Stream ecosystem resilience following extreme high-frequency summer floods in Glacier Bay, Alaska

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Submitted in accordance with

the requirements for the degree of

Doctor of Philosophy

University of Leeds

School of Geography

August 2019

The candidate confirms that the work submitted is his own and that appropriate credit has been given where reference has been made to the work of others.

Acknowledgements

I would like to acknowledge the University of Leeds for financial support of my position, as well as water@Leeds, British Society for Geomorphology and the Staffordshire Educational Endowment Fund for support of fieldwork.

The National Park Service in Glacier Bay National Park are thanked for their logistic support. In particular, thanks are offered to Todd Bruno Captain of the mv Capelin, Danny Dallas and Bruce McDonough without whom my fieldwork would have been impossible. Equally thank you to my field assistants George and Sophie.

Thank you to my supervisors Prof Lee Brown, Prof Alexander Milner, Dr Megan Klaar and Dr Jonathan Carrivick for their support, guidance, company in the field and access to data.

I offer a thanks to my friends and particularly my family, who have supported and challenged me for as long as I can remember. Finally, thanks to Kelly the greatest finding I made in Glacier Bay.

This research has been carried out by a team which has included Prof Alexander Milner, Dr Megan Klaar, Dr Svein Sønderland, Dr Leonie Clitherow and a number of MSc and BSc students. My own contributions, fully and explicitly indicated in this thesis, have been all data analyses included in research chapters, data and sample collection in the field during 2016 and 2017 and subsequent laboratory analyses of samples. I am responsible for the writing of this thesis. The other members of the group and their contributions have been as follows:

Prof Alexander Milner – establishment of long-term monitoring at all streams studied in this thesis and the collection of invertebrate community, juvenile salmon community and geomorphological (cross sections) data up to 2015 utilised throughout this thesis.

Dr Megan Klaar – collection of in-depth hydrological and geomorphological data from 2007 to 2015 central to the analyses in Chapter 3 but also utilised in Chapters 2, 5 and 6.

Dr Svein Sønderland – collection of pre-flood juvenile salmon community and dietary data utilised in Chapter 5.

Dr Leonie Clitherow – collection of juvenile salmon community and dietary data during 2014 utilised in Chapter 5.

Abstract

The frequency and magnitude of extreme hydrological disturbance events are increasing under climate change in all regions of the world. These disturbances act as significant drivers of change in ecosystems. This research sought to explore how disturbances, in particular high-frequency flooding, directly and indirectly effect stream ecosystems. Further, it sought to consider the resilience of ecological communities following the floods. High-frequency floods significantly altered ecosystems at four streams of varying geomorphological complexities, driving homogenisation of benthic macroinvertebrate community composition both within and between streams, predominantly through the processes of community reassembly. Juvenile salmon community size structure, condition and trophic linkages were significantly altered by the floods leading to a decoupling of terrestrial resources and an increasing reliance upon the selection of Chironomidae prey post-flood. The floods drove a decoupling of metrics of community stability with an increasing role of invasions observed during community reassembly. This thesis further demonstrated the capacity of multiple and linked disturbance events to sequentially degrade the resilience and decouple the metrics of stability in ecosystems. Finally, the importance of more explicitly exploring the processes which govern biological response to disturbance is highlighted. A novel conceptual perturbation pathway approach is proposed, which enables intermediary processes, which govern biological response, to be more easily and consistently defined and thus incorporated into our theoretical understanding of disturbance in ecology.

Contents

Abbreviations

GBNP – Glacier Bay National Park and Preserve

WPC – Wolf Point Creek

IVS – Ice Valley Stream

BBS – Berg Bay South Stream

RPC – Rush Point Creek

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1. Introduction

1.1 Background and context

Floods represent an important aspect of natural river flow regimes (Poff et al., 1997) and act as significant drivers of biotic communities (Junk et al., 1989, Takata et al., 2017). Anthropogenically driven climate warming, alongside increasingly extreme and unpredictable weather patterns, is altering the frequency, magnitude and distribution of precipitation and in particular rainfall (Trenberth, 2011). One consequence of these changes is the increasing frequency and magnitude of extreme floods (Donat et al., 2016), with North America experiencing a major increase in the frequency of extreme floods (Wouter et al., 2017). Extreme floods are defined as flood events driven by rare or atypical weather and climate events (Ledger and Milner, 2015). This definition is prefered to an exceedance level based description because changes in the frequency of extreme floods will make events currently considered extreme to be more regular features of flow regimes in the future.

Changes to the occurrence of extreme floods are expected to influence geomorphological and ecological processes which govern the stability of stream ecosystems (Poff, 1997). The high geological and terrestrial variability observed within low order (1-3) stream catchments provides a broad range of habitats and thus varied available niche space for freshwater taxa, leading to high beta-diversity across low order streams. Their upstream position within larger catchments makes them important to downstream ecosystem processes and function through directional transfers of nutrients and energy (Hill et al., 2014). Low order streams have varied geomorphological complexities and catchment characteristics, which could affect their resilience to floods. These characteristics alongside observed responsiveness of low order streams to extreme hydrological events (Špitalar et al., 2014) makes them ideal locations for the exploration of the resilience of freshwater ecosystems to extreme floods.

To advance general ecological theory exploring ecosystem processes in isolation from confounding factors is important. However, the extensive influence of humankind globally limits opportunities to do so, due to the presence of other disturbances and anthropogenic activities across most of the globe. Protected wilderness regions represent perhaps the best areas in which to study natural processes in isolation from anthropogenic influence. Advancements in ecological theory can then be applied to better understand the highly complex and interactive processes which govern ecological response and resilience to disturbance in anthropogenically influenced systems.

Hydrological disturbance, including floods, is a major driver of stream ecosystem and community structure (Poff, 1992, Lake, 2000, Fisher and Grimm, 1991). The magnitude, duration, frequency, timing and rate of change have all been identified as important variables in controlling the geomorphological and ecological effect of floods (Costa and O'Connor, 1995, Poff et al., 1997). Floods can have direct ecological effects such as mortality and displacement of individuals (Roghair et al., 2002), and indirect effects such as: the disruption of trophic relationships through the depletion of consumers and/or producers (Grimm and Fisher, 1989, Scrimgeour and Winterbourn, 1989); the destruction and degradation of habitat (Roghair et al., 2002, Milner et al., 2018, Chapter 3) and the disruption of meta-population dynamics (Urban, 2004). Despite the recognition of a range of potential indirect effects of floods in controlling biotic responses, resilience and the processes of community reassembly, these important research areas have rarely been addressed in the contemporary literature. A broad range of potential variables can govern ecosystem or community reassembly, and thus resilience, including: available niche space (Brown and Milner, 2012, Milner et al., 2008) the complexities of lifecycles that utilise both aquatic and terrestrial biomes (Lancaster and Downes, 2010); the extent of isolation of a disturbed system from colonising populations (meta-population processes; Brown and Swan, 2010); the capacity of potential colonisers to migrate to the disturbed systems (Brown et al., 2018) and priority-effects of the order in which species colonise a system (Little and Altermatt, 2018).

There is an increasing likelihood of hydrological disturbance events occurring in sequences and/or co-occurring with other disturbances (termed compound stressor events) under future climate projections (Wilson et al., 2006). Given our relatively poor theoretical grounding in the intermediary processes which govern ecological response to disturbance, these cases of multiple disturbances may lead to unpredictable biological responses (Buma, 2015). In addition, multiple disturbances could drive synergistic and non-linear impacts to ecosystems (Eklöf et al., 2009). One recognised aspect of multiple disturbances is the capacity of previous or already established disturbances to imprint ongoing legacy effects in ecosystems (Seidl et al., 2014), which persist beyond the cessation of the original disturbance (Foster et al., 1998). Such legacy effects can alter how ecosystems reassemble following disturbances (Ledger et al., 2006) and their subsequent response to future disturbances (Buma and Wessman, 2011, Stanley et al., 2010).

