends across stream types, there was limited evidence of contrasting climate sensitivities (Hypothesis 3).

The findings of this study present valuable evidence that highlight the complex response and recovery dynamics of stream macroinvertebrates. However, it is important to exercise caution when interpreting these results for several limitations. The primary limitation in this study was the low replication, particularly for streams characterised by broadleaf woodlands (Chapter 1, Figure 1.3). Although comparisons were made to a near-complete dataset for a subset of streams, it is possible that differences in stability were observed simply because disturbances were not equally captured. However, additional steps to mitigate this issue were taken by combining streams based on pH and canopy cover, which increased confidence in results. Additionally, besides subtle differences in HadUK-Grid data and *in situ* water temperatures recorded in some streams (Chapter 3, Section 3.3.3), this study assumed a mostly identical disturbance regime across streams. Potentially, this could mean that the effects of climate and land use on ecological stability are over- or underestimated.

Nevertheless, validation steps conducted demonstrated a high correlation in discharge values between sites located up to 40 km apart (Table A.1). This meant that differences across streams at Llyn Brianne were expected to be minimal.

Given that the primary focus of this study was to assess the nonlinear dynamics and year-to-year variation in communities, it is crucial to acknowledge random error associated with data from natural systems. For example, some variation might be due to sampling error or inherent variability of the community rather than the effects of pulse disturbances. While methods used to calculate resilience aimed to address some of this stochasticity (Ives 1995; Ives et al. 2010), other measures relying on pre-disturbance or equilibrium points where a high amount of noise is present may be less reliable. Moreover, equilibria can be difficult to identify if they are continuously shifting, or indeed do not exist (Holling 1996; Gunderson 2000; Vaughan and Gotelli 2019). Nonetheless, these issues are inherent to observational data from complex dynamical systems such as rivers, and to the field of ecological stability more generally, and simply highlight the need for ongoing monitoring and research. Moreover, given the inherent randomness and unpredictability of natural systems, the utilisation of rare, long-term data in this study further emphasises its value and importance.

In the first hypothesis, stability was expected to be the same for both taxonomic and functional indices. This was generally unsupported, and instead functional stability was found to be much higher than taxonomic, but also more complex. For example, mean inter-annual turnover of taxa was 39%, compared to just 6% for functional traits. Conversely, ellipsoid volume was 46% for functional stability, compared to 35% for taxonomic. This divergence was thought to be primarily due to lower correlations between functional persistence and other measures, and may indicate that this facet of stability is governed by different mechanisms (Hillebrand et al. 2018; Polazzo and Rico 2021). Overall, these results are suggestive of high functional redundancy, a mechanism that has been identified for conferring stability in a range of systems (Naeem 1998; Bruno et al. 2016; Biggs et al. 2020). Higher functional stability relative to taxonomic has also been shown in other aquatic systems, especially when dissimilarity measures were used (Griswold et al. 2008; Hillebrand and Kunze 2020; Polazzo and Rico 2021). Yet, the degree of average taxonomic stability might also be considered high, with similar levels seen in other headwater streams (Townsend et al. 1987; Scarsbrook 2002; Idígoras Chaumel et al. 2019). This could potentially be explained by factors such as high response diversity within communities (the variety of ways that species within the community respond to disturbances), or resistance and resilience traits, which contribute to stability (Elmqvist et al. 2003; Mori et al. 2013; Bogan et al. 2017).

The expectation that the dimensionality of stability would be low, i.e., all components would be correlated, was not supported. However, despite differences in the relative degree of stability properties between taxonomic and functional indices, overall relationships were largely conserved, meaning that stability could be reduced from nine overarching measures to just two; how communities respond and fluctuate over time, and how they recover. This suggests that the processes governing ecological stability of these stream communities are more complex than initially expected and often recognised in empirical studies. Despite this, these results are consistent with other research using a multidimensional stability approach (Donohue et al. 2013; Hillebrand et al. 2018). This consistency occurred despite differences in habitat and community type, timescales, and measurements of stability. However, while the number of dimensions corroborated other findings, the divergence of resilience from other measures contrasts with both observational and experimental studies in freshwaters (Hillebrand et al. 2018; Hillebrand and Kunze 2020; Allen et al. 2023). A number of factors could explain these results besides different underlying processes, including the contrasting ways resilience is defined and measured. For example, it is often measured over shorter timeframes, in the days, weeks, or months following a disturbance (Donohue et al. 2013; Hillebrand et al. 2018; Eagle et al. 2021; Allen et al. 2023), and in this way has often been found to correlate negatively with resistance (Harrison 1979). While there was some evidence to suggest that resilience operated at these shorter scales, i.e., years of losses were often followed by years of gains, and the dimensionality of stability changed between decades, further research would be required to identify such dynamics, including measurements over individual disturbance events where feasible.

The patterns of losses followed by gains seen in this study also warrant further investigation. For example, results from similar studies suggest that re-colonising taxa may be those able to exploit disturbed habitats, such as aerial dispersers (Eagle et al. 2021). In such cases, gains might not be indicative of community recovery, but instead invasion by generalist species. Given that, in this study, temporal reductions in taxonomic persistence were observed, and that both increasing losses and gains underpinned this trend, this could also be indicative of competitive exclusion and environmental filtering (Eagle et al. 2021), i.e., despite apparent recolonisation, strong pressures limit establishment of populations, and thus persistence.

Although the underlying processes are unknown, decreasing persistence and increasing robustness over the study were explained by the fixed effect of stream type and by climate (4-16% of explained variation in J.T, J.F, and Rb). Overall, results suggested that extreme conditions better-explained year-to-year variation than average conditions, supporting other findings from freshwaters (Sabater et al. 2022), and Hypothesis 2. In particular, the timing of events (summer or winter versus annual) revealed contrasting impacts. Variables related to higher flows in summer, and droughts in winter were significantly correlated with lower stability, supporting research that suggests atypical timing of events could have disproportionate impacts (Woodward et al. 2015).

The unexpected effects of higher flows during the driest month of the year highlight the complexity of climatic effects. Negative impacts of increased flow during the driest months might indicate that species in upland streams are adapted to low flow (except when this coincides with extreme temperatures) or that other complex processes are taking place. In chalk streams, for example, severe rainfall deficit has been shown to have little impact on macroinvertebrate communities, where flow from winter recharge of groundwater was thought to mitigate effects (Wood and Petts 1999). In the uplands, where streams are largely rain-fed, lower flow during the winter half of the year (October-March) had a negative impact to taxonomic composition, suggesting winter rainfall plays an important role in these streams too. Winter precipitation and snowmelt runoff in spring are crucial to the input and transport of organic matter (Hornberger et al. 1994; Boyer et al. 1997). Winter droughts could therefore lead to a deficit of resources and water during summer, potentially exacerbating summer high and low flow events. Despite this, functional traits persisted with changes in winter conditions, again suggesting high functional redundancy. Contrastingly, negative impacts of increased flow during dry conditions seen in summer might occur due to flash floods, sediment inputs, and mobilisation of concentrated pools of nutrients and pollutants such as heavy metals, leading to poorer water quality (Mosley 2015). These results highlight the complex and potentially interacting effects of climate change, indicating that atypical timing of events could contribute to instability.

The large taxonomic and functional shifts seen during the early 1990s have previously been attributed to a positive (warmer, wetter) phase of the NAO (Bradley and Ormerod 2001). Specifically, however, inter-annual shifts coincide with a severe summer flood event that occurred in June 1993 that was preceded by several years of low rainfall – the major drought of spring 1990 to summer 1992 (Marsh et al. 2007). This was characterised by exceptionally low groundwater levels that had not been seen for 90 years (Marsh et al. 2007). The addition of more than two decades of data since the study by Bradley and Ormerod (2001) make it possible to determine that such large reductions in inter-annual stability are uncharacteristic of NAO effects alone, but supports suggestions that positive NAO phases might exacerbate climate change effects (Durance and Ormerod 2007). During this decade, however, there appeared little impact to the dimensionality of stability, which reduced slightly for functional components. This contrasts with studies showing an increase in dimensionality following flood events (Eagle et al. 2021).

In the final hypothesis, broadleaf woodlands were predicted to enhance ecological stability relative to other, modified stream types. However, the largest dividing factor determining stability in these streams was an acid-base gradient. Specifically, coniferous streams had the largest dimensionality of stability, were the most functionally volatile, and the only stream type to display significantly greater taxonomic sensitivity to changing streamflow (Q.min). The higher dimensionality of acid and particularly conifer streams is indicative of greater stress (Donohue et al. 2013). This supports a range of studies highlighting the consequences of upland stream acidification and afforestation with conifers (Weatherley and Ormerod 1987; Donald and Gee 1992; Bunce et al. 2014; Malcolm et al. 2014). Although studies have shown some chemical recovery (Battarbee et al. 2014), the disproportionate effects of flow suggest that these streams could still be impacted by acid episodes (Kowalik and Ormerod 2006). However, further research is required to determine other potential drivers, which could relate to low nutrient inputs, excessive shading, or logging activities (Thomas et al. 2015).

The similarities seen between broadleaf and circumneutral moorland streams also supports the observations of Canning *et al* (2019), who found no differences in network structure, stability or temporal variability between grassland and forested streams. Moreover, the magnitude of changes seen in the stability of these two stream types over time were less than those of acid streams, despite limited evidence of differences in climate sensitivity. This further emphasises the acid-base divide. Despite this, changes in stability in all stream types were evident, coinciding with subtle shifts in the dimensionality of stability over the decades of this study (Donohue et al. 2013; Radchuk et al. 2019). While not without limitations, these results highlight the complex and widespread risks of climate change, that may be further exacerbated by local scale factors.

Further research should address the limitations of this study, first and foremost by expanding analyses to other sites and locations. This approach offers several benefits. Firstly, it could help to determine whether the observed patterns of stability in relation to stream type are consistent across other systems, while enhancing the statistical power and reliability of inferences. Secondly, it would facilitate the identification of potential differences in stability mechanisms at finer spatial scales. For instance, the current study may have obscured relationships between stability components due to the inclusion of streams with varying levels of modification in the same multidimensional space. Thus, investigating the dimensionality of stability within stream types, or within streams and over multiple disturbance events (Eagle et al. 2021), warrants further attention. Challenges remain however, from the widespread nature of anthropogenic pressures, as this is likely to contribute to shifting baselines and limit our ability to a) identify desired reference conditions, and b) measure stability variables that are based on equilibria (or mean) like those used in this study, as detailed above (Vaughan and Gotelli 2019).

Given the unexpected relationships between robustness and other taxonomic and functional stability variables, future studies might also benefit from more detailed network analysis. This could potentially capture multiple dimensions of stability, but would require collection of biomass and dietary data to extend beyond qualitative information and inferred connections. Likewise, although trait data are useful for separating taxonomic and functional dynamics, their use has been criticised for potentially overlooking intraspecific variation (Gonçalves-Souza et al. 2023). Genetic information, or direct measurements of functional processes such as decomposition and production, would contribute to a better understanding of stability, its underlying mechanisms, and the accuracy of generic trait data.

The UK is expecting warmer wetter winters, and hotter drier summers as climate change accelerates (IPCC 2021). However, these headline predictions should not detract from the need to investigate unexpected or atypical events such as winter droughts and summer floods, which were found in this study to correlate with community changes. Characterising climatic disturbances is challenging, however, given the complex interactions that might occur inter-seasonally, and as the culmination of multiple years of altered weather. Studies that explore these interactions are therefore crucial, and might provide a better understanding and prediction of effects from extreme events. Moreover, relationships between stability and climate could change as communities adapt to environmental pressures, and further work investigating 'ecological memory' (Hughes et al. 2019), or 'state dependency' and causal links between disturbances and stability (Sugihara et al. 2012), could be important avenues for future research.

The management implications of this study primarily relate to stream acidity rather than forest cover, and catchments afforested with conifers were considered potentially most vulnerable to change. However, the effects of conifers are not only related to acidification, and additional issues with excessive shading, and reduced quality and input of allochthonous resources (Thomas et al. 2015). This is important for land managers whose primary aim is temperature buffering or carbon sequestration since afforestation with non-native woodland could consequently make communities less stable. Although statistically significant differences were not seen between semi-natural broadleaf woodland and circumneutral moorland sites in this analysis, broadleaf woodland communities remained the most functionally persistent over time. This is also an important finding for managers aiming to maintain ecosystem functions, while broadleaves also offer a 'low regrets' option for climate adaptation (Prober et al. 2019). However, given that measures pertaining to the volatility of communities and their speed of recovery were uncorrelated, and stream type appeared not to influence the latter, management strategies aiming to enhance ecological recovery require further research.

4.6 Conclusion

In summary, this study underscores the importance of considering multiple dimensions of ecological stability and their interconnections to comprehensively assess the stability of ecosystems. Specifically, this includes measures that can quantify the volatility of communities (temporal invariability, persistence, or resistance), in addition to the resilience (rate of recovery) across taxonomic and functional indices. Both land use and climate were found to have important implications for stability, both in terms of the relative differences in stability properties, and the overall dimensionality of stability. While there were indications that broadleaf woodlands might enhance some aspects of stability, further research is required to confirm these results and understand finer scale relationships, and within-stream mechanisms involved (see Chapter 5). Overall, observed declines in taxonomic persistence and sensitivities to extreme, and potentially unexpected disturbance events, highlight the vulnerability of invertebrate communities to changing pressures and the urgent need for management.

Chapter 5: Population stability and asynchrony as mechanisms for community stability

5.1 Summary

The climate and ecological crises pose major threats to the stability of ecosystems worldwide. Although management efforts could enhance stability, little is known about the potential mechanisms involved at local scales, particularly for freshwaters.

In this study, stability was analysed at population-level, which comprised measures of resistance, engineering resilience, persistence, and invariability. Stability was calculated in 16 headwater streams of contrasting land use and chemistry (stream type) using 40 years of macroinvertebrate data. The aims were to determine the intrinsic (species-specific) and external (stream type) factors that influence the stability of populations, and how their dynamics underpin stability at community-level.

Population stability comprised two primary dimensions in these streams, the first relating to the volatility of population abundances (resistance, persistence, and invariability), and the second relating to their speed of recovery (resilience). Both the identity of taxa (characterised by their rarity and functional feeding guild, FFG), and their environment (stream type) were significantly associated with population volatility. Specifically, volatility increased near-linearly with greater rarity (low abundance, low geographic occupancy, and narrow niche), while broadleaf populations were less volatile on average, particularly compared to acid streams, and among populations of grazing and filtering taxa. Broadleaf populations were also significantly more resilient than all other stream types. Richness, population-, and community-level stability were all positively correlated, and results indicated that the combined influence of low stability and high population synchrony in these streams could be exacerbatory, particularly among populations of common taxa, those with fewer resistance and resilience traits, shredders, and their resilience.

These results highlight complex links across biological scales and components of stability, and emphasise importance of population dynamics for stability at community-level. In summary, evidence suggests that management approaches aimed at protecting the diversity of taxa and their resources may prove the most effective for enhancing overall ecological stability.

5.2 Introduction

Rivers support high biodiversity. While having intrinsic importance, riverine species are crucially responsible for ecological functions including the processing, transport and storage of carbon and other macro-nutrients (Vannote et al. 1980; Wallace and Webster 1996; Balian et al. 2008). Yet, these ecosystems are also among the most heavily impacted by human activity (Ormerod et al. 2010; Reid et al. 2018; WWF 2020), and severely threatened by climate change (Woodward et al. 2010; Reid et al. 2018). As human activities continue to degrade biodiversity worldwide, the protection of ecological stability in the face of extreme events such as floods, droughts, heatwaves, disease outbreaks, or other pulse events, has become central to global environmental policy and conservation (IPCC 2022). Stability in this context is defined multidimensionally, whereby several properties are used to describe the temporal dynamics of a system or variable in response to disturbances (Donohue et al. 2013). This multidimensional concept encompasses components such as resistance, engineering resilience, persistence, and temporal variability, which contribute to the survival of species and to the overall maintenance of community structure and function (Pimm 1984; Donohue et al. 2013). Successful efforts to maintain or enhance stability therefore require a clear understanding of the factors that influencing multiple dimensions of stability across biological scales.

Several factors have been linked to ecological stability that can interact over different spatial scales (Gunderson and Holling 2002; Allen et al. 2014; Wilcox et al. 2017). These include intrinsic factors related to individual species, communities, and metacommunities in addition to external factors related to the local habitat or larger-scale environmental conditions, e.g., the climate. Because taxonomic diversity has long been hypothesised to confer stability of ecological communities (McCann 2000), calls for natural solutions that preserve and restore biodiversity, specifically for enhancing stability, have grown (Boyer et al. 2009; Díaz et al. 2019; IPBES 2019). Yet, observed diversity-stability relationships (i.e., the positive correlation often seen between biodiversity and some aspects of stability) are inconsistent between ecosystems, at different levels of biological organisation (e.g., population versus community), and in studies comprising different timeframes (McCann 2000; Ives and Carpenter 2007). Such inconsistencies reduce the predictability of ecosystems, and therefore reduce confidence in proposed management interventions.

Differences may, in part, be due to the numerous ways in which stability is defined and measured (Ives and Carpenter 2007), but may also reflect factors operating upon individual populations. Instability of populations induced by temperature fluctuations, for example, can promote extinction risk (Duffy et al. 2022), while population dynamics can underpin stability at higher levels of biological organisation through a number of mechanisms, including trophic cascades, or the combined temporal fluctuations of their abundances (Downing et al. 2014; Wilcox et al. 2017). Thus, population-level analyses, and assessments linking population- and community-level stability are important components in advancing our understanding of ecological stability as a whole.

A range of species' characteristics may correlate with stability at the population level, including features of distribution (e.g., rarity) and ecological traits. Rare species play crucial roles within ecosystems, supporting unique and vulnerable functions (Mouillot et al. 2013; Leitão et al. 2016; Chapman et al. 2018; Basile 2022), while contributing significantly to the biodiversity of rivers (Clarke et al. 2008). In marine systems, their loss has been shown to propagate through trophic networks and destabilise the populations of other groups such as predators (Bracken and Low 2012), highlighting their potential importance for community stability.

Mounting evidence also suggests that rare taxa could face disproportionate impacts from climate change (Murphy and Romanuk 2014; Hilpold et al. 2018; Clavel et al. 2011; Domisch et al. 2011; Domisch et al. 2013; Bowler et al. 2017). Their vulnerability has been linked to reduced redundancy at low population densities, fewer conspecific interactions, and lower fitness and reproductive success (the Allee effect; Dennis 2002). Given that many rare species are also habitat specialists, climate-induced changes to disturbance regimes could undermine the stability of rare populations (Hering et al. 2009). This is a particular concern for headwater stream communities, where taxa are restricted by a 'summit trap' that precludes migration to higher, cooler altitudes (Durance and Ormerod 2007; Durance and Ormerod 2010; Bálint et al. 2011; Domisch et al. 2013).

Individual ecological traits might also account for stability at the population-level. For example, taxa with effective aerial dispersal may be better equipped to persist by recolonising quickly following pulse disturbances (Reinhardt et al. 2005; Wang and Loreau 2014; Chester et al. 2015; Dolédec et al. 2017), thereby offsetting other vulnerabilities such as rarity (Hsieh et al. 2022). Amongst stream macroinvertebrates, small body size, short lifecycles, and multivoltinism are among a range of traits linked to resistance or resilience to disturbance (Ilg and Castella 2006; Lange et al. 2014; Bogan et al. 2015; Dolédec et al. 2017; Aspin et al. 2018). In turn, a high prevalence of these traits correlates with some aspects of community-level stability, such as persistence (Poff et al. 2018).

The environment, including pulse and press disturbances, is an overarching factor influencing stability at both population and community levels. The disturbance regime, and physicochemical habitat conditions, are well-known drivers of community dynamics in river ecosystems (Brown et al. 2006). The strong connections of streams and rivers to the terrestrial landscape and riparian zone (Likens and Bormann 1974; Vannote et al. 1980), mean that land use substantially influences environmental conditions, resource dynamics, and the subsequent structure and function of communities, while also providing hydrological and thermal regulation and climate-buffering in instances where woodland is present (Weatherley and Ormerod 1990; Davies-Colley et al. 2000; Hannah et al. 2008; Broadmeadow et al. 2011). Riparian broadleaf woodlands, for example, have been increasingly promoted for their potential to enhance facets of stability of rivers such as resistance (the ability to withstand disturbance) and resilience (the ability to rapidly recover) (Broadmeadow and Nisbet 2004; Broadmeadow et al. 2011; Thomas et al. 2016; Van Looy et al. 2019; Pye et al. 2022; see Chapter 2). Conversely, populations in river systems draining other land uses might become destabilised where thermal, hydrological or chemical extremes are accentuated, such as in open or agricultural catchments (Hannah et al. 2008; Brown et al. 2010). These influences might therefore suggest ways in which land can be managed to increase the stability of river ecosystems, but this requires a sound understanding of the underlying mechanisms involved.

Community synchrony has been increasingly recognised as a potential mechanism linking population- and community-level stability. Synchrony describes the degree to which the abundances or dynamics of populations across different locations or species fluctuate in a synchronous manner over time (de Loreau and Mazencourt 2008). A primary concern regarding climate change is that the increasing frequency and/or magnitude of pulse disturbances may act to destabilise and synchronise populations simultaneously within and across communities (i.e., the metacommunity), leading to magnified fluctuations at community-level (Larsen et al. 2021). At local scale, land use and habitat conditions have been implicated in community synchrony, which could either further contribute to synchrony through processes such as biotic homogenisation (Blüthgen et al 2016; Wang et al. 2021), or promote asynchrony, which may arise with increased diversity of species and their responses to environmental change (Sasaki et al. 2019). In the latter instance, this could act to promote community stability and buffer against climatic disturbances even where population stability is low (Tilman 1996; Loreau and de Mazancourt 2013; Downing et al. 2014; Wilcox et al. 2017; Huttunen et al. 2018). However, the role of asynchrony, and its relationship with population and community stability in streams is poorly understood.

There are several major challenges to progressing understanding of ecological stability in rivers, of which three are worth highlighting. The first is that few empirical studies simultaneously assess multiple aspects of ecological stability, mostly being restricted to single components such as temporal variability (Donohue et al. 2016). Secondly, natural systems are highly variable, highlighting a need for long-term monitoring data to draw clear conclusions regarding stability. However, few freshwater studies comprise the multidecadal timeframes necessary to effectively characterise stability for many taxa, while long-term studies that do exist typically focus on temporal biodiversity trends rather than stability, or are confounded by multiple stressors from agriculture and urbanisation (Outhwaite et al. 2020). Finally, given that the environment is a key driver of community, function, and temporal dynamics, using observational data to separate the roles of intrinsic biological mechanisms from the abiotic environment upon community- and population-level stability is extremely difficult, and requires careful interpretation and methods that control for this where practically possible.

In this study, stability was examined at population- and community-levels over the 40-year dataset for each stream, using four established components; resistance, persistence, temporal variability, and engineering resilience (Pimm 1984; Donohue et al. 2013). The first part of this study assessed how species-specific characteristics – rarity, resistance/resilience (RR) traits, and functional feeding guild – and stream type influenced the stability of individual populations. Rarity can be defined in multiple ways (Rabinowitz 1981), and here, data on population abundance, occupancy, and habitat breadth were combined to provide an aggregate rarity index. The second part of the study aimed to identify the roles of diversity, asynchronous dynamics, and population-level stability in determining community-level stability. It was hypothesised that:

1. Rarer taxa, those with fewer RR traits, and those at higher trophic levels (predators) – all considered indicators of species vulnerability – would have lower population-level stability across the four stability measures.
2. In streams least modified by land use and acidification (semi-natural broadleaf woodland) average population stability would be lowest. Where the same taxa occur in all stream types, their population stability would be greater in the least modified streams.
3. Increasing diversity (taxonomic richness), mean population-level stability and asynchronous dynamics would all increase community-level stability, according to the hypothesised relationships in Figure 5.1.
4. Community stability would correlate most strongly with the dynamics of vulnerable taxa (as defined in Hypothesis 1), i.e., highlighting that in streams where vulnerable taxa are least stable, community stability would be lowest.

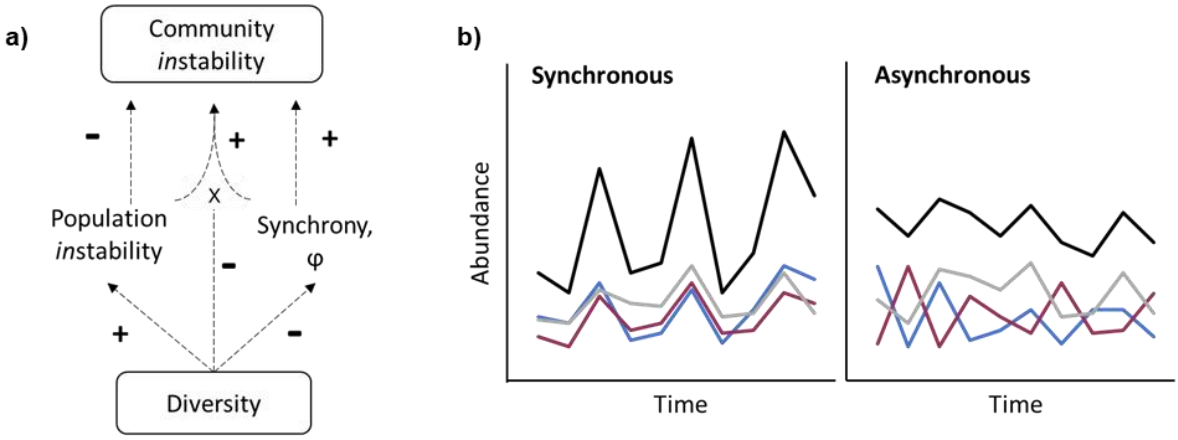


Figure 5.1 *Conceptual framework for the relationship between diversity and community stability, via population stability and local asynchrony. In **a)** dashed arrows show hypothesised relationships between components, negative (-) or positive (+). Figure adapted from Wang et al (2019) and Wang and Loreau (2014) where stability was defined as invariability (1/CV), and community CV = population CV x synchrony. In **b)** black lines show dynamics of aggregate community abundances either where population abundances (coloured lines) are changing synchronously or asynchronously over time.*

5.3 Methods

5.3.1 *Study sites and macroinvertebrate data*

Study sites comprised 16 perennial headwater streams in the uplands of Wales, UK. Streams were characterised by contrasting catchment land use and chemistry (stream type): semi-natural broadleaf woodland (BW: GI1 and GI2), coniferous woodland (AC: LI1 to LI4 and LI8), circumneutral moorland (CM: LI6 and LI7), and acid moorland (AM: CI1 to CI6 and LI5). Macroinvertebrates were kick-sampled each spring between 1981 to 2020, though some discrepancies in sample history were present across streams and stream types. A detailed description of sites and sampling methods can be found in Chapter 1, Section 1.3. For each sample, macroinvertebrates were pooled to genus-level or higher to match with trait data.

Traits relating to habitat preferences (Grinnellian niche), and biology and life-history adaptations (Eltonian niche), were used as the basis for calculating species-specific characteristics in this study (Mondy and Usseglio-Polatera 2014). These were selected from a published database of traits for European freshwater taxa (Tachet et al. 2010), and supplemented with regional data from South Wales (Durance & Ormerod *unpublished*). A fuzzy-coding approach was applied, as detailed in Chapter 3, Section 3.3.2.

Additionally, taxa were grouped into four primary functional feeding guilds (FFG; predators, shredders, grazers, filterers) according to the dominant affinity scores within this grouping feature. A set of resistance/resilience traits (RR) were also selected based on *a priori* hypotheses of their association with population stability. In this instance, small body size, short lifecycles, multivoltinism, specialised resistance forms, dispersal strategies, and respiration technique, particular locomotive strategies such as burrowing, and asexual reproduction were among the traits selected for use, since these were all considered to enhance the ability to withstand or avoid disturbances (Ilg and Castella 2006; Lange et al. 2014; Bogan et al. 2015; Dolédec et al. 2017; Aspin et al. 2018) (Table 5.1). In turn, a high prevalence of these traits among taxa is thought to correlate with some aspects of community-level stability (Poff et al. 2018). For each taxon, an RR score was assigned based on the number of RR traits where affinity was > 0, therefore indicating the total number of traits or strategies that could potentially be employed for stability.

Table 5.1 *List of biological/functional (Eltonian niche) traits. Traits were used in this study for calculation of trait specialisation, and resistance/resilience (RR). Note 'food preference' was included as a biological and an ecological trait grouping feature.*

	Grouping feature	*Trait*		Grouping feature	*Trait*
	Maximum potential size (cm)			Life cycle duration	
RR		*≤ 0.25*	*RR*		*≤ 1 year*
RR		*> 0.25-0.5*			*> 1 year*
		> 0.5-1		Respiration method	
		> 1-2			*tegument*
		> 2-4			*gill*
		> 4-8			*plastron*
		> 8	*RR*		*spiracle*
	Potential number of cycles per year (voltinism)				*hydrostatic vesicle*
		< 1		Locomotion and substrate relation	
		1	*RR*		*flier*
RR		*> 1*			*surface swimmer*
	Aquatic stages				*full water swimmer*
		Egg			*crawler*
		Larva	*RR*		*burrower*
		Nymph			*interstitial*
		Adult			*temporarily attached*
	Reproduction strategy		*RR*		*permanently attached*
		Ovoviviparity		Food preference	
		isolated eggs, free			*microorganisms*
		isolated eggs, cemented			*detritus < 1mm*
		clutches, cemented or fixed			*dead plant >= 1mm*
		clutches, free			*living microphytes*
		clutches, in vegetation			*living macrophytes*
RR		*clutches, terrestrial*			*dead animal >= 1mm*
RR		*asexual reproduction*			*living macroinvertebrates*
	Dispersal strategy				*living macroinvertebrates*
		aquatic passive			*vertebrates*
		aquatic active		Feeding habits / guild	
		aerial passive			*deposit feeder/ detritivore*
RR		*aerial active*			*shredder*
	Resistance forms				*scraper/ grazer*
RR		*eggs, statoblasts*			*filter-feeder, active*
RR		*cocoons*			*filter-feeder, passive*
RR		*housings against desiccation*			*piercer*
RR		*diapause or dormancy*			*predator*
		None			

Table 5.2 *List of ecological (Grinnellian niche) traits. Traits were used in this study for calculation of niche breadth and habitat specialisation.*

Grouping feature | *Trait*

- Food preference
  - *Microorganisms*
  - *detritus < 1mm*
  - *dead plant >= 1mm*
  - *living microphytes*
  - *living macrophytes*
  - *dead animal >= 1mm*
  - *living macroinvertebrates*
  - *living macroinvertebrates*
  - *Vertebrates*
- Transversal distribution
  - *river channel*
  - *banks, connected side-arms*
  - *ponds, pools, disconnected side-arms*
  - *marshes, peat bogs*
  - *temporary waters*
  - *Lakes*
  - *Groundwaters*
- Longitudinal distribution
  - *Crenon*
  - *Epirithron*
  - *Metarithron*
  - *Hyporithron*
  - *Epipotamon*
  - *Metapotamon*
  - *Estuary*
  - *outside river system*
- Altitude
  - *Lowlands*
  - *piedmont level*
  - *alpine level*
- Current velocity preference
  - *Slow*
  - *Medium*
  - *Fast*

Grouping feature | *Trait*

- Trophic status preference
  - *oligotrophic*
  - *mesotrophic*
  - *eutrophic*
- Substrate preference
  - *flags/boulders/cobbles/pebbles*
  - *gravel*
  - *sand*
  - *silt*
  - *macrophytes*
  - *microphytes*
  - *twigs/roots*
  - *organic detritus/litter*
  - *mud*
  - *null*
- Salinity
  - *fresh water*
  - *brackish water*
- Saprobity
  - *xenosaprobic*
  - *oligosaprobic*
  - *b-mesosaprobic*
  - *a-mesosaprobic*
  - *polysaprobic*
- Temperature
  - *psychrophilic (low temp)*
  - *thermophilic (high temp)*
  - *eurythermic (large range)*
- pH preference
  - *≤ 4*
  - *> 4-4.5*
  - *> 4.5-5*
  - *> 5-5.5*
  - *> 5.5-6*
  - *> 6*

5.3.2 *Rarity*

Species' rarity was defined according to Rabinowitz's (1981) three criteria: local abundance, geographical range, and habitat breadth. Local abundance was calculated for each taxon in each stream as its mean abundance across the complete study period. Geographical range was inferred from occupancy data obtained from Outhwaite *et al*. (2019), covering Great Britain. Annual occupancy estimates were available for 1970–2015 for most insect and mollusc groups, but excluded worms, flatworms, aquatic beetles, mites, and crustaceans. Additionally, to achieve comparable taxonomic resolution (genus level), occupancy data were averaged across taxa where multiple species were present. This was not possible for large and widespread family groups such Dipterans, and so occupancy data for these were omitted. Overall, this meant that occupancy data were available for two thirds of taxa in the Llyn Brianne dataset, for which a mean average occupancy (1970–2015) was calculated per taxon.

Habitat breadth, or niche breadth, can be defined in many ways, but generally refers to the range or diversity of environments and resources used or tolerated by species or communities (Carscadden et al. 2020). In this study, habitat breadth was calculated using two methods based on habitat preference data or Grinnellian niche traits (Table 5.2) (Grinnell 1917; Mondy and Usseglio-Polatera 2014). The first method assumed that common taxa are generalists that tolerate a wide range of environments and can co-occur with a range of other species, whilst rare species are specialists restricted in their preferred environment and number of species with which they co-occur (Ducatez et al. 2014). Not only does this account for habitat specialism based on Grinnellian niche breadth (Grinnell 1917), but also begins to indirectly incorporate biotic interactions that define the Eltonian niche (Elton 1927; Devictor et al. 2010). Species that are unable to interact with a wide range of others could face increased risk of replacement by generalists following pulse disturbances and temporary habitat degradation (Olden et al. 2004; Devictor et al. 2008), reflecting a pattern commonly observed in biotic homogenisation and loss of rare species (Rahel 2002).

For this method, trait data were simplified to presence-absence of individual traits (i.e., affinity scores >0 = 1, and 0 = 0 for each category in Table 5.2), and the habitat breadth for each taxon (β_i) was then calculated as:

$$\beta_i = \gamma/\mu(\alpha)$$

where γ was the number of taxa sharing one or more habitat types/preference traits (Table 5.2) with the focal taxon, i, and $\mu(\alpha)$ was the mean number of species in each habitat type used by the taxon (Ducatez et al. 2014). This provided a quantitative measure of habitat breadth for each taxon relative to other taxa in the streams. Higher values represented greater habitat breadth or generalism.

The second method of calculating habitat breadth used measures of ecological specialisation based on the original habitat affinity score data, as per Mondy and Usseglio-Polatera (2014). This used a Simpson's diversity index where, for each taxon and grouping feature, trait specialisation (TS) was defined as:

$$TS_{ti} = \Sigma^{k} c_{tik}{}^{2}$$

where c_{tik} was the relative use (affinity score) of each trait, t, within a grouping feature, k, by each taxon, i. Higher values reflected greater specialisation within trait groups, for example, a strong preference towards fast flowing water, whereas low values reflected greater trait diversity for a taxon, i.e., generalism. To account for differences in the number of traits within each grouping feature, TS values were normalised and then the mean TS was calculated for each taxon (Mondy and Usseglio-Polatera 2014; Larsen et al. 2018).

TS values were calculated based on both Grinnellian and Eltonian niche traits separately (Table 5.1 and 5.2), thus providing measures of habitat specialisation (TS_H) and biological or functional specialisation (TS_L) (Larsen et al. 2018) that could be compared against β (considered to incorporate aspects of both). TS_H and TH_L were weakly correlated with one another (Pearson's $r = 0.48$), while both correlated more strongly with β ($r = -0.90$ and -0.52, respectively). Habitat breadth based on species co-occurrence, β, was therefore considered an appropriate and more representative measure, effectively capturing aspects of specialisation in both Grinnellian and Eltonian niches, in addition to species co-occurrence.