The extent to which an ecosystem responds to a disturbance is associated with its stability. Ecological resilience (Harrison, 1979, Robinson, 2012b, Downing and Leibold, 2010, Buma and Wessman, 2011, Knapp et al., 2001, Vieira et al., 2004, Ibelings et al., 2007, Milner et al., 2018), a metric of ecological stability, can be utilised to explore the response of ecosystems and communities to disturbances. Resilience is defined using the approach of Holling (1973), which has been applied in both ecology (Milner et al., 2018) and policy (Hodgson et al., 2015) literature. Under the Holling model, resilience consists of two components, (1) resistance - the capacity of biota to initially persist at a site over the duration of a disturbance and (2) the ability to re-establish to pre-disturbance levels of abundance and/or diversity through reproduction of resistant individuals and recolonization through time post-disturbance. This definition is inherently multidimensional, capturing both the capacity of a biological unit to tolerate a disturbance and subsequently recover from it. As such it is a valuable metric to be explored in the study of disturbance, alongside other classic measures commonly applied in ecology such as temporal and spatial variability in density and species richness (Pimm, 1984).

Ecological stability is a concept that captures the overall dynamics of an ecosystem and importantly the ecological response of a system to disturbances (Odum, 1953, May, 1972, Pimm, 1984). Ecological stability can be considered an emergent property of ecosystems and communities (Saint-Béat et al., 2015), and a broad range of metrics have been created through which it can be explored. Stability is a complex concept yet historically it has been explored using a single metric of stability at a time (e.g. Lyons and Schwartz, 2001, Heino et al., 2004, Murry and Farrell, 2014). Donohue et al. (2013) demonstrated the limitations of such approaches and established the need for multidimensional analyses in their exploration of ecological stability. In their study of tidal communities, it was shown that ecological stability varies markedly depending upon the occurrence of disturbances (Donohue et al., 2013, Hillebrand et al., 2018) which necessitates the application of a range of stability measures, to fully comprehend how and why an ecosystem responds to disturbance in a given way. Only recently has a multidimensional approach received attention in experimental and modelling studies (Hillebrand et al., 2018, Radchuk et al., 2019, Yang et al., 2019). However, to date there have been no attempts to apply this concept to empirical data sets from the natural environment.

Geomorphological response following floods can vary depending upon pre-flood conditions including channel form, sediment availability and extent of channel modification. In some cases, channels are homogenised and deepened by floods (Magilligan et al., 2015), whilst other examples report channels becoming widened (Friedman and Lee, 2002, Pasternack and Wyrick, 2017) and that, through the recruitment of roughness elements, channel complexity increases (Steeb et al., 2017). The geomorphological response to extreme floods can persist as a legacy effect, known as post-flood relaxation, and can result in ongoing geomorphological change driven by increased sediment availability and subsequent variation in flow (Milan, 2012). This persistent channel instability could have implications for biotic response/recovery post-flood and may alter ecosystems resilience however to date there has been little research directly exploring these processes.

Ecological resilience to extreme floods varies between individual events (e.g. Mundahl and Hunt, 2011, Milner et al., 2013) and between taxa/communities (Scrimgeour and Winterbourn, 1989, Ming-Chih and Mei-Hwa, 2012, Roghair et al., 2002, Schwendel et al., 2010). The timing (George et al., 2015) and magnitude (Ming-Chih and Mei-Hwa, 2012) of a flood in controlling its direct ecological effects are recognised as important. More recently, the indirect effects of floods have begun to be explored more explicitly in the literature, with studies assessing changes to resource utilisation (Larson et al., 2018), habitat availability (Carlson et al., 2016) and trait-based approaches (Ming-Chih and Mei-Hwa, 2012, Bae and Park, 2016 , Poff et al., 2018).

The geomorphological complexity of a stream has been associated with conferring ecological resilience to communities through for example increased availability of refugia during extreme flows (Pearsons et al., 1992, O'Neill and Thorp, 2011). Enhancing such complexity could therefore be considered as an approach to enhancing the resilience of river and stream ecosystems by freshwater resource managers. However, the capacity of complexity to confer resilience to floods of different forms has not been explored in the literature, with the majority of studies addressing complexity in the context of individual high-magnitude floods. For instance, Szczerkowska-Majchrzak et al. (2014) demonstrated increased resilience in winter emerging Chironomidae to extreme high-magnitude floods in more complex river channels but did not address other magnitudes or frequencies of flood events.

Whilst there is abundant literature addressing the response of stream ecosystems to extreme floods, the majority of papers address high-magnitude floods (> 1 in 50 year peak flow event). However, extreme floods can take a range of forms and recently the capacity of high-frequency floods to drive ecological change have been reported by Milner et al. (2018) for one heavily studied stream in Glacier Bay National Park and Preserve (GBNP), a wilderness area in southeast Alaska. GBNP is recognised as an important site for the study of primary succession (Cooper, 1923, Chapin et al., 1994, Fastie, 1995, Buma et al., 2017) and as such a number of extensive and highly relevant stream datasets are available in which to study ecological response to disturbance events.

1.2 Overall thesis aim

The aim of this research was to address the resilience of stream ecosystems to high-frequency summer floods across a gradient of catchments with varied geomorphological and habitat complexities in an environment free from additional anthropogenic stressors. This was addressed through five specific objectives, from which specific hypotheses were developed within each research chapter.

1.3 Objectives

- Identify the capacity of high-frequency summer floods to drive hydrogeomorphological change in stream channels and identify the implications of such change for habitat heterogeneity post-flood.
- Explore the resilience of stream benthic macroinvertebrate communities to extreme high-frequency floods and evaluate the processes governing their response.
- Identify the implications of extreme high-frequency summer floods for juvenile salmon communities, size structure and available niche space.
- Compare the impacts of high-magnitude versus high-frequency floods on stream benthic macroinvertebrate community composition using a long-term data set and explore the potential for legacy effects of an initial extreme winter flood, which could alter community response to subsequent high-frequency summer floods.
- Consider the dimensionality and drivers of changing ecological stability during community reassembly process following high-magnitude and high-frequency floods.

1.4 Thesis structure

This thesis takes a multidisciplinary approach to highlight the complex intermediary processes which govern biological response and thus system resilience to extreme hydrological disturbances, linked to alterations of the available niche space via changing geomorphology and resource availability (Figure 1.1). Past research in the GBNP study region was reviewed and evidence of the extreme high-frequency flood occurrence, the main focus of this thesis, is presented (**Chapter 2**). Analyses in the main research **Chapters 3 to 7** (or a subset thereof - **Chapters 6 and 7**) focuses on four streams of varying geomorphological complexity and successional stage. It is hypothesised that these streams could respond to high-flow events differently depending upon the pre-flood availability of refugia, stability of channels, community compositions and how channels respond through time post-flood.

Chapter 3 explores the geomorphological and hydrological response of the study streams to the high-frequency floods and ongoing change post-flood. These analyses address response at two spatial scales, segment (10^3m) and Channel Geomorphological Units (CGU; 10^1 m), and reveal differences in the geomorphological and habitat resilience of systems. The chapter highlights significant post-flood instability in channel position at all streams, whilst a divergent habitat response between lower and higher complexity streams is reported and linked to stream form and availability of instream wood pre-flood. This chapter suggest that high-frequency floods can act to boost paraglacial processes, through increased sediment availability, that have slowed as catchments become stabilised by vegetation and glacier loss. It thus demonstrates that floods can represent an important driver of continued geomorphological and habitat development.