Although studies suggest aspects of rarity can be correlated (Slatyer et al. 2013; Olsen et al. 2022), there was no strong evidence here to corroborate this (Pearson's $r < 0.3$). Therefore, rather than a dimensionality reduction method (e.g., principal component analysis), a classification-based approach was considered more appropriate for summarising rarity (Rabinowitz 1981; Yu and Dobson 2000). Each of the three rarity variables was dichotomised into above- and below-median values, allowing each taxon in each stream to be classified from 1 (most rare) to 4 (most common) according to the scheme in Table 5.3. For taxa with missing occupancy data, an average of the other two rarity scores was calculated and added to the total, giving increments of 0.5 for some taxa. Despite some acknowledged limitation, this allowed for the remaining third of taxa to be included in the dataset. A final comparison between rarity and the other niche specialisation measures (TS and β) showed a weak to moderate relationship (r = -0.51 to -0.55).

Table 5.3 *Rarity index classification table based on geographical range, habitat breadth, and local abundance. A rarity score of 1 indicates that taxa are rare in all three forms, small range, narrow habitat tolerance or use, and low abundance, while a score of 4 indicates that a taxon is common. Table adapted from Rabinowitz (1981) and Yu and Dobson (2000).*

Geographical range		Large		Small	
Habitat breadth		Broad	Narrow	Broad	Narrow
Local abundance	High	4	3	3	2
	Low	3	2	2	1

5.3.3 *Population stability*

For each taxon in each stream, four commonly assessed measures of population stability were calculated (Donohue et al. 2016): variability, resistance, persistence, and engineering resilience. Calculation of all measures except persistence required populations to be present on multiple occasions. Taxa present on less than four sampling occasions were therefore removed from the dataset for each stream, thereby excluding the least prevalent and some of the rarest taxa. This meant that 59 of the original 86 taxa were included in subsequent analyses, while 73 taxa were impacted by removal from one or more streams. Given these differences in the prevalence and composition of taxa across streams, a subset of ubiquitous taxa was derived from the dataset, i.e., that were present in all streams excluding higher taxonomic groupings such as those at family level due to potential compositional differences. This dataset comprised seven taxa: *Amphinemura* (shredder), *Isoperla* (predator), *Leuctra* (shredder), *Nemoura* (shredder), *Plectrocnemia* (predator), *Protonemura* (shredder), and *Siphonoperla* (shredder). All of these were considered ‘common’ taxa with low RR.

For each taxon and stream, persistence was calculated as the sampling occasions that a taxon was present as a proportion of the samples for each stream (Soininen and Heino 2005), ranging from 0 (not persistent) to 1 (persistent). To calculate variability in abundance, the coefficient of variation was used: $CV = \sigma/\mu$, where σ was the standard deviation, and μ the mean abundance in each stream. CV was also calculated after detrending data using a linear model over time, to remove any influence of a trend (Tilman et al. 2006). However, for all but some of the least persistent populations, this made little difference to CV values and CV based on raw, rather than detrended data were used. Resistance was calculated as the absolute inter-annual change in abundance, divided by μ, giving a continuous scale from zero (maximum resistance). Values from consecutive zero-abundance years were excluded before calculating an overall mean resistance per taxon per stream.

Lastly, engineering resilience, λ, was calculated using autoregressive moving average (ARMA) models as per Ives *et al*. (2010). For each taxon in each stream, linear mixed-effect models were fitted using the *lme4* package in R (version 1.1.31) (Bates et al. 2015). As the dependent variable in each model, abundance data were log(x + 1)-transformed and first detrended using linear models to ensure a stationary timeseries for each population and stream. To determine the AR (p) and MA (q) components of the model, five models were fitted with varying combinations of p = 1-2 and q = 0-2. The final model was selected based on the lowest Akaike's Information Criterion for small sample sizes (AICc). In most instances, this was the simplest model, p = 1, q = 0. Resilience, as characteristic return time $||\lambda||$, was defined as the dominant eigenvalue of the covariance matrix containing the estimated MA and/or AR coefficients. Values ranged from 0 (high resilience) to 1 (no resilience, i.e., random walk behaviour and no return to equilibrium).

Principal component analysis (PCA) was used to the assess relationships between the four stability measures and as a dimensionality reduction step. Two main components, PC1, which described changes in persistence, resistance, and invariability, and PC2, which described changes in engineering resilience, were retained for further analysis. Together, these components explained 87% of the variation in population stability, each with eigenvalues > 1. Higher principal component (PC) scores reflected greater stability.

5.3.4 *Community stability and asynchrony*

Most studies assessing the relationships between diversity, population stability, synchrony, and community stability focus on temporal variability in biomass or abundance (Wang et al. 2019). Here, this was extended to include engineering resilience – the second, distinct dimension identified at both population- (Section 5.3.3) and community-levels (see Chapter 4). Given that at both population- and community-level, measures of persistence and resistance were correlated with temporal variability, it was not considered necessary to include these. To address Hypotheses 3 and 4, community stability was assessed as temporal variability (coefficient of variation in total abundance, CV), and community resilience (characteristic return time, $||\lambda||$, in total abundance, hereafter λ, calculated using the same ARMA model approach as for individual populations; Section 5.3.3) over the timeseries for each stream. To determine whether population stability and asynchrony were related to community stability, single values for each were calculated for each stream. Firstly, the weighted mean population stability, V_P, was calculated as:

$$V_P = \sum_i V_i \times \mu_i/\mu_\Sigma$$

where V_i was the stability (CV and λ, separately with increasing values corresponding to less stable populations) of each taxon, i, and μ_i/μ_Σ was the mean relative abundance of each taxon in each community, as per Wang et al (2019). Secondly, synchrony, φ, was calculated as per Loreau and de Mazencourt (2008):

$$\varphi = \frac{\sigma_{x_T}^2}{(\Sigma_i \sigma_{x_i})^2}$$

where $\sigma_{x_T}^2$ was the temporal variance of the community-level variable (in this case, total abundance), and σ_{x_i} was the temporal variance of each population abundance within the community. This provided a measure between 0 (perfect asynchrony) and 1 (perfect synchrony).

In addition to population stability and community synchrony for the whole community, values were calculated for: *i*) rare taxa versus common taxa (below-median or less than or equal to two forms of rarity, and > 2 forms of rarity, respectively), *ii*) high versus low RR taxa (above- and below-median RR, respectively), and *iii*) each FFG (shredder, grazer, predator, filterer).

5.3.5 *Statistical analyses*

Statistical analysis comprised three stages. The first aimed to evaluate relationships between species-specific characteristics and stream type against population-level stability metrics of all taxa, addressing Hypotheses 1 and 2. One of the limitations of using natural community data, however, is that each stream supports a compositionally different community, making untangling the effects of species traits and stream effects challenging. A second analysis was therefore conducted using the subset of ubiquitous taxa present in all streams to test whether the stability of the same taxa differed between stream types, described in Section 5.3.3. Lastly, analyses were conducted to assess the linkages between diversity and community stability, via population stability and synchrony (Hypotheses 3 and 4).

In the first stage, linear mixed-effect models were used to test the effects of species-specific characteristics and stream type on population-level stability (PC1 and PC2), constructed using the R package *lme4,* (version 1.1.31) (Bates et al. 2015). Models included random effects to control for taxon and stream identity. Values of PC2 were $\log_{10}$(max(x+1)-x)-transformed to meet the assumptions of a Gaussian distribution. For both stability variables for all taxa, i, and streams, x, a global model was constructed, allowing for potential interactions between variables:

V_{x_i} ~ rarity*stream type + RR*stream type + FFG*stream type + rarity*RR + FFG*RR

The significance of each interaction was assessed through a process of stepwise deletion, from the least to most significant term. In each step, the simplified model was compared to the previous using likelihood ration tests (LRT), and interactions were excluded where not statistically significant ($p > 0.05$) to simplify the interpretation of main effects. Results were obtained from models fitted with restricted maximum likelihood (REML). Significant effects were further investigated through *post-hoc* Tukey tests of pairwise comparisons between groups, using the R package *emmeans,* (version 1.8.4.1) (Lenth et al. 2023).

Secondly, for the cross-stream comparisons of stability using ubiquitous taxa, linear regression was used to test the significance of taxon identity, stream type, and the interaction between these for each aspect of population stability. The relative importance of taxon versus stream type was determined by calculating the ΔR^2 between models with and without each term.

Finally, to test relationships between diversity, population stability, synchrony, and community stability (Figure 5.1), Pearson's correlation coefficients were used. Diversity was defined as the mean taxonomic richness across years for each stream (Thibaut et al. 2013; Wang et al. 2019). For each stability variable, 5 pairwise correlations were assessed, in addition to the correlation between diversity and synchrony, corresponding to the dashed lines in Figure 5.1. Pairwise assessments were made ensuring that increasing values corresponded to decreasing stability and increasing synchrony.

5.4 Results

5.4.1 *Community composition*

Streams at Llyn Brianne were dominated by species categorised as common, those with few RR traits, shredders, and grazers (Table 5.4). Across stream types, BW and CM streams were the most biodiverse, with ca. 25-30 taxa per sample at genus-level or above. These stream types also had the largest community abundance on average, nearing 1000 individuals per sample. In contrast, acid streams had < 20 taxa per sample, and > 50% fewer individuals, with the lowest numbers occurring in AC streams. Acid streams had proportionally more common taxa, and those with high RR, in addition to shredders, which were dominant in AC streams (72% of individuals). Acid streams also supported proportionally more predatory taxa compared to other stream types, albeit lower absolute numbers. While being the most diverse of all stream types, the distribution of taxa among FFGs, e.g., grazers: shredders, appeared more balanced in BW communities than in other stream types, including CM streams where diversity was similar.

Table 5.4 Summary of species groups (rarity, resistance/resilience, and functional feeding guild) within each stream type, as percentages of mean community richness and abundance. ***A)*** *mean and standard error in brackets, for richness (S) and abundance (N) of macroinvertebrate taxa.* ***B)*** *percentage of taxa belonging to different groups: rare v. common taxa, high v. low prevalence of RR traits, and FFG, expressed in terms of S and N. Highlighted cells show highest values for each group across stream types for S (grey/green) and N (purple/blue).*

	BW		AC		CM		AM	
	S	N	S	N	S	N	S	N
A								
Total	28 (1)	895 (108)	14 (0.3)	384 (26)	27 (0.6)	827 (53)	18 (0.4)	421 (25)
B (%)								
Rare	24	14	8	2	22	18	10	2
Common	76	86	92	98	77	82	90	99
High RR	36	27	47	22	33	15	42	39
Low RR	64	73	53	78	67	85	57	62
Grazers	33	37	15	6	38	59	27	18
Shredders	30	35	45	72	28	27	31	45
Predators	22	15	31	11	23	10	34	20
Filterers	14	13	8	11	11	4	8	16

5.4.2 *The effects of species-specific characteristics and stream type on population stability*

Both intrinsic (species-specific characteristics) and external factors (stream type) were found to relate to population stability. The strongest evidence was for PC1 (population volatility), where the linear mixed-effect models revealed statistically significant effects of stream type, rarity, and the interaction between stream type and FFG (Table 5.5). For PC2 (population resilience), only stream type was significantly related, after controlling for other variables. These models explained 40 and 8% of the variation in PC1 and PC2, respectively, further highlighting a larger amount of unexplained variation in population resilience.

Across steam types, BW were the most stable for both PC1 and PC2 (Figure 5.2) i.e., they varied less year-to-year (lower volatility) and recovered more rapidly from perturbations (greater resilience). Pairwise differences in PC1 were statistically significant between populations in BW and AC streams (t = 4.1, p = 0.005), and between BW and AM (t = 4.35, p = 0.004). Although all stream types had low characteristic return times ($\lambda < 0.4$), PC2 was significantly lower in BW ($\lambda = 0.21$) compared to other stream types (AC: $t = 3.99$, $p = 0.008$; CM: $t = 3.89$, $p = 0.03$; AM: $t = 4.15$, $p = 0.01$). There was a strong, highly significant ($p < 0.0001$) relationship between rarity and PC1, with a near-linear relationship over a gradient of rare to common taxa (Figure 5.2b). The rarest populations (group 1), reflecting low local abundance, narrow habitat breadth, and small geographical range, were significantly more volatile than all others, except for the next rarest group, 1.5, which was likely to include some overlap where occupancy data were unavailable. There was a significant interaction between FFG and stream type in the PC1 model ($F = 2.8$, $p = 0.004$). Within FFGs, BW filterers were the least volatile compared to other stream types (Figure 5.2c), particularly acid streams (BW-AM $t = 3.3$, $p = 0.006$; BW-AC $t = -2.8$, $p = 0.03$). Similarly, for communities in BW and CM, grazers were significantly less volatile than in acid streams (BW-AC $t = 4.0$, $p = 0.0008$, BW-AM $t = 4.0$, $p = 0.002$, CM-AC $t = 3.4$, $p = 0.008$, CM-AM $t = 3.2$, $p – 0.02$). Within stream types, the only significant pairwise differences were seen between AC grazers and shredders, where populations of grazers were more volatile, on average ($t = 2.8$, $p = 0.03$).

Overall, some of the least stable taxa, both in terms of PC1 and PC2, were triclads, e.g., *Crenobia*, while highly volatile groups also included megalopteran and hemipteran taxa, i.e., water boatmen and skaters. In addition to grazers, results also showed that higher affinities towards low voltinism, flying, obligate aquatic life histories, and cemented or fixed egg clutches were the most strongly associated with greater volatility, albeit relationships were generally weak (Pearson's $r = -0.2–0.3$). Conversely, populations of Diptera, such as tipulids and chironomids, and Oligochaetes were the least volatile. Generally, those with affinities towards acidic conditions (pH < 4), burrowing behaviours, warm waters, multivoltinism, free egg clutches, and alpine habitats were least volatile (PC1; $r = 0.2\text{-}0.3$). There were no clear relationships with PC2.

Cross-stream comparisons of ubiquitous taxa

The stability of ubiquitous taxa differed significantly between stream types for both PC1 ($F_{3,84} = 7$, $p < 0.0001$) and PC2 ($F_{3,84} = 2.7$, $p = 0.049$). The effects of stream type largely reflected those found for the full analyses (Figure 5.3). Moreover, a significant interaction between stream type and taxon revealed differences between taxa in the way that stability (PC1; $F_{18,84} = 4.4$, $p < 0.0001$) varied across stream types. Specifically, the shredders

Amphinemura and *Protonemura* were least stable in AM streams, whereas *Isoperla* was least stable in AC streams (Figure 5.3c). When comparing across taxa, three phylogenetically similar shredders (*Amphinemura, Protonemura,* and *Nemoura*) were the least stable (PC1) compared to other taxa, while *Protonemura* was also the least resilient. Overall, factors relating to the identity of taxa were around twice as important as their environment (stream type), based on the strength of evidence from ΔR^2 (Table 5.6).

Table 5.5 *Results of linear mixed-effect models for the effects of stream type and taxon characteristics on population stability.*

Stability component	Model term	Sum sq.	Mean sq.	df	F	p	R^2
PC1	Stream type	20.73	6.91	3,14	7.86	*0.003*	0.40 ^{a},
	Rarity	92.42	15.40	6,179	17.51	*< 0.0001*	0.69 ^{b}
	RR	0.01	0.01	1,49	0.01	0.9	
	FFG	1.88	0.63	3,47	0.71	0.5	
	FFG : Stream type	22.06	2.45	9,416	2.79	*0.004*	
PC2	Stream type	0.57	0.19	3,461	7.20	*< 0.0001*	0.08 ^{a},
	Rarity	0.16	0.03	6,97	1.01	0.4	0.11 ^{b}
	RR	0.07	0.07	1,40	2.54	0.1	
	FFG	0.19	0.06	3,41	2.38	0.08	

^{a} Marginal, ^{b} Conditional

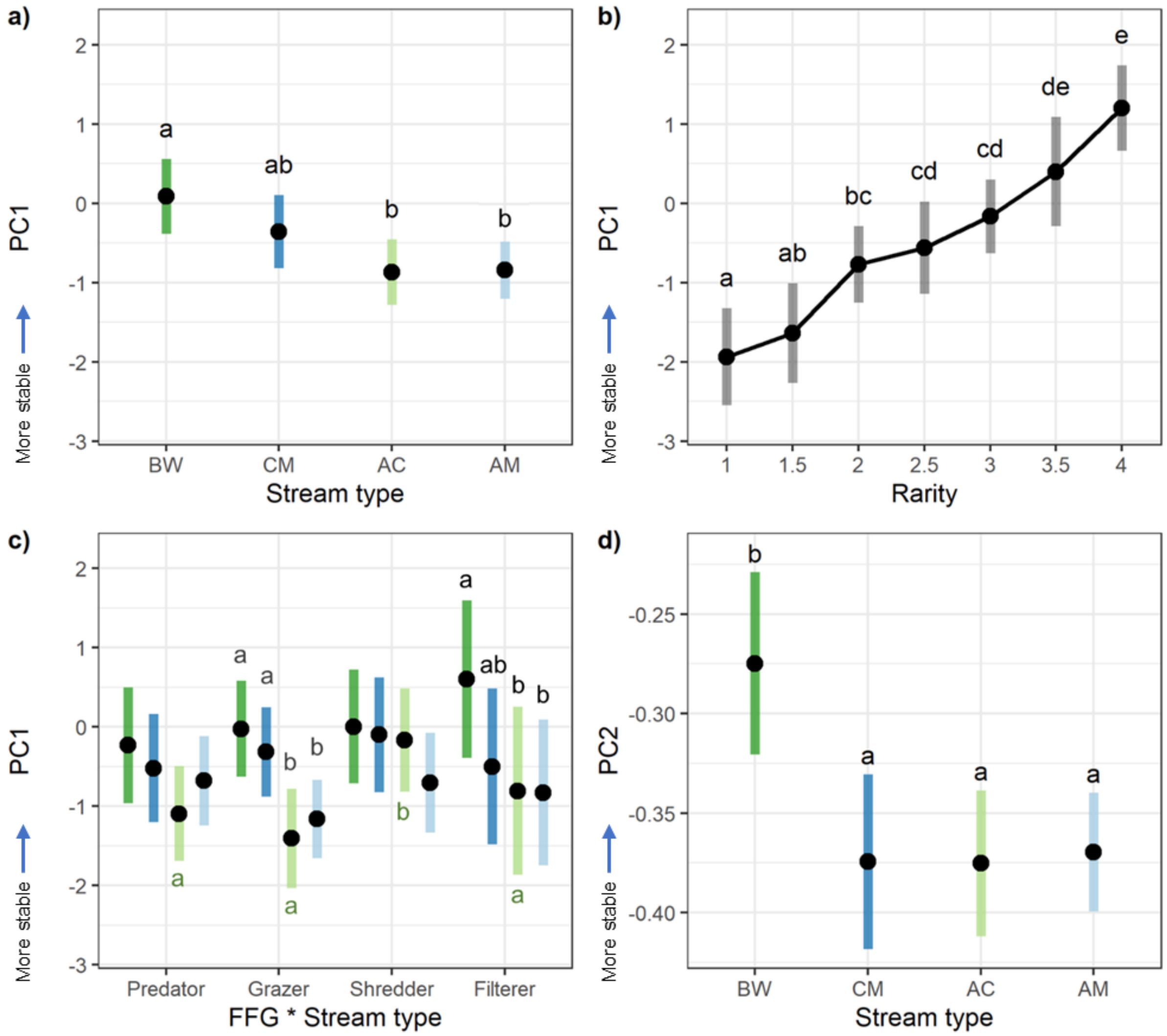


*Figure 5.2 Estimated partial effects of stream type and taxon characteristics on population stability. Plots **a**-**c)** show effects on PC1 (volatility), and plot **d)** shows effects on PC2 (resilience). Plot **b)** highlights differences in PC1 within each form of rarity (1 = rarest, 4 = most common). Results were derived from linear mixed-effect models. Groups whose letters differ are significantly different according to results from Tukey's post-hoc tests. For plot c), colours represent stream type, following the same colour scheme as panels a, b and d, and comparisons between FFGs within stream types are shown below 95% confidence limits, and between streams within FFGs are shown above.*