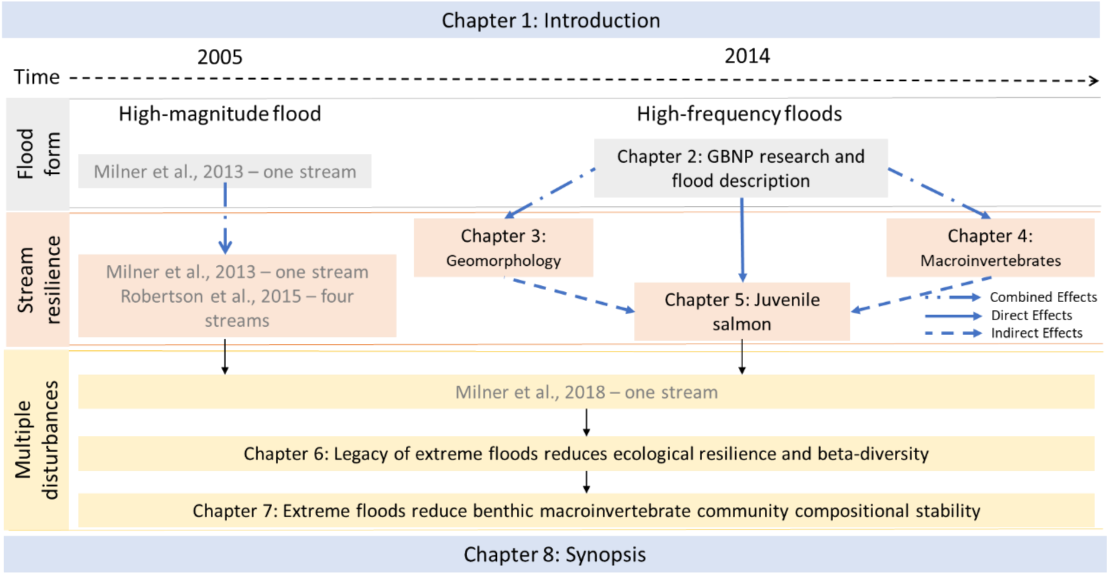


Figure 1.1. Schematic depiction of the thesis structure noting how it builds on published literature for the study area and flood events that were studied. Colours identify chapters or additional literatures predominant theme: theoretical – blue, flood form – grey, stream resilience – orange and multiple disturbances – yellow.

Chapter 4 explores the response of benthic macroinvertebrate communities to the floods and demonstrates low ecological resilience across streams irrespective of differences in pre-flood community composition. Ongoing post-flood convergence of community composition both within and between streams is linked to the processes of community reassembly, and the changing availability of niche space and post-flood dispersal patterns, rather than direct effects of the floods.

The response of juvenile salmon communities as well as altered trophic interactions are explored in **Chapter 5**, in the context of changing niche space (**Chapters 3 and 4**) and time since the last extreme flood. This chapter reports significant and persistent decreases in fish condition following the floods. Further, it identifies the capacity of floods to significantly alter trophic interactions and terrestrial to aquatic subsidies. Low freshwater prey availability and shorter times since a flood event are associated with communities dominated by smaller (0+) individuals.

The cumulative impact of an extreme high-magnitude flood in 2005 and the subsequent high-frequency floods (2014) are considered in **Chapter 6**. The chapter identifies a flood legacy in the ecological community, which has persisted for almost a decade. In addition, **Chapter 6** demonstrates that both extreme flood events drove convergence of community composition between and within streams. It is proposed that the contrasting initial responses of taxa richness and density between the two floods are associated with differences in flood form. Whilst the low resilience of communities to the high-frequency floods, may suggest that past extreme flood events do not act as powerful environmental filters and do not increase resilience of subsequent communities.

The multidimensionality of ecological stability is explored during pre- and post-flood time periods at the most heavily studied stream, Wolf Point Creek (WPC), using a 17-year data set (**Chapter 7)**. This chapter considers how the relationships between metrics vary following each flood event and demonstrates an increased coupling of invasions to other metrics of stability during community reassembly. This coupling occurred despite increased dimensionality of ecological stability. Increased dimensionality suggests significant alterations to the processes governing community (re)assembly following each flood, which then persist temporally.

An overall final synthesis of the research within the context of the literature is provided in **Chapter 8**. Further, it provides a novel conceptual approach to explore ecosystem resilience to extreme floods and highlights the capacity of extreme floods to drive change in communities at the local and regional scales. Important areas for future research are discussed.

1.5 References

BAE, M.-J. & PARK, Y.-S. 2016 Responses of the functional diversity of benthic macroinvertebrates to floods and drought at small streams with different flow permanence. *Inland Waters,* 6**,** 461-475.

BROWN, B. L. & SWAN, C. M. 2010. Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology,* 79**,** 571-580.

BROWN, L. E., KHAMIS, K., WILKES, M., BLAEN, P., BRITTAIN, J. E., CARRIVICK, J. L., FELL, S., FRIBERG, N., FÜREDER, L., GISLASON, G. M., HAINIE, S., HANNAH, D. M., JAMES, W. H. M., LENCIONI, V., OLAFSSON, J. S., ROBINSON, C. T., SALTVEIT, S. J., THOMPSON, C. & MILNER, A. M. 2018. Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nature Ecology & Evolution,* 2**,** 325-333.

BROWN, L. E. & MILNER, A. M. 2012. Rapid loss of glacial ice reveals stream community assembly processes. *Global Change Biology,* 18**,** 2195-2204.

BUMA, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere,* 6**,** art70.

BUMA, B., BISBING, S., KRAPEK, J. & WRIGHT, G. 2017. A foundation of ecology rediscovered: 100 years of succession on the William S. Cooper plots in Glacier Bay, Alaska. *Ecology,* 98**,** 1513-1523.

BUMA, B. & WESSMAN, C. A. 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere,* 2**,** art64.

CARLSON, A. K., FINCEL, M. J., LONGHENRY, C. M. & GRAEB, B. D. S. 2016. Effects of historic flooding on fishes and aquatic habitats in a Missouri River delta. *Journal of Freshwater Ecology,* 31**,** 271-288.

CHAPIN, F. S., WALKER, L. R., FASTIE, C. L. & SHARMAN, L. C. 1994. Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska. *Ecological Monographs,* 64**,** 149-175.

COOPER, W. S. 1923. The Recent Ecological History of Glacier Bay, Alaska: The Present Vegetation Cycle. *Ecology,* 4**,** 223-246.

COSTA, J. E. & O'CONNOR, J. E. 1995. Geomorphically Effective Floods. *Natural and Anthropogenic Influences in Fluvial Geomorphology.* American Geophysical Union.

DONAT, M. G., LOWRY, A. L., ALEXANDER, L. V., O'GORMAN, P. A. & MAHER, N. 2016. More extreme precipitation in the world's dry and wet regions. *Nature Climate Change,* 6**,** 508.

DONOHUE, I., PETCHEY, O. L., MONTOYA, J. M., JACKSON, A. L., MCNALLY, L., VIANA, M., HEALY, K., LURGI, M., O'CONNOR, N. E. & EMMERSON, M. C. 2013. On the dimensionality of ecological stability. *Ecology Letters,* 16**,** 421-429.

DOWNING, A. L. & LEIBOLD, M. A. 2010. Species richness facilitates ecosystem resilience in aquatic food webs. *Freshwater Biology,* 55**,** 2123-2137.

EKLÖF, J. S., MCMAHON, K. & LAVERY, P. S. 2009. Effects of multiple disturbances in seagrass meadows: shading decreases resilience to grazing. *Marine and Freshwater Research,* 60**,** 1317-1327.

FASTIE, C. L. 1995. Causes and Ecosystem Consequences of Multiple Pathways of Primary Succession at Glacier Bay, Alaska. *Ecology,* 76**,** 1899-1916.

FISHER, S. G. & GRIMM, N. B. 1991. Streams and Disturbance: Are Cross-Ecosystem Comparisons Useful? *In:* COLE, J., LOVETT, G. & FINDLAY, S. (eds.) *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories.* New York, NY: Springer New York.

FOSTER, D. R., KNIGHT, D. H. & FRANKLIN, J. F. 1998. Landscape Patterns and Legacies Resulting from Large, Infrequent Forest Disturbances. *Ecosystems,* 1**,** 497-510.

FRIEDMAN, J. M. & LEE, V. J. 2002. EXTREME FLOODS, CHANNEL CHANGE, AND RIPARIAN FORESTS ALONG EPHEMERAL STREAMS. *Ecological Monographs,* 72**,** 409-425.

GEORGE, S. D., BALDIGO, B. P., SMITH, A. J. & ROBINSON, G. R. 2015. Effects of extreme floods on trout populations and fish communities in a Catskill Mountain river. *Freshwater Biology,* 60**,** 2511-2522.

GRIMM, N. B. & FISHER, S. G. 1989. Stability of Periphyton and Macroinvertebrates to Disturbance by Flash Floods in a Desert Stream. *Journal of the North American Benthological Society,* 8**,** 293-307.

HARRISON, G. W. 1979. Stability under Environmental Stress: Resistance, Resilience, Persistence, and Variability. *The American Naturalist,* 113**,** 659-669.

HEINO, J., LOUHI, P. & MUOTKA, T. 2004. Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure. *Freshwater Biology,* 49**,** 1230-1239.

HILL, B. H., KOLKA, R. K., MCCORMICK, F. H. & STARRY, M. A. 2014. A synoptic survey of ecosystem services from headwater catchments in the United States. *Ecosystem Services,* 7**,** 106-115.

HILLEBRAND, H., LANGENHEDER, S., LEBRET, K., LINDSTRÖM, E., ÖSTMAN, Ö. & STRIEBEL, M. 2018. Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters,* 21**,** 21-30.

HODGSON, D., MCDONALD, J. L. & HOSKEN, D. J. 2015. What do you mean, 'resilient'? *Trends in Ecology & Evolution,* 30**,** 503-506.

HOLLING, C. S. 1973. Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics,* 4**,** 1-23.

IBELINGS, B. W., PORTIELJE, R., LAMMENS, E. H. R. R., NOORDHUIS, R., VAN DEN BERG, M. S., JOOSSE, W. & MEIJER, M. L. 2007. Resilience of Alternative Stable States during the Recovery of Shallow Lakes from Eutrophication: Lake Veluwe as a Case Study. *Ecosystems,* 10**,** 4-16.

JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E. 1989. The Flood Pulse Concept in River-Floodplain Systems. *Canadian Special Publication of Fisheries and Aquatic Science,* 106**,** 110 - 127.

KNAPP, R. A., MATTHEWS, K. R. & SARNELLE, O. 2001. RESISTANCE AND RESILIENCE OF ALPINE LAKE FAUNA TO FISH INTRODUCTIONS. *Ecological Monographs,* 71**,** 401-421.

LAKE, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society,* 19**,** 573-592.

LANCASTER, J. & DOWNES, B. J. 2010. Linking the hydraulic world of individual organisms to ecological processes: Putting ecology into ecohydraulics. *River Research and Applications,* 26**,** 385-403.

LARSON, E. I., POFF, N. L., ATKINSON, C. L. & FLECKER, A. S. 2018. Extreme flooding decreases stream consumer autochthony by increasing detrital resource availability. *Freshwater Biology,* 0.

LEDGER, M., M L HARRIS, R., MILNER, A. & ARMITAGE, P. 2006. *Disturbance, biological legacies and community development in stream mesocosms*.

LEDGER, M. E. & MILNER, A. M. 2015. Extreme events in running waters. *Freshwater Biology,* 60**,** 2455-2460.

LITTLE, C. J. & ALTERMATT, F. 2018. Do priority effects outweigh environmental filtering in a guild of dominant freshwater macroinvertebrates? *Proceedings of the Royal Society B: Biological Sciences,* 285**,** 20180205.

LYONS, K. G. & SCHWARTZ, M. W. 2001. Rare species loss alters ecosystem function – invasion resistance. *Ecology Letters,* 4**,** 358-365.

MAGILLIGAN, F. J., BURAAS, E. M. & RENSHAW, C. E. 2015. The efficacy of stream power and flow duration on geomorphic responses to catastrophic flooding. *Geomorphology,* 228**,** 175-188.

MAY, R. M. 1972. Will a Large Complex System be Stable? *Nature,* 238**,** 413-414.

MILAN, D. J. 2012. Geomorphic impact and system recovery following an extreme flood in an upland stream: Thinhope Burn, northern England, UK. *Geomorphology,* 138**,** 319-328.

MILNER, A. M., PICKEN, J. L., KLAAR, M. J., ROBERTSON, A. L., CLITHEROW, L. R., EAGLE, L. & BROWN, L. E. 2018. River ecosystem resilience to extreme flood events. *Ecology and Evolution,* 0.

MILNER, A. M., ROBERTSON, A. L., MCDERMOTT, M. J., KLAAR, M. J. & BROWN, L. E. 2013. Major flood disturbance alters river ecosystem evolution. *Nature Climate Change,* 3**,** 137-141.

MILNER, A. M., ROBERTSON, A. L., MONAGHAN, K. A., VEAL, A. J. & FLORY, E. A. 2008. Colonization and development of an Alaskan stream community over 28 years. *Frontiers in Ecology and the Environment,* 6**,** 413-419.

MING-CHIH, C. & MEI-HWA, K. 2012. Application of r/K selection to macroinvertebrate responses to extreme floods. *Ecological Entomology,* 37**,** 145-154.

MUNDAHL, N. D. & HUNT, A. M. 2011. Recovery of stream invertebrates after catastrophic flooding in southeastern Minnesota, USA. *Journal of Freshwater Ecology,* 26**,** 445-457.

MURRY, B. A. & FARRELL, J. M. 2014. Resistance of the size structure of the fish community to ecological perturbations in a large river ecosystem. *Freshwater Biology,* 59**,** 155-167.

O'NEILL, B. J. & THORP, J. H. 2011. Flow refugia for the zoobenthos of a sand-bed river: the role of physical-habitat complexity. *Journal of the North American Benthological Society,* 30**,** 546-558.

ODUM, E. 1953. *Fundamentals of Ecology,* Philadelphia, PA, Saunders.

PASTERNACK, G. B. & WYRICK, J. R. 2017. Flood-driven topographic changes in a gravel-cobble river over segment, reach, and morphological unit scales. *Earth Surface Processes and Landforms,* 42**,** 487-502.

PEARSONS, T. N., LI, H. W. & LAMBERTI, G. A. 1992. Influence of Habitat Complexity on Resistance to Flooding and Resilience of Stream Fish Assemblages. *Transactions of the American Fisheries Society,* 121**,** 427-436.

PIMM, S. L. 1984. The complexity and stability of ecosystems. *Nature,* 307**,** 321-326.

POFF, N. L. 1992. Why Disturbances Can Be Predictable: A Perspective on the Definition of Disturbance in Streams. *Journal of the North American Benthological Society,* 11**,** 86-92.

POFF, N. L., ALLAN, J. D., BAIN, M. B., KARR, J. R., PRESTEGAARD, K. L., RICHTER, B. D., SPARKS, R. E. & STROMBERG, J. C. 1997. The Natural Flow Regime. *BioScience,* 47**,** 769-784.

POFF, N. L., LARSON, E. I., SALERNO, P. E., MORTON, S. G., KONDRATIEFF, B. C., FLECKER, A. S., ZAMUDIO, K. R. & FUNK, W. C. 2018. Extreme streams: species persistence and genomic change in montane insect populations across a flooding gradient. *Ecology Letters,* 21**,** 525-535.

RADCHUK, V., LAENDER, F. D., CABRAL, J. S., BOULANGEAT, I., CRAWFORD, M., BOHN, F., RAEDT, J. D., SCHERER, C., SVENNING, J.-C., THONICKE, K., SCHURR, F. M., GRIMM, V. & KRAMER-SCHADT, S. 2019. The dimensionality of stability depends on disturbance type. *Ecology Letters,* 0.

ROBINSON, C. T. 2012. Long-term changes in community assembly, resistance, and resilience following experimental floods. *Ecological Applications,* 22**,** 1949-1961.

ROGHAIR, C. N., DOLLOFF, C. A. & UNDERWOOD, M. K. 2002. Response of a Brook Trout Population and Instream Habitat to a Catastrophic Flood and Debris Flow. *Transactions of the American Fisheries Society,* 131**,** 718-730.

SAINT-BÉAT, B., BAIRD, D., ASMUS, H., ASMUS, R., BACHER, C., PACELLA, S. R., JOHNSON, G. A., DAVID, V., VÉZINA, A. F. & NIQUIL, N. 2015. Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review. *Ecological Indicators,* 52**,** 458-471.

SCHWENDEL, A. C., FULLER, I. C. & DEATH, R. G. 2010. Morphological dynamics of upland headwater streams in the southern North Island of New Zealand. *New Zealand Geographer,* 66**,** 14-32.

SCRIMGEOUR, G. J. & WINTERBOURN, M. J. 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia,* 171**,** 33-44.