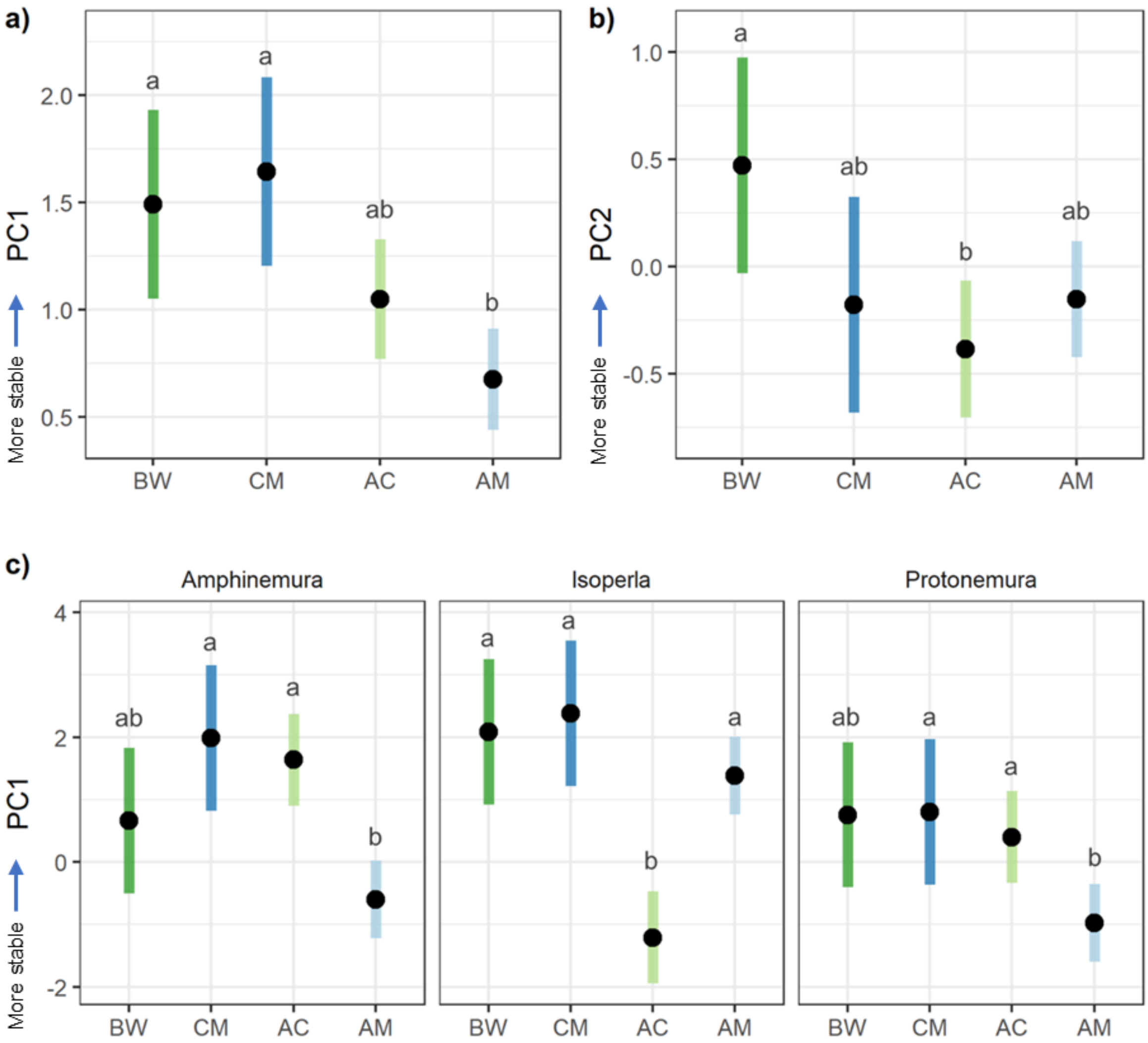


*Figure 5.3 Estimated partial effects of stream type and taxon identity on the population stability ubiquitous taxa. Plot **a)** shows significant effects and pairwise comparisons of stream type on population PC1 (volatility), **b)** PC2 (resilience), and **c)** the interaction between stream type and taxon identity on PC1. Results were derived from linear models. Groups whose letters differ are significantly different according to results from Tukey's post-hoc tests.*

Table 5.6 Significance and importance of taxon, and stream type on population stability of ubiquitous taxa. Relative importance was determined through ΔR^2 between global models and models with terms removed individually. *Note that the sum of* ΔR^2 *may not equal overall model* R^2 *due to the presence of the interaction term.*

Stability component	Model term	df	*F*	*P*	R^2-adj	ΔR^2
PC1	Taxon	6	16.9	*< 0.0001*	0.61	0.56
	Stream type	3	7.0	*< 0.0001*		0.29
	Taxon * Stream type	18	4.4	*< 0.0001*		
PC2	Taxon	6	2.6	*0.021*	0.12	0.08
	Stream type	3	2.7	*0.049*		0.04
	Taxon * Stream type	18	0.98	0.48		

5.4.3 *Effects of diversity, population stability and asynchrony on community stability*

Key components of community and population stability increased significantly with taxonomic richness (Figure 5.4a). Contrasting with the hypothesised relationships, both the mean population λ and mean population CV within each stream were positively related to respective variables at community-level ($r > 0.5$). Although synchrony was not significantly correlated with richness (Pearson's $r = -0.21$), there was evidence of a positive relationship between synchrony and community instability, particularly with regards to λ ($r = 0.56$, $p = 0.02$). Moreover, despite no clear relationship between synchrony and population instability (Figure 5.4b and c), there was evidence that their combined effects correlated more strongly with community-level instability than either variable alone.

With regards to community CV, additive effects of population CV and synchrony were apparent, resulting in the strongest correlation seen for any pairwise comparison ($r = 0.9$, $p < 0.0001$). The sum of mean weighted population CV and synchrony also correlated more strongly with richness ($r = -0.74$, $p = 0.0009$) than either variable on its own. Similarly for community λ, the effects of population λ and synchrony were also additive ($r = 0.66$), but more strongly associated with a multiplicative effect ($r = 0.72$) (Figure 5.4d and e). For example, streams with both low resilience and high synchrony, such as some acid streams, also had the lowest community resilience. Conversely, greater asynchrony in some streams, notably LI6 (CM), appeared to moderate effects of low population resilience. However, this combination of variables was not clearly associated with richness (*r* = -0.45, *p* = 0.08). Likewise, BW streams had higher synchrony on average, but with no clear consequence of this to community stability based on the current timeframe of analysis.

Further analyses to address Hypothesis 4, revealed variations in the strength of relationships between the mean weighted population stability and synchrony within different subsets of taxa, richness and community stability (Figure 5.5). Community CV was most strongly positively correlated with shredders, grazers, and common taxa CV (*r* = 0.65, 0.64, and 0.71, respectively), but also correlated with the population abundances of both high and low RR taxa (*r* = 0.51 and 0.6). Reflecting overall results, additive effects of population CV and synchrony on community CV were apparent, despite no significant relationships between synchrony and community CV. In this instance, the sum of synchrony and population CV among common, and low RR taxa (*r* = 0.89 and 0.78, respectively), i.e., the most abundant groups, correlated most strongly with CV, and a relationship with rare taxa was also revealed (*r* = 0.73). Even though populations of rare taxa were found to be more volatile, on average (Section 5.4.2), low synchrony suggests that these additive effects were mediatory, except in some woodland streams (Figure 5.6).

Shredders, common taxa, and high RR taxa were also the only groups whose weighted mean population λ was significantly correlated with community λ (*r* = 0.53-0.55) (Figure 5.5). Moreover, community λ was most strongly correlated with the multiplication of synchrony and population λ, which again revealed a previously unseen relationship with rare taxa, and low RR taxa (*r* = 0.64). Unlike for community CV, relationships between within-group synchrony and community λ were apparent for shredders (*r* = 0.51), common taxa (*r* = 0.52), and low RR taxa (*r* = 0.59). The only significant relationship between synchrony and population stability among any of the groups was for shredders, where increasing synchrony was associated with reduced resilience (*r* = 0.71, *p* = 0.0021). Moreover, shredder populations were the most synchronous of all groups (Figure 5.6).

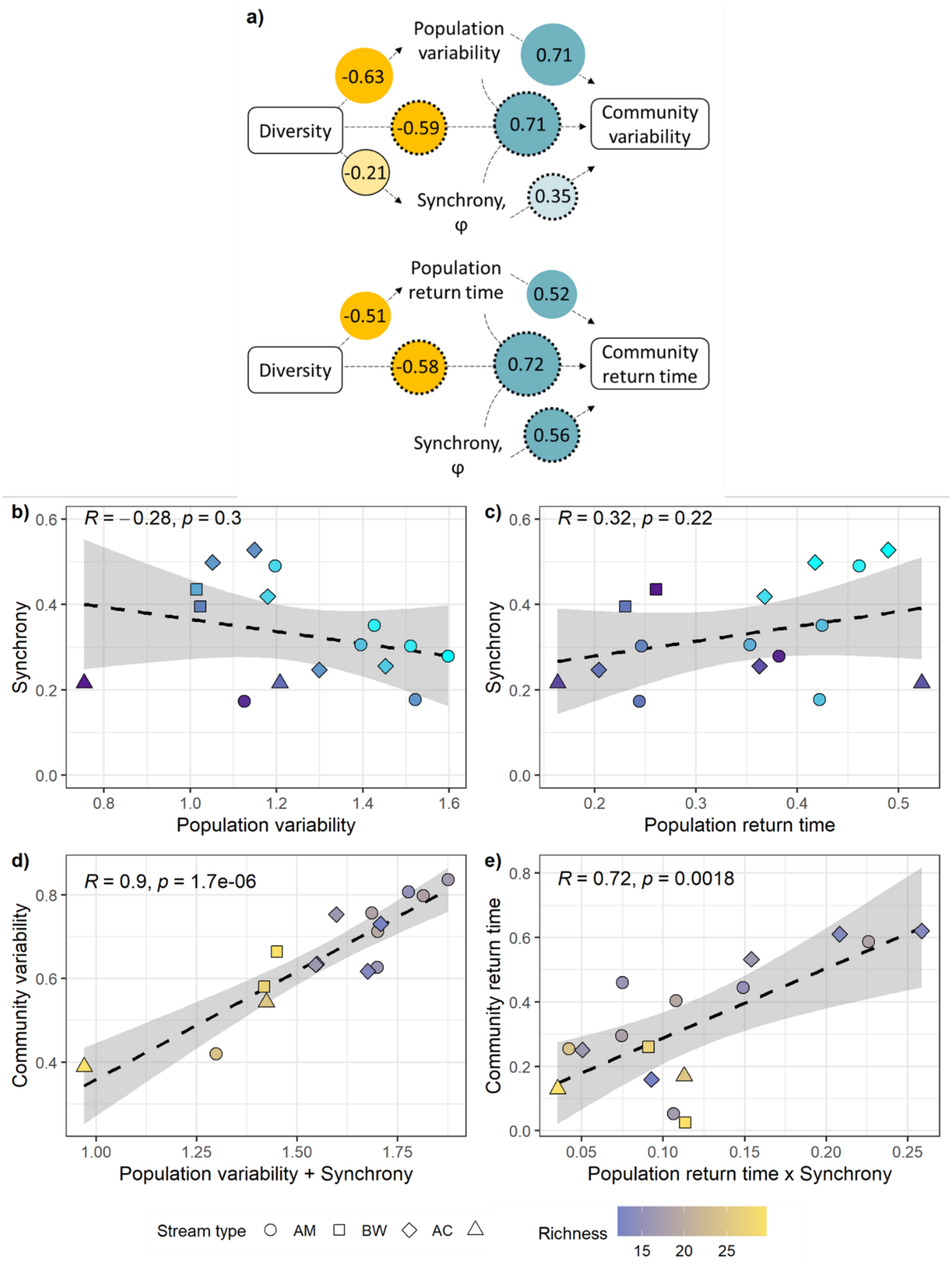


Figure 5.4 *Relationships between community richness (diversity), population stability, synchrony, and community stability. Plot* ***a)*** *shows Pearson's correlation coefficients based on hypothesised relationships in Figure 5.1. Colours highlight direction of relationship, bold colours indicate statistical significance ($p < 0.05$), and dashed circles show were results confirmed hypotheses. Plots* ***b-c)*** *show the relationship between weighted-mean population variability and synchrony, and weighted-mean population resilience and synchrony, with points coloured by respective community-level stability values, low stability = light, high stability = dark. Plot* ***d)*** *shows their additive effects on community variability, and* ***e)*** *shows their multiplicative effects on community resilience.*

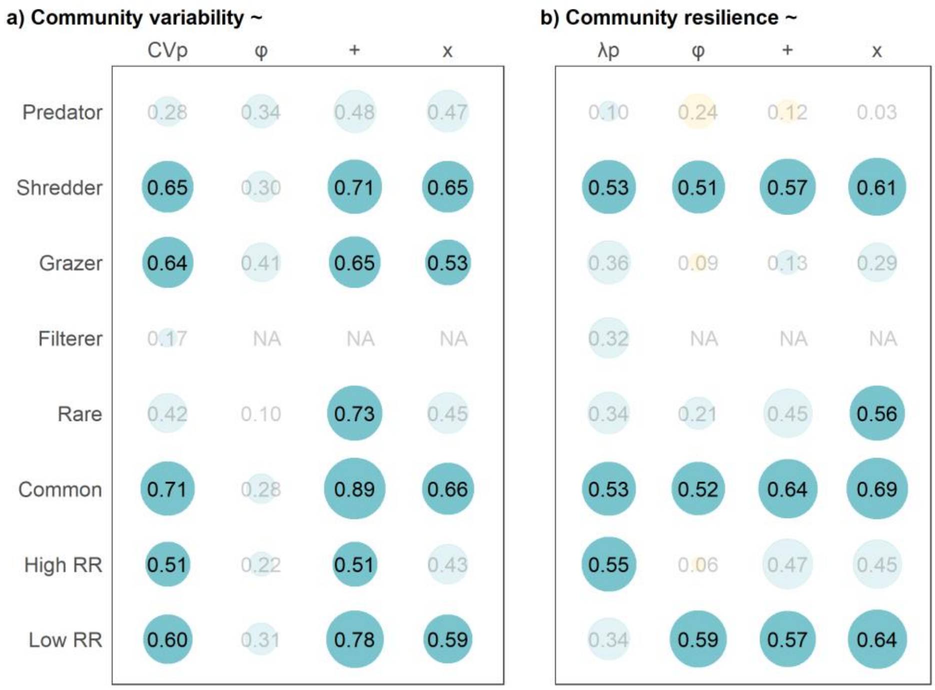


Figure 5.5 Pearson's correlation coefficients for pairwise comparisons between community stability and population dynamics of species groups (rarity, resistance/resilience, and functional feeding guild). Colour represents direction of relationship, blue = positive, yellow = negative, and bold indicates statistical significance ($p < 0.05$). Note: filterer richness was too low to calculate synchrony.