SEIDL, R., RAMMER, W. & SPIES, T. A. 2014. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. *Ecological Applications,* 24**,** 2063-2077.

ŠPITALAR, M., GOURLEY, J. J., LUTOFF, C., KIRSTETTER, P.-E., BRILLY, M. & CARR, N. 2014. Analysis of flash flood parameters and human impacts in the US from 2006 to 2012. *Journal of Hydrology,* 519**,** 863-870.

STANLEY, E. H., POWERS, S. M. & LOTTIG, N. R. 2010. The evolving legacy of disturbance in stream ecology: concepts, contributions, and coming challenges. *Journal of the North American Benthological Society,* 29**,** 67-83.

STEEB, N., RICKENMANN, D., BADOUX, A., RICKLI, C. & WALDNER, P. 2017. Large wood recruitment processes and transported volumes in Swiss mountain streams during the extreme flood of August 2005. *Geomorphology,* 279**,** 112-127.

TAKATA, L., SOMMER, T. R., LOUISE CONRAD, J. & SCHREIER, B. M. 2017. Rearing and migration of juvenile Chinook salmon (Oncorhynchus tshawytscha) in a large river floodplain. *Environmental Biology of Fishes,* 100**,** 1105-1120.

TRENBERTH, K. E. 2011. Changes in precipitation with climate change. *Climate Research,* 47**,** 123-138.

URBAN, M. C. 2004. Disturbance heterogeneity determines freshwater metacommunity structure *Ecology,* 85**,** 2971-2978.

VIEIRA, N. K. M., CLEMENTS , W. H., GUEVARA, L. S. & JACOBS, B. F. 2004. Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire. *Freshwater Biology,* 49**,** 1243-1259.

WILSON, S. K., GRAHAM, N. A. J., PRATCHETT, M. S., JONES, G. P. & POLUNIN, N. V. C. 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology,* 12**,** 2220-2234.

WOUTER, R. B., EMMA, E. A., JOSHUA, R. L., RALPH, T. & ROSS, A. W. 2017. Recent changes in extreme floods across multiple continents. *Environmental Research Letters,* 12**,** 114035.

YANG, Q., FOWLER, M. S., JACKSON, A. L. & DONOHUE, I. 2019. The predictability of ecological stability in a noisy world. *Nature Ecology & Evolution,* 3**,** 251-259.

2. Glacier Bay National Park and Preserve research: succession and disturbance

2.1 Introduction

Glacier Bay National Park and Preserve (GBNP), in southeast Alaska (58°10′–59°15′ N.; 135°15′–138°10′ W.), is dominated by a ‘Y’ shaped tidal fjord 150 km long and 20 km wide (. GBNP covers an area of 11,030 km^2 and has a maritime climate with average annual precipitation of 1400 mm. Since approximately 1700 a Neoglacial ice sheet, which covered large swathes of GBNP, has retreated northwards exposing the modern-day fjord and surrounding landscape.

The retreat of the Neoglacial ice sheet is one of the most rapid glacial retreats globally, up to 15 times greater than other tidewater glaciers (Field, 1947, Hall et al., 1995). Deglaciation timing has been accurately recorded through historical, dendrochronological, and geological data, with ground exposed following glacial retreat facilitating the re-establishment of complex and coupled physical and ecological processes associated with primary succession (Chapin et al., 1994, Milner et al., 2007). The region has been studied since pioneering vegetative work in the 1920s by WS Cooper who established long term monitoring plots (Cooper, 1923a, Cooper, 1923b, Cooper, 1923c). Since then studies of terrestrial development in the region have remained at the core of the terrestrial primary succession literature (Field, 1947, Ugolini, 1968, Fastie, 1995, Crocker and Major, 1955, Bormann and Sidle, 1990, Goldthwait et al., 1966, Lawrence et al., 1967, Reiners et al., 1971, Walker et al., 1993, Chapin et al., 1994, Boggs et al., 2010, Klaar et al., 2015).

2.1.1 Terrestrial succession

Succession incorporates the processes which control the accumulation and replacement of species within a community through time. Succession has a number of key recognised stages in GBNP (Chapin et al., 1994), beginning with the development of a crust of blue-green algae, lichens, liverworts, forbs, mountain avens (*Dryas drummondii)* and sparse willows (*Salix spp.*). Mountain avens is an effective fixer of nitrogen and as a result dominates early-stage successional landscapes, alongside individuals of willow and cottonwood (*Populus trichocarpa*). By 50 years ice free, Sitka alder (*Alnus crispa*) and willow are the dominant plant species and mountain avens is typically lost. After 100 years, Sitka spruce (*Picea sitchensis*) generally dominates with an increasing contribution of Western hemlock (*Tsuga heterophylla*) through time. This forest stage is, under the correct environmental conditions, followed by muskeg dominated by *Sphagnum* mosses (Noble et al., 1984). However, this process takes thousands of years and is therefore yet to be seen locally along GBNP's tidal fjord.

2.1.2 Aquatic succession

As in the terrestrial biome, aquatic systems demonstrate physical and ecological development that are fundamentally linked (Sidle and Milner, 1989, Milner and Gloyne-Phillips, 2005, Milner et al., 2000, Milner et al., 2007, Milner et al., 2008). Following glacial retreat, unstable geomorphological conditions dominate (Ballantyne, 2002, Eichel et al., 2016), as glacial foreland landscape elements and sediments are reworked. Under such conditions catchment sediment yields are higher than those typical of local non-glaciated catchments, as sediment deposited by receding glaciers is available in the short term (Ballantyne, 2002) and sediments have high bulk density and erosion rates (Crocker and Major, 1955, Klaar et al., 2015). These dynamic sediment conditions, low water temperature (associated with glacial inputs) alongside species' life history traits (principally dispersal capacity) act as direct factors in early ecological development of streams (Brown and Milner, 2012, Milner et al., 2008, Milner et al., 2011, Brown et al., 2018). These factors control ecosystem composition, with early colonising taxa that successfully establish showing tolerance of harsh environmental conditions and a high capacity for dispersal (Milner, 1987, Milner and Bailey, 1989, Flory and Milner, 2000, Brown and Milner, 2012, Milner et al., 2000, Milner et al., 2008, Milner et al., 2011). Typically, proglacial/upstream lakes are present in young catchments (< 100 years ice free), which can increase water temperature and channel stability for a period (Sidle and Milner, 1989, Milner et al., 2000, Milner et al., 2008). These lakes also remove coarse sediments and buffer maximum flows during flood events (Milner et al., 2007). Young streams are typically dominated by fast and shallow habitat types and high suspended sediment loads (Sidle and Milner, 1989, Klaar et al., 2009).

With the loss of catchment glacial cover, streams continue to warm, whilst the depletion and stabilisation of formerly deposited glacial sediment results in decreasing suspended sediment loads and increased channel stability (Ballantyne, 2002). During this period dispersal limitation remains the principal factor in controlling stream community assembly (Brown and Milner, 2012, Brown et al., 2018). However, following the establishment of riparian forests, biotic processes become more important in controlling both the physical and ecological development of streams (Milner and Gloyne-Phillips, 2005, Klaar et al., 2009, Klaar et al., 2011). Older, forested catchments intercept precipitation more effectively than bare ground and provide a buffer to run-off during storm events (Hornbeck et al., 1970, Swank et al., 1988). The initial development of trees in the riparian corridor acts to stabilise banks as their roots bind soils, and ground cover decreases erosion (Eichel et al., 2016) which in turn increases stream channel stability.

Once recruited into the stream channel, trees act locally as points of channel structural and positional change (Trimble, 1997, Gregory and Davis, 1992, Gurnell and Gregory, 1995, Fetherston et al., 1995, Zaimes et al., 2004). As riparian wood is accumulated into the stream channel it provides a roughness element, causing significant local (10^1 m) and reach scale (10^2 m) alterations in hydraulics (Klaar et al., 2011, Wenzel et al., 2014). Through this process, instream wood facilitates the continued development of instream geomorphic and hydraulic habitat (Milner and Gloyne-Phillips, 2005, Klaar et al., 2011). Instream wood can more closely couple a river to its floodplain by linking terrestrial and aquatic ecosystems, although this is dependent upon instream wood being of sufficient size to significantly alter flow hydraulics (Klaar et al., 2011). Given its capacity to alter velocity locally, instream wood can act as a site of fine sediment accumulation and its presence is known to drive pool formation (Sidle and Milner, 1989, Abbe and Montgomery, 1996, Montgomery et al., 1995, Yarnell et al., 2006, Klaar et al., 2011). As low velocity habitat types (such as pools) develop and streams begin to occupy a more complex and stable channel, high velocity habitat types found earlier are reduced. This results in a peak in habitat complexity of streams at an intermediate age: as instream wood begins to accumulate but channels still support high velocity habitat types (Klaar et al., 2009).

Table 2.1. Physical characteristics of study streams. Adapted from Klaar et al. (2015), including newly delineated catchment boundaries to calculate catchment size from USGS 5 m DEM.

Site	Stream age (in 2014)	Stream length (km)	Catchment size (km^2)	Average Discharge (m^3/s)	Stream order	Dominant substrate type	Dominant riparian vegetation	Geology
WPC	70	5.6	29.8	2.29	2	Boulder	Alder	A/W
IVS	146	8.3	19.2	3.02	2	Cobble	Alder/ Cottonwood	A/W
BBS	186	7.2	27.3	4.95	3	Gravel	Sitka spruce	A/W
RPC	211	6.6	26.3	7.51	2	Gravel	Sitka spruce	A/W

2.1.3 Scientific importance of Glacier Bay

Since Cooper's early work in the 1920's a space for time substitution approach has been applied in terrestrial, lotic, lentic and intertidal successional studies within Glacier Bay (Fastie, 1995, Weishampel and Sugart, 1994, Reiners et al., 1971, Milner et al., 2000, Fritz et al., 2004, Chapin et al., 1994, Milner et al., 2007, Klaar et al., 2015). This facilitates studies over short time periods (months to years) to explore processes which occur over decades to centuries (Foster and Tilman, 2000). Specifically, in GBNP, >500 years of physical and ecological development can be studied across the length of the tidal fjord (150 km). Although, this space-for-time approach has received criticism for failing to represent empirically observed ecological succession in some cases (Johnson and Miyanishi, 2008), the relationships observed in GBNP have been validated by long term monitoring (Milan, 2012, Walker et al., 2010, Klaar et al., 2015). This validation is possible because GBNP also has the longest running terrestrial and lotic ecological successional datasets known globally (Buma et al., 2017, Milner et al., 2018).

The combination of space-for-time substitution and long term monitoring has enabled a deep understanding of the processes of community assembly (Flory and Milner, 2000, Milner et al., 2000, Milner et al., 2008) to be developed. Species colonisation following glacial retreat is dependent upon various deterministic (niche) and stochastic (neutral) assembly processes specific to each potential colonising species (Brown and Milner, 2012). Depending upon the traits of each potential colonising species, generalists (both habitat/trophic) may arrive under assembly processes associated with dispersal ability/limitation (Brown et al., 2018). In contrast, the recruitment of specialists (habitat/trophic) may be more dependent upon habitat and resource availability (Flory and Milner, 2000), associated with environmental/niche filtering (Poff, 1997). At this stage ecosystems show high taxa retention through time, resulting in the development of functional redundancy in macroinvertebrate communities (Brown and Milner, 2012).Whilst more recently the response to both predictable and unpredictable change has been explored (Brown and Milner, 2012, Milner et al., 2011, Milner et al., 2013, Robertson et al., 2015).

2.1.4 Major historic flooding in Glacier Bay

The role of disturbances in controlling biotic community and geomorphological composition within GBNP streams has received attention following a major flood event across the park in 2005 (1 in 100 year storm; Milner et al., 2013). Evidence of response to the 2005 floods suggested streams of varying complexities responded in drastically different ways to the floods. Lower complexity streams demonstrated greater impacts to taxa richness and density than more complex streams (Robertson et al., 2015). Whilst the impacts of flooding have been studied across the globe (Molles, 1985, Matthews, 1986, Milan, 2012, Pearsons et al., 1992, Roghair et al., 2002, Bertoldi et al., 2010, Fryirs et al., 2015, Lojkásek et al., 2005, Schwendel et al., 2010) there are no examples outside of GBNP that can contextualise a flood’s physical and ecological impacts or subsequent responses in the context of extensive pre-flood data sets which also capture primary successional processes. This provides the opportunity to develop novel insights into the differences between primary and secondary successional processes (Milner et al., 2013, Robertson et al., 2015). These impacts of the 2005 floods will be incorporated into this thesis and examined with respect to the 2014 floods in Chapter 6, 7 and 8.

2.1.5 Recent flooding in Glacier Bay

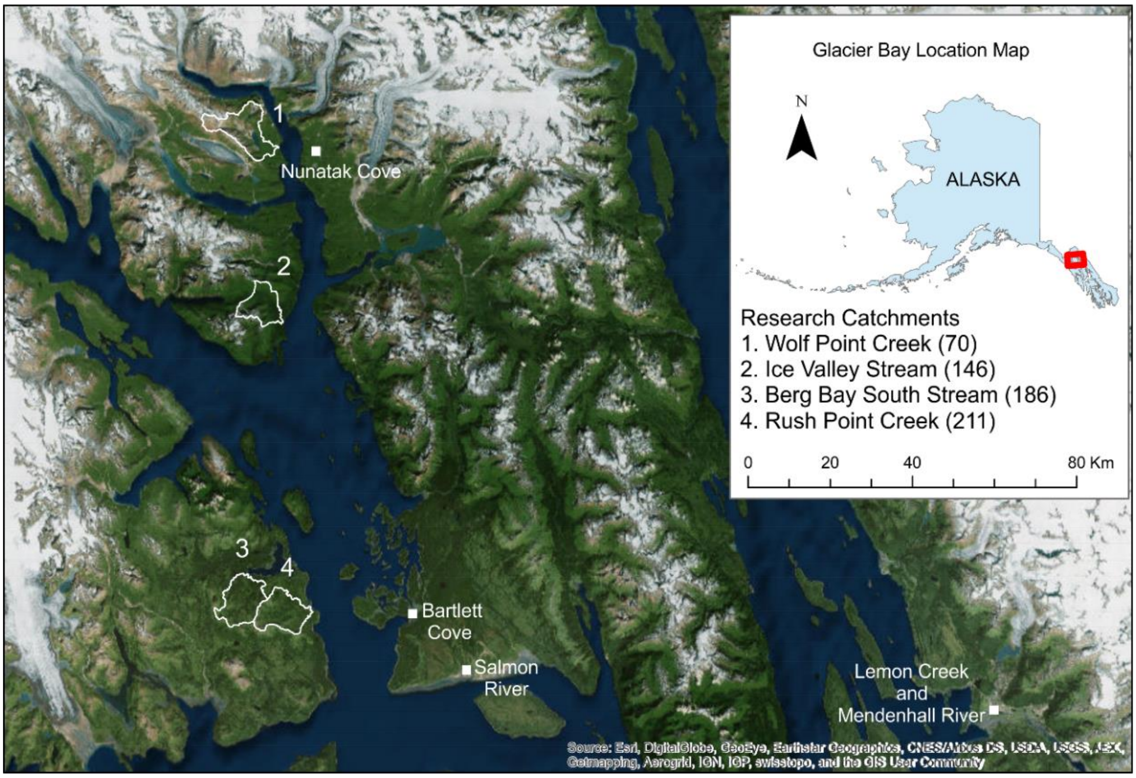
The summer of 2014 saw recurrent atypical heavy precipitation in GBNP (Figure 2.2). Similar wet conditions were reported during the summer of 2014 elsewhere in southeast Alaska (Milner et al., 2018). This heavy precipitation is thought to have been driven by the Pacific warm surface water anomaly ('Pacific blob') which persisted off the west coast of North America from 2012 until 2015 (Cavole et al., 2016). The blob's capacity to alter weather patterns has been documented and more specifically it has been shown to have driven increased precipitation along the Pacific coastline during 2014 (Bond et al., 2015).