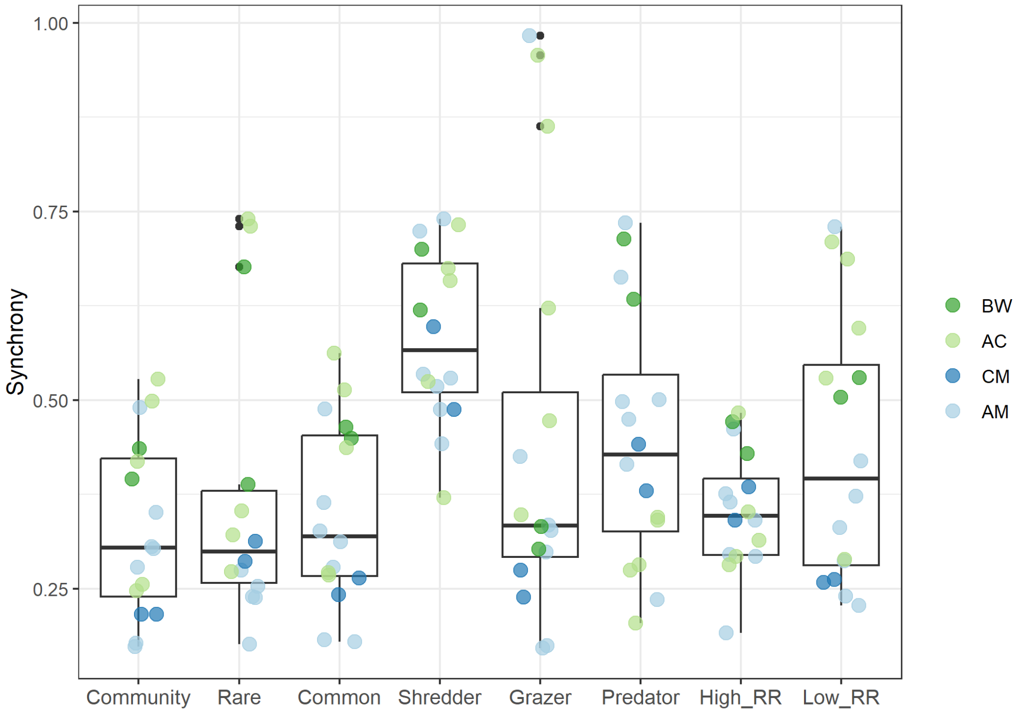


Figure 5.6 Boxplots of population synchrony within species groups (rarity, resistance/resilience, and functional feeding guild). Note: filterer richness was too low to calculate synchrony.

5.5 Discussion

The climate and ecological crises pose major threats to the stability of ecosystems worldwide. However, little is known about the mechanisms promoting multiple aspects of stability at local scales, particularly for freshwaters. To date, few datasets exist that comprise the taxonomic resolution and timescales necessary for analysing and understanding ecological stability and its underlying drivers. Such long-term datasets are required to draw patterns from the background of variability inherent to natural systems, and especially rivers. Despite limited spatial replication and some differences in the sampling history of streams, these analyses begin to disentangle the possible processes responsible for stability. This is among the first freshwater studies to apply multidecadal ecological monitoring data to assess several facets of stability simultaneously (Eagle et al. 2021; Allen et al. 2023), and to link dynamics across biological scales (Downing et al. 2014). In identifying the factors associated with population-level stability, and subsequently how the dynamics of these populations underpin stability at the level of the whole community, this study contributes to much-needed empirical evidence for the management of upland waters. Still, one of the main caveats to this study was the significantly shorter timeseries and limited sites available for broadleaf woodland streams, and these results are therefore treated with caution.

In this analysis, two main components of macroinvertebrate population stability, representing temporal fluctuations or volatility, and rate of recovery (engineering resilience), were found to be significantly related to both intrinsic (species-specific) traits such as rarity and functional feeding guild (Hypothesis 1), in addition to the local environment (stream type; Hypothesis 2). Subsequently, the combined influence of population stability and within-stream asynchrony was found to be an important determinant for stability of aggregate community abundance (Hypothesis 3). However, these relationships were not necessarily reflective of vulnerabilities observed at population-level, such as the characteristic of being rare. Rather, dominant groups, such as shredders, those categorised as ‘common’, and those with few resistance and resilience life-history traits correlated most strongly with community stability (Hypothesis 4), with evidence of potentially exacerbatory effects where synchrony and low stability occurred simultaneously. Results also suggested that the underlying mechanisms responsible for stability may differ relative to local conditions and to each component of stability.

Populations of rarer taxa, characterised by low local abundance, small geographical range, and a narrow habitat breadth, were more volatile. This partially supports Hypothesis 1, highlighting potentially disproportionate risks of pulse disturbances to rare taxa. Moreover, there was no clear distinction in population resilience over a gradient of rarity, which might otherwise offset the risks of volatility. The near-linear relationship seen between rarity and volatility might partly be explained by a sampling effect (i.e., that rare taxa are statistically less likely to be sampled and thus inherently more variable or less persistent; Bradley and Ormerod 2002a; Mykrä et al. 2011), or changes in mean population size. For example, decreases in CV can result from increases in the denominator for the ratio of the standard deviation to the mean (Hector et al. 2010; Blüthgen et al. 2016). However, by using a rarity index comprising other forms besides abundance, this issue was addressed to some extent. Moreover, direct comparison of PC1 with each aspect of rarity showed the pattern to be largely preserved, despite aspects being uncorrelated. Results might therefore reflect increased vulnerabilities of rare and specialist taxa noted from other studies, such as Allee effects and niche restriction (Dennis 2002; Hering et al. 2009; Domisch et al. 2013; Hilpold et al. 2018). However, the exact mechanisms are unknown, including whether fluctuations correspond to anthropogenic stressors such as climate change or to natural and stochastic processes. Although other factors such as resistance and resilience traits were also predicted to enhance population stability, there was no clear evidence for this besides very weak correlations with individual trait affinities ($r = 0.2$-0.3). This may in part reflect limitations in the quality of trait data, and how well they capture underlying mechanisms (Gonçalves-Souza et al. 2023).

In the second hypothesis, external factors relating to differences in land use and chemistry were predicted to influence population stability. Contrary to expectations (Figure 5.1), broadleaf woodland streams had the highest population-level stability on average, corresponding to community-level results (Chapter 4). This contradicted Hypothesis 2, despite BW communities having the highest proportion of rare, and seemingly least stable, taxa. While volatility was greater in acid streams, population resilience was greater in broadleaf streams compared to all other stream types. This suggests that characteristics of the habitat are potentially more important than diversity, given the similarities between BW and CM streams. This supports similar findings that habitat complexity and stability can promote population stability of fish (Terui et al. 2018), and stream macroinvertebrates (Mykrä et al. 2011), including rare taxa (Death and Winterbourn 1994). The divergence in population resilience between BW and CM streams might also reflect the speed of recovery in course particulate organic matter (CPOM) standing stocks seen after hydrological disturbances (Pye et al. 2022; Thomas et al. 2016), or differences in the balance between green and brown food webs and species interactions (McCann et al. 1998; Zou et al. 2016). Additionally, the lower stability in acid streams suggest that populations are still exposed to acid episodes, or could suffer from the legacy effects of acidification with biological recovery further impeded by climate change (Kowalik and Ormerod 2006; Ormerod and Durance 2009; Battarbee et al. 2014).

There was a significant interaction between functional feeding guild and stream type, which partially supported Hypothesis 2. Grazers were significantly less stable (PC1 only) in acid streams compared to BW and CM streams. This potentially reflects smaller population sizes or acid sensitivity of algae (Planas 1996) and consumers such as *Baetis* (Kowalik and Ormerod 2006), and further supports evidence for ongoing acid events. Similarly, lower stability of filterers in acid streams compared to BW is likely to reflect the acid sensitivity of trichopterans such as *Diplectrona* and *Wormaldia* (Ormerod and Durance 2009). However, this could also indicate reductions in flow velocity, decreased oxygen levels, and sedimentation that are the consequence of drought and known to impact these taxa (Philipson 1954).

Separating species-specific traits such as feeding guild from environmental influences is challenging. While this was partly addressed by controlling for site-level differences in mixed-effect modelling, data were restricted to a universal subset of taxa for comparison across sites. Analysis using these taxa revealed differences in stability in relation to stream type across both components (PC1 and PC2). One of the key findings was that, among these ubiquitous taxa, three phylogenetically similar shredders (*Amphinemura, Protonemura,* and *Nemoura*) fluctuated most over time. This could result from the organic matter dynamics to which these taxa respond, and the likely effects of discharge and warming (Pye et al. 2022). For example, increasing flow intermittency during summer could reduce CPOM availability and potentially increase competition with other shredders (Piano et al. 2020). This might also explain why *Amphinemura* and *Protonemura* were the most volatile in AM compared to other stream types, particularly given the dominance of shredders in these streams.

Contrary to Hypothesis 3, population and community stability were positively correlated, this contributes to a large body of literature suggesting both positive and negative relationships are possible across biological scales (McCann 2000). However, there have remained knowledge gaps in relation to aspects of population and community dynamics such as resilience, with most studies focused solely on temporal variability (Thibaut et al. 2013; Donohue et al. 2016; Wang et al. 2019). This positive relationship suggests that within-stream asynchrony may not be a dominant mechanism for stability in these streams (Downing et al. 2014). However, given the data limitations it is not possible to determine this fully. Mechanisms might also differ in relation to local conditions, for which greater spatial replication is required to better understand. Moreover, asynchrony operating at larger scales such as the regional metacommunity is likely to play a stabilising role (Downing et al. 2014; Wang et al. 2019), and may be more important than within-community asynchrony (Hammond et al. 2020). Despite these findings, the combination of low stability with high synchrony may be particularly detrimental to resilience, as observed in some AC streams. Likewise, despite high resilience in BW streams, high synchrony could either signal low importance relative to other mechanisms (Downing et al. 2014), or that large-scale environmental stressors are acting to synchronise dynamics. This warrants further investigation.

Results of this study showed that the dynamics of the most abundant taxa correlated most strongly with community stability. This might be expected given the larger contribution to aggregate community abundance (Arnoldi et al. 2019). However, predictions that population stability of rare taxa and predators would correlate with community stability was not strongly supported. Across functional feeding guilds, the stability of grazers was found to be significantly correlated with community variability, but not with resilience. This distinction might reflect the short-term boom and bust dynamics of algal resources and their consumers (Müller-Navarra et al. 2000; Taylor et al. 2002; Torres-Ruiz et al. 2007; Lau et al. 2009). Conversely, over the longer timescales these dynamics may be less important, and instead slower-growing populations such as shredders were related to resilience.

Given the importance of shredders to multiple aspects of community stability in upland streams, and as fundamental functional groups responsible for carbon and nutrient cycling (Covich et al. 1999), future research on these populations should be a priority. Ultimately, this might allow for more targeted and cost-effective management approaches. Future risks from climate change should be carefully considered, given that climate change is predicted to decrease the nutritional quality of organic matter inputs into streams, potentially impacting dominant functional groups such as decomposers or shredders (Fenoy et al. 2020; Fenoy et al. 2021). Changes to resource availability, and the slower generation times of allochthonous material compared to algae may explain why shredder population stability and synchrony were found to be correlated, where this relationship was not found for any other group. Assessment of long-term trends in nutrient levels would also be important, since loss of nutritional quality could reduce population sizes further (Domisch et al. 2011), and contribute to vulnerabilities associated with rarity. Worldwide declines have already been witnessed for many common invertebrates (Sánchez-Bayo and Wyckhuys 2019), which, alongside rare taxa, are also crucial for the taxonomic and functional diversity of ecosystems (Chapman et al. 2018). Understanding whether trends are also present in synchrony or other potential mechanisms would help to address knowledge gaps (Downing et al. 2014). Additionally, questions remain around the importance of other groups, such as predators, which are likely to contribute in ways that were not able to be determined fully in this study (Arnoldi et al. 2019; Ross et al. 2022), and studies that include measures of biomass might better emphasise subtle differences in community structure and population stability compared to abundance.

5.6 Conclusion

This study provides insights into how both intrinsic and external factors contribute to ecological stability at multiple biological scales. It reveals that circumneutral streams draining broadleaved woodland were more stable than other stream types at both population and community levels, though broadleaf populations were more resilient. Results also highlight the lower stability of acidified coniferous catchments, in addition to the widely studied reductions in diversity (Weatherley and Ormerod 1987; Ormerod et al. 1993). Yet, the high proportions of potentially sensitive rare taxa and high population synchrony found in broadleaf streams could indicate that these habitats are also at risk of some losses, and that local scale management solutions may not be enough to prevent climate change impacts. Understanding how wider-scale factors influence stability, including metacommunity dynamics and changes in terrestrial biomass and nutrient inputs into streams are therefore priorities for future research.

Chapter 6: General Discussion

6.1 Overview and research purpose

The actions of humans have resulted in a profound alteration of life on Earth. The past few decades have witnessed unparalleled rates of biodiversity decline on a global scale, accompanied by rapid changes in climate and land use. These developments have raised substantial concerns and heightened the need for immediate action (Foley et al. 2005; Díaz et al. 2019; IPCC 2021). Freshwaters are among the most threatened of all ecosystems, the resilience of which - the ability to maintain the current state in spite of disturbance (Holling 1973) - is vital to many functional processes upon which we rely (Vörösmarty et al. 2010; Reid et al. 2018; IPBES 2019). In light of these concerns, the objective of this thesis was to evaluate the ecological resilience of upland stream macroinvertebrate communities in relation to local land management and climatic changes over the past 40 years. Particular emphasis was placed on understanding the role of native riparian broadleaf woodland in enhancing ecosystem resilience, which has been increasingly promoted as a nature-based solution to these issues (Ormerod 2009; Thomas et al. 2016; Griscom et al. 2017).

Chapter 2 of this thesis comprised a literature review aimed at providing general background to the field, and identifying gaps in current knowledge. Subsequently, three studies were conducted to address the following questions, **1)** what are the long-term trends in upland stream macroinvertebrate structure and function, and to what extent can climate and stream type (land use and chemistry) explain these trends? (Chapter 3), **2)** what are the effects of climate and stream type on the ecological stability of upland stream communities? (Chapter 4), and **3)** what are the factors influencing the stability of populations, and how do their dynamics relate to community stability? (Chapter 5). In this chapter, results are synthesised and accompanied by recommendations for future research.

6.2 Synthesis

In Chapter 3, a comprehensive assessment of macroinvertebrate community structure and function revealed significant and widespread changes in all stream types at Llyn Brianne over the past four decades. These findings align with a growing body of research indicating rapid declines in insect and macroinvertebrate communities (Dirzo et al. 2014; Ceballos et al. 2017; Sánchez-Bayo and Wyckhuys 2019; Rumschlag et al. 2023), even in relatively undisturbed systems (Hallmann et al. 2017; Baranov et al. 2020). However, observed declines contrast with evidence of increasing trends in other freshwater systems that appear to be recovering from pollution (Vaughan and Ormerod 2012; van Klink et al. 2020; Outhwaite et al. 2020; Pilotto et al. 2020; Pharaoh et al. 2023). This underscores the importance of monitoring programmes in smaller waterbodies and headwaters that are relatively free from anthropogenic stress, and which have typically been overlooked (Riley et al. 2018).

Among the indices analysed, the most prominent declines were observed in abundance. Conifer streams experienced a significant 53% loss in 37 years, while broadleaf woodland, circumneutral moorland, and acid moorland streams faced declines of 46%, 22%, and 21% respectively. Additionally, circumneutral streams exhibited a decline in functional diversity, highlighting the need to prioritise the conservation of exposed and potentially vulnerable communities. Across all streams, compositional shifts were seen reflecting declines in plecopteran detritivores. Although some of these changes could be attributed to climate, a significant portion of the observed variation remained unexplained, emphasising the complex nature of ecosystems, their nonlinear dynamics, and a large amount of noise at local scale (Jourdan et al. 2018; Baranov et al. 2020). Of the effects detected, warm summers were the most striking, linked to declines in abundance and richness, with an estimated 33% loss in abundance for every 1°C rise, and a net loss of two taxa, on average. Additionally, warm, and especially wet winters were linked to increased taxonomic and functional diversity, contrasting with previous findings (Durance and Ormerod 2007).

Chapter 4 investigated the nonlinear response and recovery dynamics of community-level taxonomic and functional diversity indices. Based on an overarching concept of ecological stability (Pimm 1984), a multidimensional approach was taken combining measures of resistance, persistence, food web robustness, temporal variability, and engineering resilience

(Donohue et al. 2013). Results indicated that stability in upland stream communities is more complex than often recognised in empirical studies, where typically only single components are assessed (Donohue et al. 2013; Donohue et al. 2016). Here, two dimensions of stability, one describing the volatility of communities (resistance, persistence, invariability) and the other their rate of return to equilibrium state (engineering resilience), were identified, while results for robustness were unexpectedly connected to both and also more strongly correlated with functional measures of stability. Results indicated a high degree of functional redundancy in streams at Llyn Brianne, but a clear divide between acid and neutral streams in terms of volatility. In this instance, there were indications that acid stream communities were more volatile than BW and CM streams, particularly with regards to functional traits. Moreover, increasing taxonomic turnover (declining persistence) was seen across streams, building on previous findings where this trajectory was not yet apparent (Bradley and Ormerod 2001).

Similar to the findings of Chapter 3, Chapter 4 revealed some effects of high temperatures (Tw.max), but most striking were the impacts of increased discharge during the driest months (typically summer). In addition, lower stability in years of reduced winter minimum discharge were seen, that might typically be the wettest period of the year. These results suggest extreme, rather than mean conditions may be a key factor contributing to community instability, and that unexpected timing of events, such as winter droughts or increased flow during what would otherwise be the driest months, might disproportionately impact communities. This corroborates evidence from a meta-analysis showing that extreme events pose a greater threat to river biodiversity than gradual change (Sabater et al. 2022). Moreover, both analyses highlighted the potentially complex interface between stream drying and re-wetting, which may contribute to the release of harmful heavy metals and other particulates (Dawson et al. 2008; Mosley 2015).

The final data analysis chapter, Chapter 5, focused on stability at the population-level, aiming to unravel some of the mechanisms influencing the stability of total community abundance. Results highlighted the significance of both intrinsic, species-specific factors and external habitat conditions in maintaining ecological stability across multiple biological scales. Additionally, the findings emphasised the potential vulnerability of rare taxa to disturbances, supporting the notion that rare and specialist taxa could face disproportionate impacts from climate change (Clavel et al. 2011; Hilpold et al. 2018). Consistent with findings from previous chapters, this study identified potentially detrimental effects of conifer forestry on ecological stability, contrasting with enhanced population stability in broadleaf streams. Moreover, the stability of the most abundant populations, including shredders and those classified as common, was found to be closely linked with community-level stability. This highlights the potential importance of shredders in ecological stability, and contributes to results in Chapter 3 demonstrating their role in compositional shifts. Despite greater stability in broadleaf streams, the high abundance of both common and rare taxa, and notable population synchrony, could indicate an elevated risk posed by climate change in these streams and their need for support from the wider landscape.