To interpret the impacts of disturbance events, such as floods, it is necessary to have an understanding of their magnitude, duration and timing, as these factors are known to influence both the physical and ecological impacts of floods (e.g. Junk et al., 1989, Poff et al., 1997, Milner et al. 2013). In this chapter, precipitation and stream discharge conditions in GBNP during the summer of 2014 are described through two steps. Initially, relationships between precipitation and stream flow records across the southeast Alaska region during pre-flood and post-flood time periods are described. Subsequently, regional precipitation and stream flow conditions during the summer of 2014 are correlated, to demonstrate the consistent weather and streamflow patterns across the region and more specifically GBNP during the summer of floods.

2.2 Regional setting and available data

The majority of GBNP is a wilderness area and thus a range of federal laws and policies regulate installations that are considered long-term (Congress, 1964). As a result, there have been limited opportunities to establish permanent monitoring equipment, such as stream gauges or weather stations, at sites within the park. Consequently, few long-term precipitation data sets are available in GBNP, in spite of the scientific importance of the park. The lack of stream flow monitoring poses a problem when trying to describe flooding events.

Despite this, GBNP and southeast Alaska have some long term (>30 years), as well as short term (<2 years) precipitation and stream discharge records. These include a gap free, consistently monitored, daily, point source precipitation record for Bartlett Cove (southeast GBNP; Figure 2.1. Map of Glacier Bay, Alaska. Study catchments outlined in white. since 1987. A 33-year stream discharge record at Lemon Creek (LC; Juneau; Figure 2.1) and a discharge record for the Salmon River (SR; Gustavus; Figure 2.1) were established in 2014. Additionally, in 2015/16 the National Parks Service and United States Geological Survey installed weather stations across GBNP. One station at Nunatak Cove is proximal to the most remote research site Wolf Point Creek (WPC), whilst a new precipitation dataset was also made available at Bartlett Cove. In 2010-2011, previous stream research in GBNP established stream discharge at three sites WPC, Ice Valley Stream (IVS) and Rush Point Creek (RPC) for periods of 8 to 13 months. Finally, discharge data for the Mendenhall River (Juneau) was available for a complimentary period to the WPC 2010-2011 data set. These two streams have upstream lakes and therefore are expected to share more similar flow regimes when compared to streams without lakes, although the presence of a lake-terminating glacier on Mendenhall Lake is likely to result in some differences in stream discharge between WPC and Mendenhall River (MR), particularly during dry warm periods. All the datasets used in this description of hydrological conditions are summarised in Table 2.2.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 2.1. Map of Glacier Bay, Alaska. Study catchments outlined in white.

2.3 Methods

Precipitation data was accessed from online repositories from National Oceanic and Atmospheric Administration (NOAA) and the Western Regional Climate Center (RAWS data).

Discharge data for gauged streams were accessed from the United States Geological Survey (USGS; USGS Data, 2019) online repository (see

Table 2.2 for descriptions of temporal availability). Once collated, data was processed manually using a consistent quality control approach to identify erroneous values, missing data and outliers. This process initially entailed removing periods of data which did not match temporally with another data set. High and low flows were checked and, where extreme, were cross-referenced back to NOAA, RAWS and USGS internal quality control checks. Where data failed to meet internal quality control standards, and following communications with the given organisation, data was excluded from analyses. Extreme high and low values based on histograms of binned flow and precipitation data were visually inspected, compared to values over the preceding and succeeding days and where necessary were checked against local media to corroborate flood and drought periods. Where there was no evidence to support an event that time period was removed from the data set. Following these steps, the quality-controlled data was taken forward into correlation analyses.

2.3.1 Trends in regional weather and streamflow patterns through time

Spearman’s rank correlation coefficients were used to explore regional correlations in discharge data collected at WPC, IVS and RPC in 2010-2011 and gauged streams LC and the MR (WPC only) to explore regional patterns in stream flow during a pre-flood time period. In addition, precipitation data from Nunatak Cove (northeast GBNP) weather station was compared to precipitation from the new Bartlett Cove (south GBNP) gauge to assess if precipitation was significantly correlated across GBNP (Figure 2.1.) during a post-flood time period.

Table 2.2. Precipitation and stream discharge data sets utilised in this chapter. NOAA = National Oceanic and Atmospheric Administration, USGS = United States Geological Survey and RAWS = Western Regional Climate Center. Distance from IVS is reported because IVS is located near the centre of GBNP and as such offers a central point from which to compare distances of sampling locations.

Name	Data type	Units	Temporal availability	Station record number	Source	Latitude Longitude	Distance from IVS (km)
Bartlett Cove Inner Dock	Point Source Precipitation	mm	01/1987 – 12/2014	USC 00503294	NOAA	58° 27’ 22" -135° 52' 09”	41
Lemon Creek (LC)	Gauged Discharge	m^3/s	08/1951 – 09/1973 & 05/2002 – 01/2018	USGS 15052000	USGS	58° 23' 30" -134° 25' 15"	115
Salmon River (SR)	Gauged Discharge	m^3/s	05/2014 – 02/2018	USGS 15057596	USGS	58° 26' 42” -135° 44' 24"	49
Mendenhall River (MR)	Gauged Discharge	m^3/s	07/2010 – 06/2011	USGS 15052500	USGS	58°25'47" -134°34'22"	110
Nunatak Cove Upper	Point Source Precipitation	mm	06/2016 – 02/2018	NPS 3962C6E6	RAWS	58° 59' 01" -136° 06' 01"	19
Bartlett Cove Inner Dock	Point Source Precipitation	mm	09/2015 – 07/2017	NPS 3962D590	RAWS	58° 27' 23" -135° 52' 11"	41
Wolf Point Creek (WPC)	Discharge	m^3/s	07/2010 – 06/2011	n/a	M.J. Klaar unpub data	58° 59' 46" -136° 10' 43"	26
Ice Valley Stream (IVS)	Discharge	m^3/s	06/2010 – 07/2011	n/a	M.J. Klaar unpub data	58° 48' 11" -136° 09' 34"	0
Rush Point Creek (RPC)	Discharge	m^3/s	08/2010 – 04/2011	n/a	M.J. Klaar unpub data	58° 28' 15" -136° 06' 22"	37

2.3.2 Weather and stream discharge conditions during the summer of 2014 within GBNP and across the southeast Alaska region

Summary statistics were calculated for summer precipitation (June to August) in the Bartlett Cove long-term record. Annual, monthly and weekly totals were calculated across the data set to assess timing and volume of precipitation. From precipitation data, return intervals were calculated for daily and weekly periods to assess the temporal likelihood of any individual rainfall event occurring. These summary statistics were then used to contextualise the overall conditions during the summer within the long-term data and identify specific periods where rainfall was particularly intense in GBNP overall and specifically in 2014.

Discharge from May to September 2014 was analysed at LC to establish if the trends seen in the precipitation data were also recorded in stream discharge when compared to a long-term historic record. Daily 2014 data were compared to 33-year median values to identify differences in discharge as used in Milner et al. (2013) and Milner et al. (2018).

Discharge and precipitation were plotted temporally to allow for visual comparisons of records. Subsequently, Spearman's rank correlation coefficients were calculated for comparisons of 2014 summer discharge at LC and SR with precipitation in GBNP. Cross correlation analyses were used to identify if temporal shifts were present in the data, as might be expected if a storm moves across the region, rather than establishes and persists across the entire region.