6.3 Strengths and limitations

Although limitations unique to each chapter are addressed individually, several common themes occur throughout. Firstly, it is important to note that the use of observational data restricts this study to establishing correlations rather than causation. Furthermore, field systems are inherently variable and lack experimental control, introducing potential confounding factors and often a low signal-to-noise ratio that can influence the results. A notable limitation in this context is the challenge of confidently identifying reference conditions, as well as the impact of shifting baselines on the analysis of ecological resilience based on traditional, equilibrium-based measures (Holling 1996; Van Meerbeek et al. 2021). Moreover, despite the extensive, multidecadal nature of the data, low spatial replication reduces statistical power for some stream types, notably broadleaf woodlands. These limitations underscore the need to exercise caution when interpreting the findings, while also highlighting the widespread nature of habitat degradation within the region.

Despite these challenges, the study provides valuable insights into the complex dynamics of upland stream communities and contributes to the existing body of knowledge in several fields of research, including freshwater ecology, human impacts, and ecological stability. Additionally, the challenges faced at Llyn Brianne, including extensive habitat loss, atmospheric deposition of acidic compounds, pollution from trace metals and organic matter, ongoing forestry and other intensive land management regimes, and threats from nitrogen deposition and climate change, are common across UK uplands and those of Western Europe

(Curtis et al. 2014), highlighting that research using these study streams is representative of upland waters more broadly. Furthermore, the study benefits from the relative proximity of the selected sites, as well as their similar altitude, size, underlying geology, climate, and specifically their upland location. This advantageous aspect helps minimise numerous confounding factors that are often encountered in studies conducted in more polluted lowland areas or across larger spatial distributions (Ormerod et al. 2010; Vaughan and Ormerod 2014; Outhwaite et al. 2020). By focusing on a controlled and homogeneous setting (as much as practically possible), results provide more robust insights into the specific research questions at hand. This approach aligns with the growing demand for rigorous data to substantiate claims of an ecological "Armageddon" or an impending mass extinction (Leather 2018; Sánchez-Bayo and Wyckhuys 2019; Thomas et al. 2019). Moreover, observational datasets of the length used here are extremely unique in many ways, and play a vital role in connecting theoretical and experimental findings of ecological stability and climate change impacts to the real world.

6.4 Implications

The findings of this research have significant implications for the uplands, rivers, and their management in the face of climate change, as well as for our understanding of ecological stability and resilience in general. Firstly, the observed speed and extent of biodiversity declines, coupled with changes in functional traits, could have far-reaching impacts to ecosystem processes on which we depend, such as the provision of clean water and nutrient cycling. That these changes were seen in the uplands specifically, also has potentially important implications to downstream ecology. For example, export of processed organic matter from the headwaters is crucial for downstream communities (Vannote et al. 1980), and indications of decline and high synchrony among shredder populations highlight a particular risk to brown energy pathways. These results may also provide an early warning signal for other river systems, such as downstream sections that are dependent upon headwaters, and also larger rivers that may be less sensitive to current changes in temperature variation (Caissie et al. 1998).

The distinct divergence observed between acid and neutral streams provides compelling empirical evidence that a legacy of poor water quality and ongoing land use activities confound relationships between biodiversity and climate (Durance and Ormerod 2009; Vaughan and Ormerod 2014; Baranov et al. 2020). Moreover, results highlighted the impacts to community composition and diversity more generally, with the encroachment of conifer forestry exerting particularly deleterious effects on stream ecosystems, as previously demonstrated (Thomas et al. 2016). Additionally, the findings from this study revealed the influential role of high temperatures and increased discharge during the driest months of the year, that may exacerbate local acidification effects.

In spite of the adverse effects, the observed nonlinear trends and potential recovery seen within acid moorland streams serve as an indication of high engineering resilience of stream communities, and a potential for recovery under appropriate management (Vaughan and Gotelli 2019). However, this study highlighted the need to assess multiple facets of stability across taxonomic and functional properties, where simplified approaches (i.e., single measures or proxies) may be insufficient. These are important results for practitioners and policymakers looking to extend upon current frameworks for resilience, e.g., DECCA (see Chapter 2; Garrett et al. 2021), which have so far been limited to measuring attributes and proxies rather than using quantifiable and direct measures (Pimm et al. 2019; Prober et al. 2019; Sanderson Bellamy et al. 2021). Based on these analyses, at least two facets of stability, including measures of the volatility of communities (resistance, persistence, or temporal variability) in addition to engineering resilience should be used at a minimum, whilst also considering traditional biodiversity indices (namely abundance) alongside functional aspects.

The results of this study highlight a clear need to mitigate against climatic extremes, and to halt the significant declines in abundance and compositional shifts seen across streams. This may require interventions at multiple scales. At local scale, managers may choose to prioritise interventions based on water quality improvements and regulation of extremes if their goal is stress mitigation and biodiversity promotion. But for those whose primary aim is temperature buffering or carbon sequestration, extreme caution should be exercised when considering afforestation with non-native conifers, which were related to the largest declines in community abundance through time, and the lowest levels of ecological stability at community and population-scales. For managers aiming for enhanced ecological resilience and ecosystem functioning, broadleaf woodlands demonstrated the greatest functional persistence and highest population resilience. Even in the absence of conclusive evidence of increased resilience at community-level, broadleaf woodlands offer a ‘low regrets’ option for climate adaptation (Prober et al. 2019).

Despite benefits of local-scale intervention, extensive declines across streams indicate that larger-scale management strategies beyond the immediate riparian zone are necessary. These observations align with prior research findings and reinforce recommendations regarding catchment-scale interventions (Thomas et al. 2016). Currently, upland areas in Wales are predominantly utilised for sheep farming, which has a significant land footprint, requiring nearly 200 m^2 per 100 g of protein (Poore and Nemecek 2018). This creates a largely homogenous landscape that could be a contributing factor to biodiversity loss, certainly when viewed in a historical context. Sheep grazing also has a larger water footprint compared to any other crop product with equivalent nutritional value (Mekonnen and Hoekstra 2012), while animal agriculture as a whole is among the leading drivers of climate change, responsible for at least 14.5% of carbon emissions (Gerber 2013).

This offers a unique and pivotal opportunity for Wales to address the challenges of climate change and biodiversity loss, and to enhance resilience at larger geographical scales. For example, transitioning towards regeneration of woodlands in upland areas holds considerable potential not only to alleviate pressures on ecosystems, but to improve carbon sequestration, increase connectivity, promote recovery, and enhance resilience of freshwater systems and the landscapes they traverse. Transitions towards resilient and biodiverse uplands is imperative for aligning with legislative mandates and ethical principles, and for safeguarding vital ecosystems for future generations (Sanderson Bellamy et al. 2021). There are a number of routes by which this could be achieved.

In Wales, the government has made a recent commitment to the National Forest, which aims to create a connected network of woodlands across the country. This commitment includes various schemes for farmers and landowners who are interested in tree-planting to either create, restore, or expand woodlands in upland areas. Some of these schemes, such as Glastir, The Woodland Investment Grant (TWIG), and Coetiroedd Bach (Tiny Forests), offer financial incentives for forestry activities that contribute to the woodland network (Welsh Government 2021). Additionally, there have been proposed updates to the UK Forestry Standards that would restrict the maximum percentage of any one tree species in commercial plantations to

65%. This change is intended to promote greater diversity of tree species, which can enhance resilience of the woodland and support climate adaptation efforts (Welsh Government 2022). Building on the findings of this study, a more targeted approach could be developed, which might include guidance on managing or establishing riparian woodland corridors as part of the National Forest. Such an approach would offer multiple benefits to both terrestrial and freshwater ecosystems.

Another recommended approach for restoring habitat heterogeneity and connectivity, which can support insect dispersal and enhance stream resilience, is rewilding. This strategy also reduces the ongoing need for human management. In upland areas, rewilding would entail reducing grazing pressure and potentially removing non-native conifers. An example of this approach can be seen less than 40 kilometres north of the Llyn Brianne reservoir at the Gilfach nature reserve in the Marteg Valley (Rewilding Britain 2023). While installing fences can keep grazers out of specific designated areas, it does not address grazing pressure as a whole. Achieving more extensive habitat regeneration at landscape-scale would require a significant reduction in sheep numbers. Implementing such a strategy would necessitate changes in policies that reduce the demand for animal-based foods and facilitate the return of land to its natural state.

It follows, that numerous influential organisations, including the United Nations, the Intergovernmental Panel on Climate Change, and the Climate Change Committee, along with various climate advocacy groups, have called for an urgent transition away from animal-based foods in favour of more sustainable, healthy, plant-rich diets. This shift is seen as crucial to alleviating land pressures, reducing environmental impacts, and combating the climate and biodiversity crisis (IPCC 2023, UN 2023, CCC 2023). A growing body of research supports this stance, indicating that transitioning from typical Western diets to more environmentally sustainable dietary patterns could have profound benefits. This includes potentially reducing global land use for agriculture by 75%, cutting greenhouse gas emissions by up to 70-80%, and halving water use. Additionally, such dietary shifts could lead to various human health benefits, including reductions in overall mortality risk, potentially saving up to 8 million human lives by 2050 (Aleksandrowicz et al. 2016; Springmann et al. 2016; Poore and Nemecek 2018; Crippa et al. 2021; Ritchie 2021). Policies that promote these dietary changes have the potential to make a significant contribution to reducing the environmental footprint of the UK, and enabling the restoration of natural habitats (Scarborough et al. 2023).

To facilitate transitions like these, additional government support is essential to mitigate potential negative impacts on farmers and rural communities. For instance, subsidies currently allocated to sheep farming could be redirected to further incentivise environmentally sustainable practices. However, it is crucial to also consider the potential adverse effects of tree-planting to headwaters. Some studies indicate that deciduous trees, due to their deeper roots, evaporation rates, and canopy interception, might lead to soil moisture deficits compared to grass, potentially resulting in reduced run-off, streamflow, and groundwater recharge (Finch 2000). Therefore, any tree-planting or natural regeneration programs must be subject to careful monitoring. Nevertheless, trees continue to play a vital role in freshwater ecosystems by providing organic matter, shade, and regulating flow and temperature. These functions support aquatic food webs and promote the diversity of species and functional groups (Vannote et al. 1980; Hannah et al. 2008; Broadmeadow et al. 2011; Nisbet et al. 2011). Although the statistical evidence for the importance of native broadleaf woodlands in this study may have limitations, the findings here align with a growing body of literature that underscores the critical role of these woodlands in enhancing freshwater resilience.

Interpretation of resilience is not without challenges, however, given that it can only be understood so far in relative terms, with no clear baseline for a ‘resilient’ system. This leads to a fundamental question concerning the nature of resilience and its constituent elements, and specifically whether they should be universally perceived as positive attributes. For instance, the notion of resilience and related components could be detrimental in instances where a system is trapped in an undesired state, or if this limits the ability to adapt or redirect resources during perturbations. Thus, river assessments would need to be considered on a case-by-case basis, keeping in mind the individual stressors at play and current ecological status of the system, whilst contextualising results against other habitats.

Some aspects of resilience may also be considered detrimental from a societal perspective. For example, resistance to change is perhaps the biggest barrier to the transformative shifts necessary for averting global catastrophe (Díaz et al. 2019). Strong connections within the economic system, bystander effects, cognitive dissonance, social norms, and a diffusion of responsibility are among factors that can contribute to a rigid adherence to the status quo or an aversion to change within individuals and larger societal scales (Latane and Darley 1968; Rees 2010; Jiang et al. 2021). This could potentially lead to a devastating underestimation or collective denial of the current state of emergency, and at least partly explains the inaction by national and international organisations thus far (Rees 2010).

With this perspective in mind, it is evident that a comprehensive reassessment of our relationship with and utilisation of the natural world is imperative. It is crucial to recognise the pressing need to restore equilibrium between us and other species within socio-ecological networks, and identify avenues for achieving this objective. While some of these have been discussed, ultimately this requires a paradigm shift in our attitudes, practices, and policies away from current industrial agricultural practices and anthropocentric perspectives, towards those that are ecologically and socially responsible (Griscom et al. 2017; Piccolo et al. 2018; Kassam and Kassam 2021). Strategies that involve local communities and prioritise smaller-scale interventions emphasise the importance of connecting people with nature and empowering individuals. Such an approach may help accelerate collective action and can be implemented with immediate effect (Scheffer et al. 2015; Jiang et al. 2021).

6.5 Future research

Future studies on ecological resilience in freshwater systems should aim to assess whether the observed patterns identified in this study are applicable to other ecosystems. Conducting similar analyses in different sites would enhance the robustness of stability assessments across various stream types (Donohue et al. 2013). Furthermore, including additional components in dimensionality analyses, such as inter-annual losses and gains, would improve comparability with recent research utilising observational data in riverine systems (Eagle et al. 2021; Allen et al. 2023), and enhance our understanding of relative invasion and extinction risks.

An important question that remains to be investigated is the relationship between short-term and long-term dynamics, as well as the influence of stability measures operating at different timescales (e.g., days, weeks, or months following a disturbance event) (Domínguez-García et al. 2019). Further research could employ moving-window analyses to explore phenomena associated with tipping points (Scheffer et al. 2009), state dependency (Sugihara et al. 2012), or ‘ecological memory’ (Johnstone et al. 2016; Hughes et al. 2019; Jackson et al. 2021), which can alter the relationships between biodiversity and disturbances over time.

Although abundance has proven to be a valuable indicator of change, future studies would benefit from incorporating biomass data in analyses. This would help to provide insights into energy transfer or direct consequences to ecological functions such as production, which information on abundance can only imply. Furthermore, researchers seeking to incorporate interaction strength into food web models and derive more precise measures of robustness would greatly benefit from biomass data (Dunne et al. 2002b; Dunne et al. 2002a; Memmott et al. 2004), in addition to dietary information which could be obtained from Next Generation Sequencing of gut contents (Pompanon et al. 2012). These assessments might also consider species’ temperature tolerance limits, enabling more accurate predictions of disturbance effects. Further research using network approaches may be beneficial, given the potential to capture multiple aspects of ecological stability.

Further work is required to better characterise climate-related disturbance events, and complex interactions between variables over spatial and temporal scales. Moreover, while complete discharge and water temperature records were obtained from short runs of stream data and the linear relationship with air temperature and precipitation, it is possible that these relationships will change in time with differences in cloud cover, wind, water volume, and water colour. For example, increased browning from dissolved organic carbon that is predicted to rise with climate change (Kritzberg et al. 2020; Lee et al. 2020), or shifts in macrophyte and algal composition and dominance could alter absorption and release of short- and long-wave radiation (Houser 2006). Close monitoring of stream temperatures and flow alongside spectrophotometry data collection would be an interesting and important route for further study.

To determine wider ecological drivers of change that could also indirectly reflect climate change, e.g., phenological mismatch and changing nitrogen levels, future studies will need to consider factors such as C:N ratios and species emergence times (Hassall et al. 2007; Fenoy et al. 2020; Zhang et al. 2022). Additionally, research into the loss of genetic diversity through reduced connectivity and dispersal limitation across the landscapes (Bálint et al. 2011; Firmiano et al. 2021), or other investigations of metacommunity dynamics such as between-stream synchrony would be beneficial (Larsen et al. 2021). Likewise, research to identify other potential mechanisms for resilience beyond in-stream synchrony would help to better understand these systems (Downing et al. 2014). Research should also include monitoring of stream-level environmental variables, such as water quality, streambed stability, water depth and flow velocity over flood and drought events. This would help to disentangle the contributions of intrinsic, community-based properties from the influence of environmental variability on measures of ecological stability.

6.6 Final conclusions

In summary, the broad geographical extent, small size, and unique connection of headwater streams to the terrestrial landscape makes them especially vulnerable to climate change and land use. The results presented in this thesis elucidate the significant structural and functional shifts taking place in upland headwaters, which can be attributed, at least in part, to these factors. While there were indications that riparian broadleaf woodlands enhanced certain aspects of ecological resilience, the widespread declines in abundance, compositional shifts, and diminishing community persistence underline the need for a combination of local and broader-scale interventions.

These findings emphasise the importance of prioritising upland headwaters in policy and practice, for biodiversity, water security, and the preservation of vital ecosystem processes. Overall, results shed light on the intricate dynamics within stream ecosystems, highlighting the need for multifaceted assessments and careful interpretation of outcomes when relying solely on single stability components, or traditional measures such as richness. This thesis exemplifies the value of ongoing long-term monitoring and the utilisation of historical data to predict future response and potential recovery, and further research will help to forecast the consequences of climate change and biodiversity loss more accurately.

Overall, however, natural systems are highly complex and often unpredictable, and we should not underestimate their fragility, their importance, and the urgent need for immediate action to safeguard ecosystems and the wellbeing of future generations. How we choose to utilise, value, and nurture our connection with the natural environment will be key to addressing the challenges that lie ahead.

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Appendix

Table A.1 Cross-checks of environmental data used in this study. ***a)*** *shows details of pairwise relationships between HadUK-Grid precipitation and air temperature data with local records.* ***b)*** *shows relationships between discharge from the flume at LI1 and two other sites.*

a)

Variable	Source	Location information	Distance from furthest stream	Dates	r	Intercept	slope	*p*
Precipitation (daily)	Natural Resources Wales	Crump weir at Ystradffin (SN785472, station number 60008)	< 12 km	1980 to 2017	0.98	0.046	1	< 0.0001
Precipitation	Natural Resources Wales	Nant Y Maen (LI1)	< 11 km	2008 to 2020	0.91	0.4	0.82	< 0.0001
Air temperature (monthly mean)	Forestry Commission	Llyn Brianne area	n.a.	July 2009 to December 2014	0.94	1.7	1.1	< 0.0001

b)

Source	Location information	Distance from flume	r	Intercept	slope	*p*
Natural Resources Wales	Afon Twrch at Ddol Las, SN650439, station number 60012	18 km south-west	0.92	22	1.3	< 0.0001
Centre for Ecology and Hydrology	Hafren flume, Plynlimon, SN843878	< 40 km north	0.9	16	0.74	< 0.0001

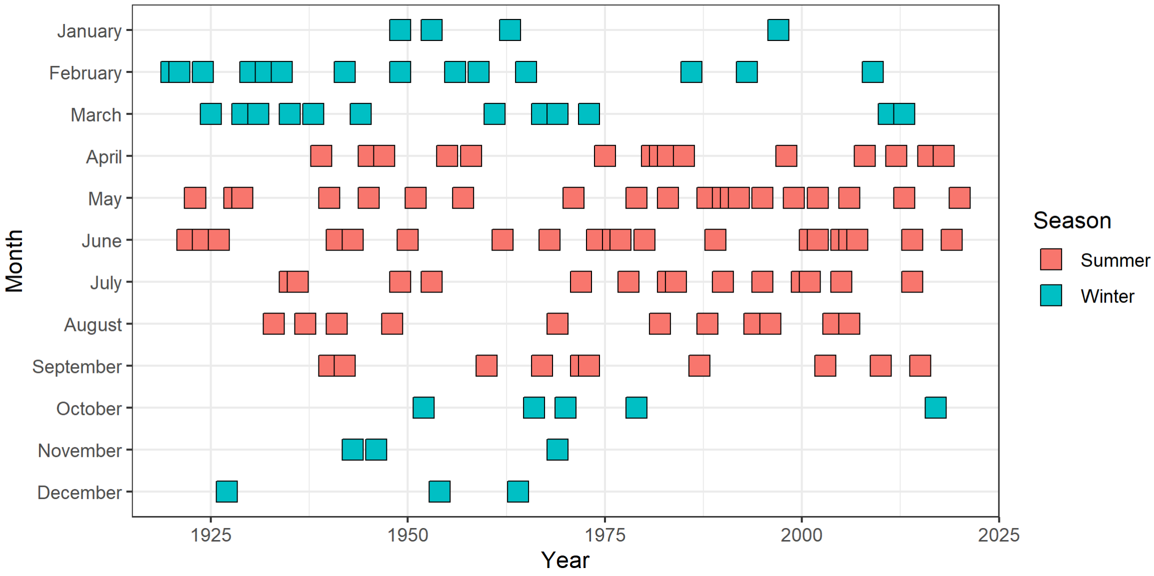


Figure A.1 *Occurrence of the lowest discharge (driest) month of each year from 1920 to 2018.*

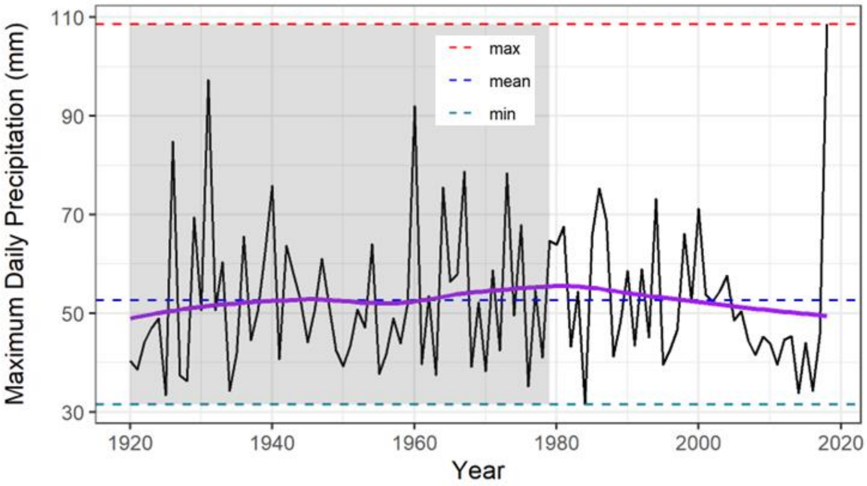


Figure A.2 *Volume of highest daily precipitation in each year from 1920 to 2018. Purple trendline was fitted with a loess smoother.*

Table A.2 Comparison of adjusted R^2 values from models constructed with annual and seasonal scale climate variables, and with the winter North Atlantic Oscillation (NAO) Index. Blue cells highlight the best model, where ΔR^2 values were > 1% above the base model (stream type only). Note, some differences due to rounding.

Group	Community variable	Base	Annual	Seasonal	NAO	ΔR^2
Taxonomic	Abundance	0.18	0.30	0.28	0.22	0.12
	Richness	0.51	0.58	0.57	0.54	0.06
	Rarefied Richness	0.24	0.27	0.25	0.25	0.03
	Composition NMDS1	0.60	0.63	0.69	0.61	0.09
	Composition NMDS2	0.35	0.48	0.45	0.38	0.13
Functional	FRic	0.51	0.51	0.51	0.51	< 0.01
	FDis	0.18	0.22	0.20	0.18	0.04
	SES FRic	0.01	0.03	0.05	0.01	0.04
	SES FDis	0.30	0.31	0.31	0.31	0.01
	Composition NMDS1	0.36	0.46	0.40	0.37	0.10
	Composition NMDS2	0.62	0.67	0.66	0.62	0.04

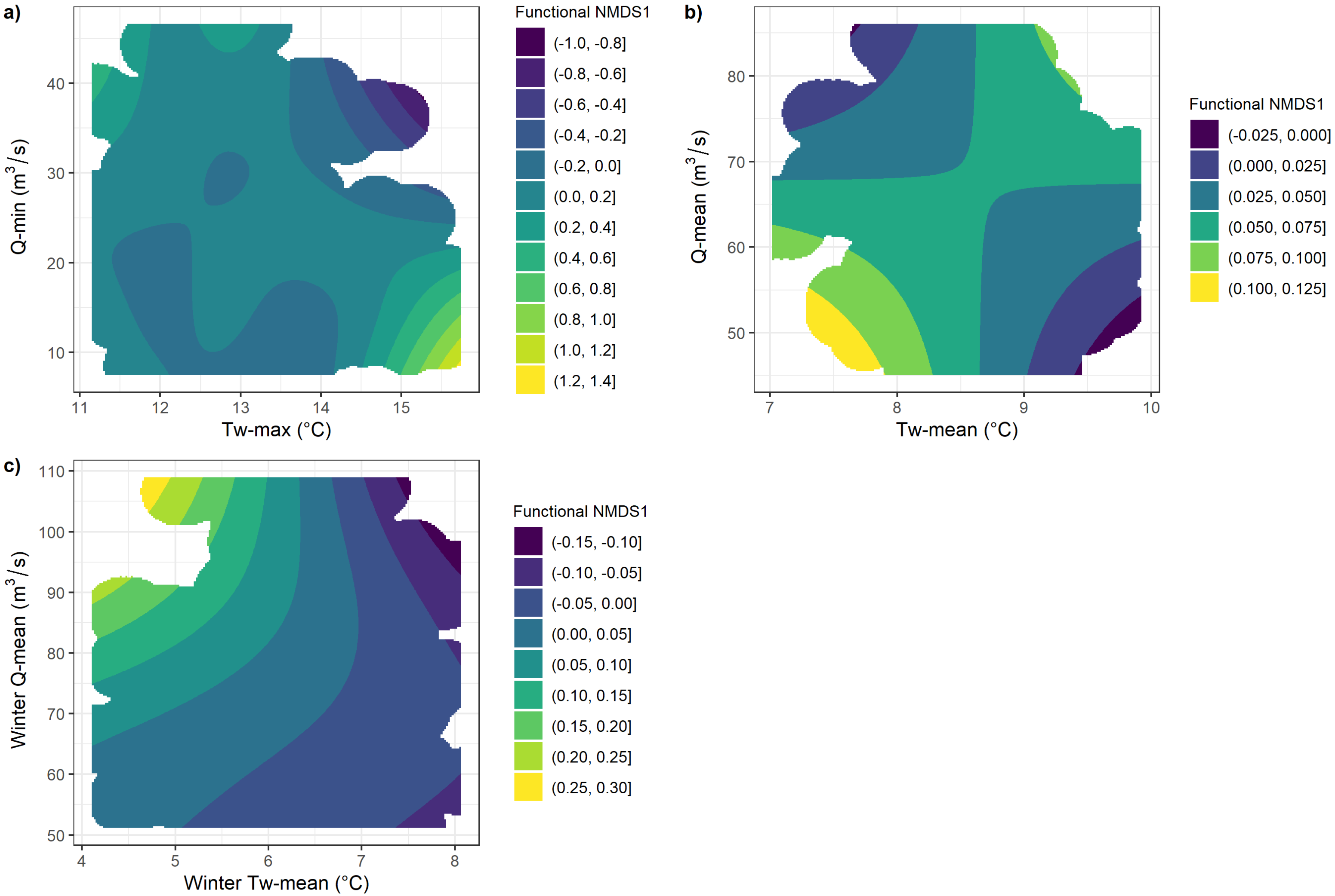


*Figure A.3 Predicted partial effects of winter conditions on functional composition (NMDS1) in coniferous streams. Plots **a-b)** show interactive effects of annual scale climate variables, a) Tw.max * Q.min, b) Tw.mean * Q.mean, controlling for other variables in the model. Plot **c)** shows interactive effects of winter Tw.mean (Tw.W), and winter Q.mean (Q.W) coloured by NMDS score. Higher values (yellow) reflect communities characterised by secondary consumers, and lower values (blue) reflect communities characterised by predatory taxa.*

Table A.3 *Prediction accuracy of climate models for taxonomic diversity and composition in each stream type. Results show comparison of root-mean squared error (RMSE) and proportion (p) of observed change in taxonomic indices between 1982 and 2018 estimated from annual and seasonal climate variables, and the NAO. Bold values highlight statistical significance of observed trend.*

Community variable	Stream type	Observed change	Annual			Seasonal			NAO		
			RMSE	nRMSE	p	RMSE	nRMSE	p	RMSE	nRMSE	p
Abundance	BW	-529	582	0.18	0.28	599	0.19	0.41	607	0.19	0.2
	CM	-210	323	0.1	0.62	363	0.11	0.93	399	0.12	0.46
	AC	**-219**	312	0.1	0.24	328	0.1	0.36	327	0.1	0.18
	AM	**-23**	268	0.08	2.32	268	0.08	3.43	280	0.09	1.75
Richness	BW	-3	4.68	0.13	-0.11	4.68	0.13	0.21	4.83	0.13	0.19
	CM	-4	4.52	0.12	-0.08	4.74	0.13	0.16	4.76	0.13	0.14
	AC	-1	3.04	0.08	-0.3	3.21	0.09	0.56	3.27	0.09	0.49
	AM	**1**	4.05	0.11	0.57	4.19	0.11	-1.09	4.17	0.11	-0.95
Rarefied Richness	BW	**-0.22**	0.53	0.09	-2.04	0.61	0.1	-0.71	0.65	0.11	0.1
	CM		0.84	0.14	1.49	0.93	0.15		0.95	0.16	
	AC		0.92	0.15	0.93	0.97	0.16		0.98	0.16	
	AM		0.84	0.14	0.12	0.87	0.14		0.88	0.14	
Composition NMDS1	BW	**0.03**	0.11	0.22	-0.27	0.11	0.2	-0.46	0.12	0.24	-0.81
	CM		0.1	0.15	0.91	0.11	0.15	-0.73	0.1	0.15	
	AC		0.18	0.13	0.92	0.18	0.13	-0.52	0.19	0.13	
	AM		0.19	0.12	1.59	0.16	0.1	20.8	0.23	0.14	
Composition NMDS2	BW	**-0.39**	0.12	0.17	0.26	0.16	0.23	0.4	0.17	0.24	0.1
	CM		0.14	0.14	0.25	0.14	0.15		0.16	0.16	
	AC		0.18	0.09	0.31	0.2	0.1		0.21	0.11	
	AM		0.18	0.12	0.26	0.19	0.13		0.21	0.14	

Table A.4 *Prediction accuracy of climate models for functional diversity and composition in each stream type. Results show comparison of root-mean squared error (RMSE) and proportion (p) of observed change in functional indices between 1982 and 2018 estimated from annual and seasonal climate variables, and the NAO. Bold values highlight statistical significance of observed trend.*

Community variable	Stream type	Observed change	Annual RMSE	nRMSE	p	Seasonal RMSE	nRMSE	p	NAO RMSE	nRMSE	p
FRic	BW	-0.0021	0.0057	0.23	-0.08	0.0057	0.23	-0.39	0.0053	0.22	0.23
	CM	**-0.0071**	0.0052	0.17	-0.02	0.0055	0.18	-0.11	0.0052	0.17	0.07
	AC	-0.0008	0.0048	0.18	-0.21	0.005	0.19	-1.02	0.005	0.19	0.59
	AM	**0.0041**	0.0064	0.19	0.04	0.0064	0.19	0.2	0.0062	0.19	-0.11
FDis	BW	-0.0028	0.028	0.28	1.79	0.027	0.27	-4.16	0.028	0.29	0.51
	CM	-0.0314	0.043	0.24	0.16	0.039	0.22	-0.38	0.04	0.22	0.05
	AC	**0.0273**	0.067	0.18	-0.19	0.07	0.19	0.43	0.073	0.2	-0.05
	AM	-0.023	0.047	0.17	0.22	0.046	0.17	-0.51	0.048	0.17	0.06
SES FRic	BW	-0.33	0.57	0.19	-0.42	0.55	0.18	0.29	0.60	0.20	-0.09
	CM	**-0.76**	0.71	0.23	-0.18	0.69	0.22	0.92	0.71	0.23	-0.04
	AC	0.06	0.43	0.19	2.15	0.42	0.19	0.15	0.43	0.19	0.48
	AM	**0.57**	0.70	0.18	0.24	0.67	0.17	0.62	0.71	0.19	0.05
SES FDis	BW	**0.37**	0.68	0.19	0.03	0.69	0.20	0.22	0.67	0.19	0.22
	CM		0.69	0.21		0.65	0.20		0.66	0.21	
	AC		0.94	0.16		0.93	0.16		0.95	0.17	
	AM		0.87	0.18		0.87	0.18		0.87	0.18	
Composition NMDS1	BW	0.059	0.04	0.23	-0.34	0.04	0.23	0.03	0.04	0.23	-0.10
	CM	0.025	0.04	0.21	-0.43	0.04	0.20	-0.47	0.04	0.20	-0.24
	AC	**-0.136**	0.07	0.10	0.30	0.09	0.12	0.53	0.10	0.13	0.04
	AM	-0.002	0.07	0.10	8.52	0.07	0.10	4.47	0.07	0.11	3.35
Composition NMDS2	BW	**-0.059**	0.02	0.15	0.39	0.02	0.13	0.40	0.03	0.30	-0.02
	CM		0.03	0.19	0.46	0.03	0.20		0.03	0.22	
	AC		0.04	0.11	0.25	0.05	0.12		0.05	0.12	
	AM		0.05	0.14	0.41	0.06	0.15		0.12	0.16	

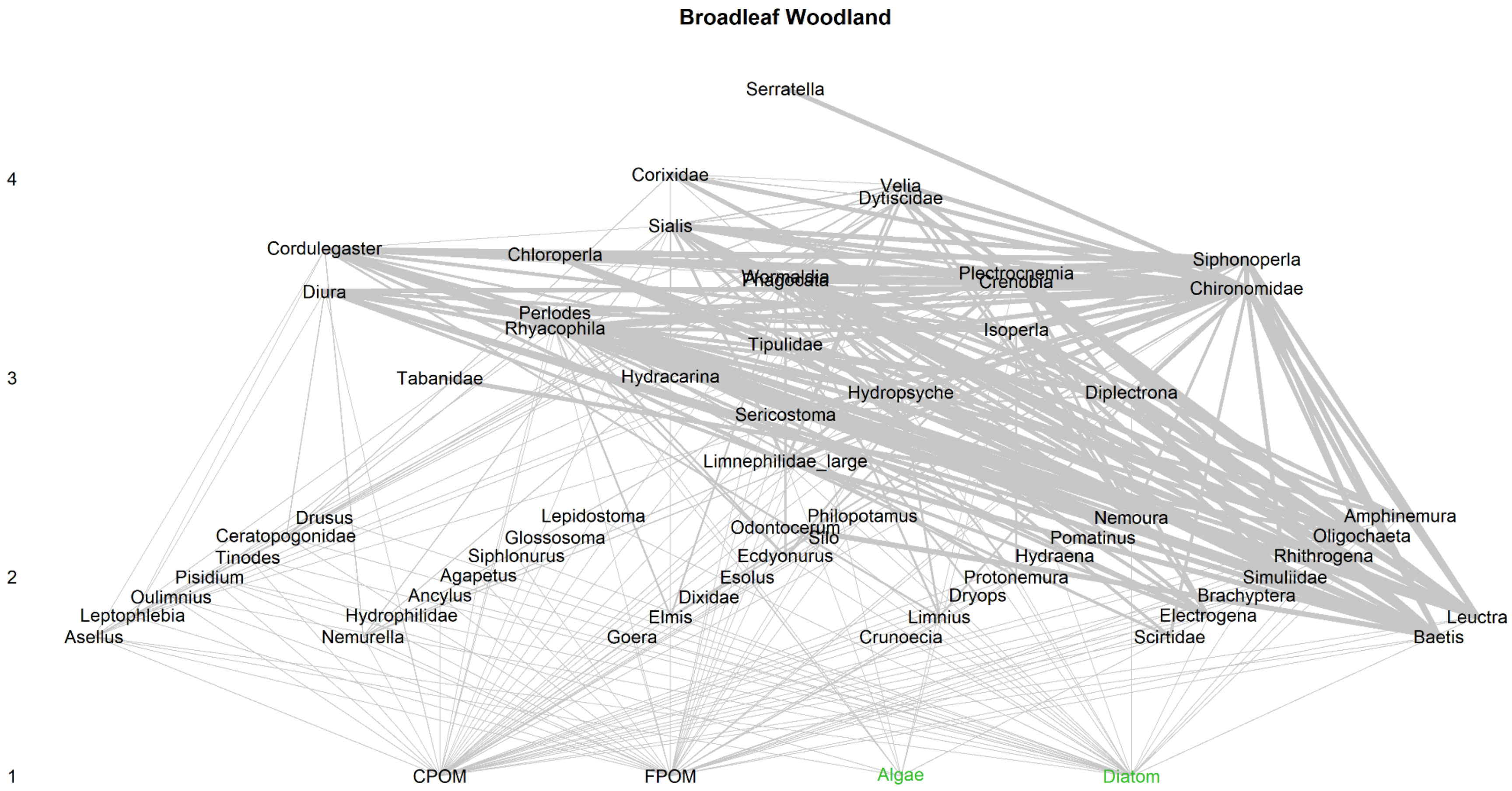
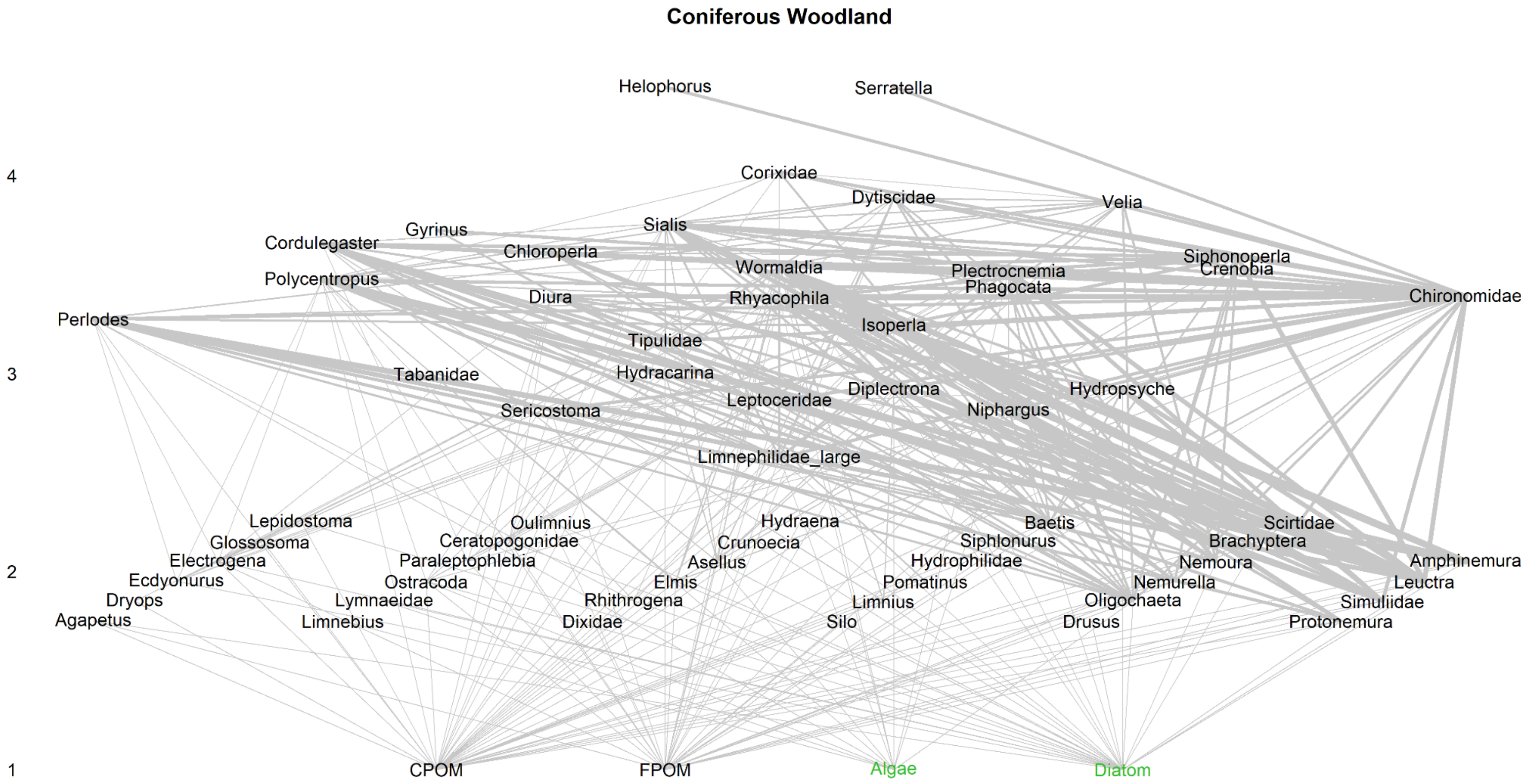


Figure A.4 *Aggregate prey-averaged food web for broadleaf woodland streams. Link width indicates mean abundance of resource node.*



Coniferous Woodland

Figure A.5 Aggregate prey-averaged food web for coniferous woodland streams. Link width indicates mean abundance of resource node.

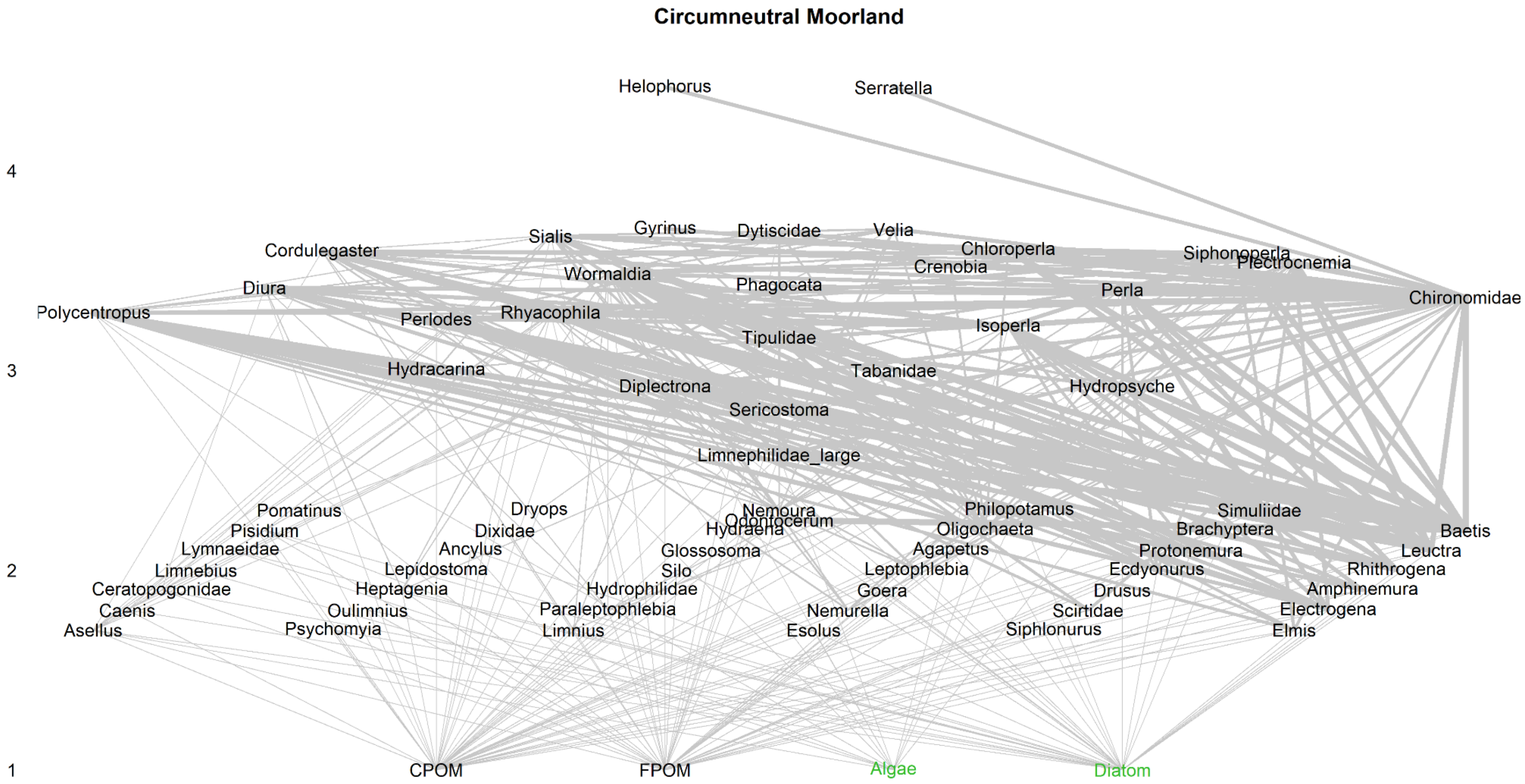

Circumneutral Moorland

Figure A.6 Aggregate prey-averaged food web for circumneutral moorland streams. Link width indicates mean abundance of resource node.

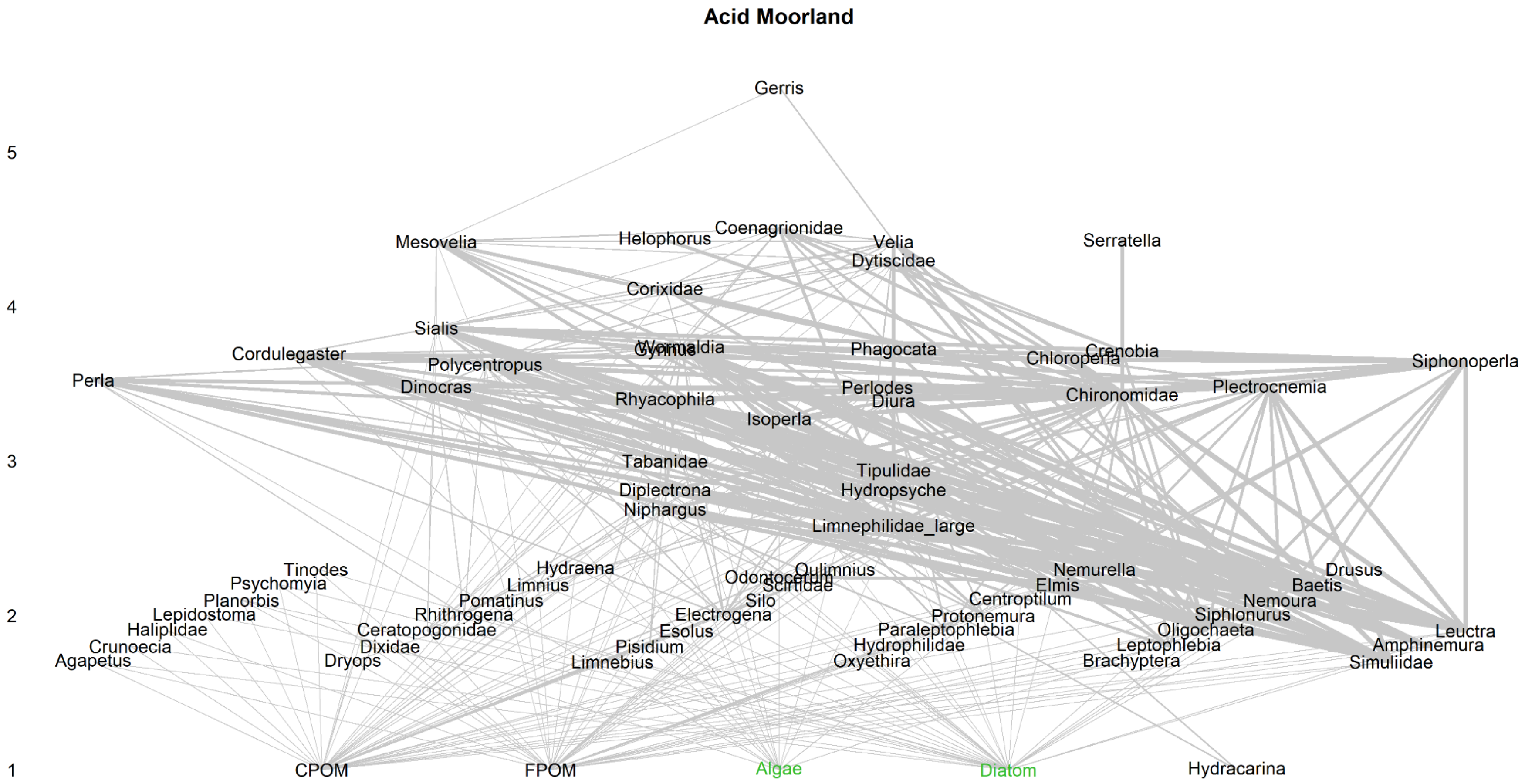


Figure A.7 Aggregate prey-averaged food web for acid moorland streams. Link width indicates mean abundance of resource node.

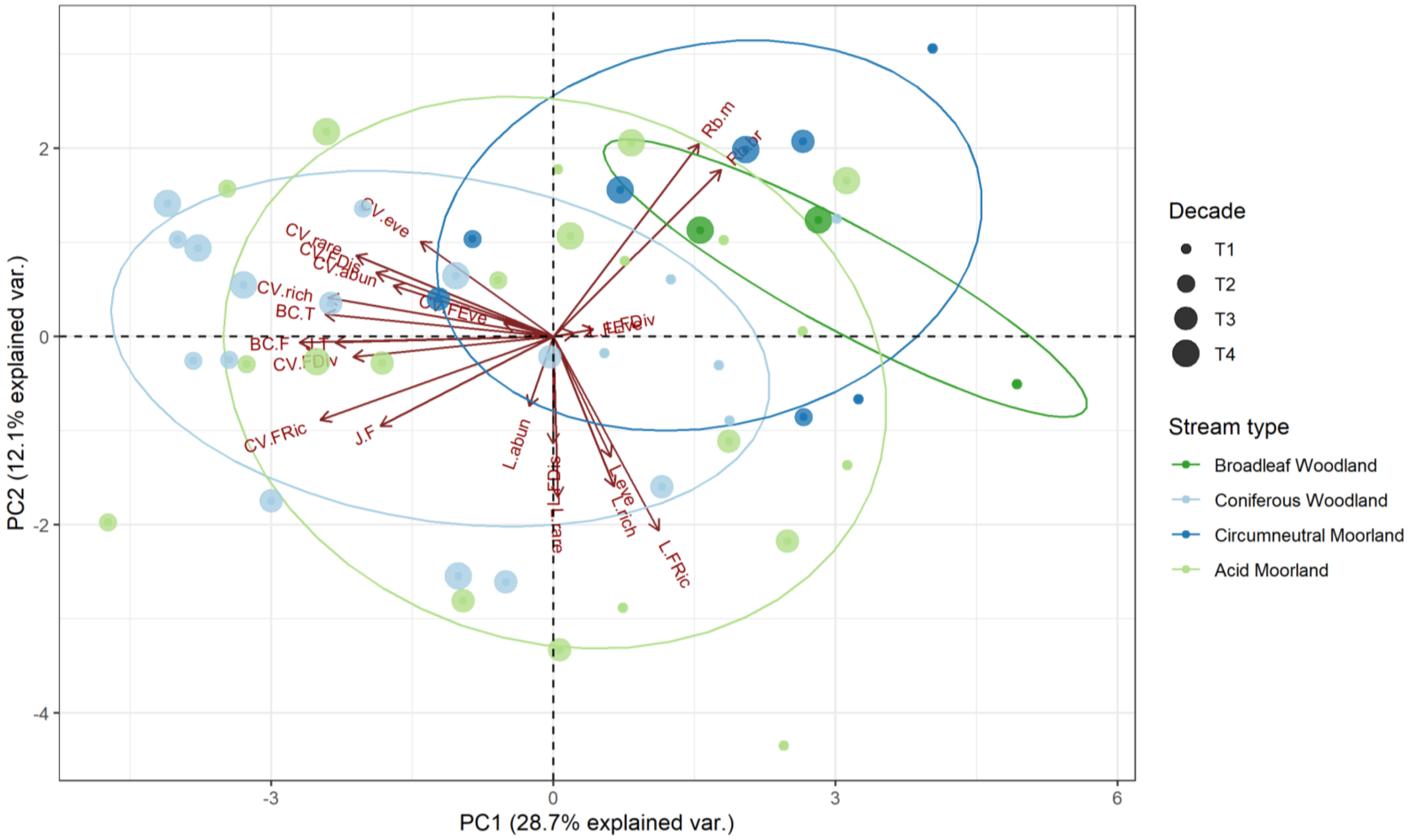


Figure A.8 Ordination of the first two components of all measured aspects of community stability for each decade and stream. 95% ellipses are shown for each stream type. Direction of arrows indicates decreasing stability. L = λ.

Table A.5 *Variable loadings for the first two principal components of principal component analysis within groups (acid and neutral streams, and each decade). PCAs were conducted for taxonomic and functional stability separately. Darker shades highlight larger loadings. Dimensions with eigenvalues >1 are reported and the % explained variation for each PC.*

pH group	Stability variable	Taxonomic			Functional		
		Dim	PC1	PC2	Dim	PC1	PC2
Acid		2	*45%*	*25%*	2	*48%*	*22%*
	BC		0.62	-0.03		0.46	0.30
	J		0.60	-0.19		0.53	-0.14
	CV		0.45	0.32		0.56	0.05
	λ		-0.13	-0.73		-0.09	-0.85
	Rb		-0.19	0.57		-0.42	0.41
Neutral		2	*62%*	*24%*	1	*56%*	*19%*
	BC		0.54	-0.13		0.55	-0.17
	J		0.49	-0.29		0.45	0.34
	CV		0.49	0.29		0.47	0.43
	λ		-0.05	0.87		-0.24	0.81
	Rb		-0.47	-0.25		-0.46	0.14

Decade	Stability variable	Taxonomic			Functional		
		Dim	PC1	PC2	Dim	PC1	PC2
T1		2	*52%*	*24%*	2	*48%*	*23%*
	BC		0.60	0.10		0.49	-0.44
	J		0.48	-0.03		0.20	-0.10
	CV		0.47	0.37		0.53	0.41
	λ		0.08	-0.86		-0.44	-0.60
	Rb		-0.43	0.35		-0.49	0.51
T2		2	*43%*	*39%*	1	*62%*	*20%*
	BC		0.52	-0.42		0.46	-0.17
	J		0.58	-0.34		0.49	-0.21
	CV		-0.42	-0.45		0.54	0.06
	λ		0.46	0.33		-0.17	-0.96
	Rb		0.11	0.63		-0.48	0.03
T3		2	*44%*	*31%*	2	*44%*	*27%*
	BC		0.62	-0.11		0.55	-0.23
	J		0.63	-0.01		0.38	-0.62
	CV		0.33	-0.58		0.58	0.14
	λ		0.26	0.48		0.15	0.58
	Rb		-0.22	-0.65		-0.43	-0.45
T4		2	*52%*	*27%*	2	*57%*	*22%*
	BC		-0.55	0.23		0.49	-0.34
	J		-0.55	0.16		0.38	0.51
	CV		-0.46	-0.35		0.53	0.02
	λ		0.23	-0.67		0.35	-0.67
	Rb		0.36	0.59		-0.46	-0.43