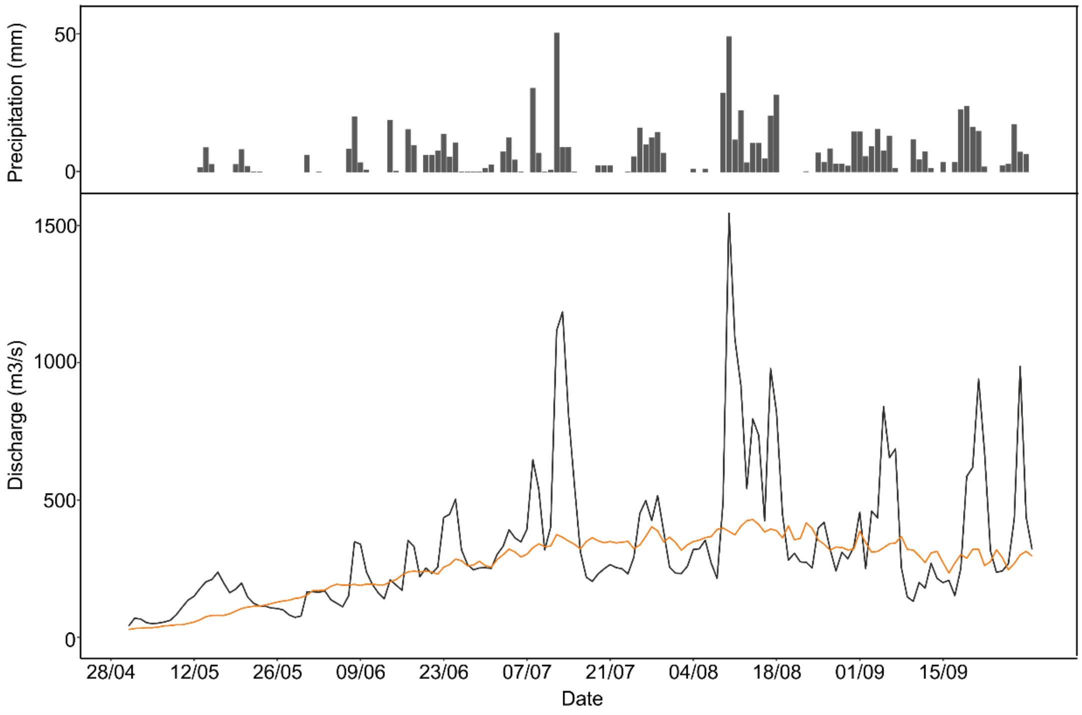


Figure 2.2. Bartlett Cove precipitation data (top) and Lemon Creek hydrograph (black) for the summer of 2014 and 33-year median (orange; bottom).

2.4 Results

2.4.1 Precipitation and streamflow across GBNP and SE Alaska during pre- and post-flood time periods

Cross correlation analysis was not applied to 2010-2011 discharge or 2015-2017 precipitation data, due to the presence of a large number of outliers, missing and/or unreliable data points, leaving an incomplete time series. Spearman's rank correlation analyses demonstrated significant positive relationships in discharge between LC, IVS and RPC pre-flood (Table 2.3.). No significant relationship was found between LC and WPC discharges. However, a significant relationship was found between MR and WPC discharges. Additionally, precipitation data for Nunatak Cove (<5 km from WPC) and Bartlett Cove during the post-flood period demonstrated a strong and significant positive correlation.

2.4.2 Weather and stream discharge conditions during the summer of 2014

Cross correlation analyses demonstrated that the relationship between all pairs of variables were greatest at a lag of 0 days. Subsequent analyses were therefore performed on the original data set with no temporal adjustment. Significant positive correlations were identified between each pair of variables (Table 2.4.).

*Table 2.3. Spearman's rank correlation coefficients of non-flood period discharge (top) and precipitation (bottom) data sets. ** p<0.001, *p<0.01*

Correlation	Lemon Creek Discharge (m3/s)	Mendenhall River Discharge (m3/s)
Wolf Point Creek Discharge (m3/s)	-0.13	0.37*
Ice Valley Stream Discharge (m3/s)	0.58**	
Rush Point Creek Discharge (m3/s)	0.42**	

Correlation	Bartlett Cove Precipitation (mm)
Nunatak Creek Precipitation (mm)	0.78**

The long-term precipitation record at Bartlett Cove (GBNP) indicated the summer of 2014 was the wettest on record (1987-2014). June and July were the second wettest months and August the fourth wettest month on record. Whilst precipitation was consistent across the summer (Figure 2.2), two periods of particularly intense precipitation were identified. A total of 109 mm of precipitation fell in one week in July (8th-14th), an event with a 5-year return interval. Whilst during a two-week period in August (5th-18th), 193 mm of precipitation were recorded, individual weeks with return intervals of 2.5- and 3-years respectively. Within these periods the fifth (12th July, 51 mm) and sixth (10th August, 50 mm) wettest summer days on record occurred, with 5 - and 4 -year return intervals. During the same period gauged streams recorded high flows (see Figure 2.2) across southeast Alaska. The 12th of July and 10th of August saw discharge four times the median at LC. These high flows and precipitation levels were consistent across Bartlett Cove, SR and LC records (Table 2.4).

*Table 2.4. Spearman's rank correlation coefficients for flood time period precipitation and stream discharges across southeast Alaska. ** p < 0.01*

Data	Bartlett Cove Precipitation mm	Lemon Creek Discharge m^3/s
Lemon Creek Discharge m^3/s	0.66**	-
Salmon River Discharge m^3/s	0.54**	0.64**

2.5 Discussion

2.5.1 General trends across GBNP and regional precipitation and stream discharge

In this analysis significant positive relationships were identified, during all time periods, between precipitation and stream discharge both regionally and within GBNP. This suggests that summer precipitation and subsequently stream discharge were associated with weather trends that act regionally across southeast Alaska (Bond et al., 2015, Cavole et al., 2016). As a result of these relationships, general trends identified regionally and specifically within the available GBNP precipitation data can be considered to describe overall trends within GBNP generally and more specifically during the summer of 2014.

The non-significant relationship between stream discharge at the research stream WPC and long-term gauged stream LC represents the one outlier in this regional relationship. However, given the relatively young age of WPC and the presence of an upstream lake, its discharge can be expected to respond to precipitation in a different manner to other streams in the analyses. This is supported by the significant relationship between WPC and the MR, which also has a lake upstream of its gauging station. Such lakes act as a buffer to peak flows, due to the lake's capacity to hold water and regulate its release from constricted outflows (Mielko and Woo, 2006). Consequently, streams with upstream lakes may demonstrate less variable hydrographs with extended periods of high flow following precipitation. These differences in water availability to streams helps explains the lack of positive relationship for mean daily discharge between streams with and without upstream lakes, even where precipitation is known to be similar across streams (such as identified here in precipitation at Bartlett Cove and Nunatak

Creek). However, given the known relationship between peak and duration of stream discharge and total energy available for geomorphic change (Leopold and Maddock Jr, 1953, Costa and O'Connor, 1995), the smoothed hydrograph of a stream with an upstream lake can still be expected to be effective at driving change to downstream geomorphology and ecology.

2.5.2 Weather and stream discharge conditions during the summer of 2014

During the summer of 2014, this study identified strong positive correlations between precipitation in GBNP and stream discharge in the region's gauged streams. This suggests that the high levels of precipitation recorded in Bartlett Cove during this period occurred across a large spatial scale driving elevated stream discharges and was not the result of localised intense precipitation events, consistent with the effects of the Pacific blob (Bond et al., 2015, Cavole et al., 2016). This is supported by comparisons of timings of peak precipitation days in the summer precipitation record at Bartlett Cove and regional stream discharges. The two peak precipitation days recorded during the summer of 2014 at Bartlett Cove (12th July and 10th August) had the two highest stream discharges at both LC and SR. Consequently, variation in precipitation and discharge, at long-term monitoring sites LC and Bartlett Cove, are considered to describe general conditions across the region through the summer of 2014.

Comparisons within the long-term precipitation record at Bartlett Cove demonstrate the summer (June to August) of 2014 to be the wettest on record. All individual months showed high precipitation, whilst comparisons of return intervals for individual weeks and days suggest the presence of intense short-term periods of precipitation as well as prolonged periods of wet weather. Intense precipitation often followed weeks of persistent wet weather. This is further supported by precipitation data presented in Milner et al. (2018). Precipitation was the highest on record during June and second highest in July in Juneau, 150 km away (ACRC, 2014), whilst precipitation in Bartlett Cove was identified as the second wettest June and July on record. These conditions are unique in the historic data set where generally summer precipitation fell over shorter time periods. As such, the weather conditions during the summer of 2014 were not only likely to drive high stream discharges but also can be expected to result in significant wetting out of soils over long periods of the summer (Osman and Barakbah, 2006). Elsewhere, under such wet antecedent conditions lower magnitude precipitation events have been shown to have the capacity to drive significant floods (Marsh, 2008).

Importantly, such saturated soils were likely to have been exposed to very intense short-term summer precipitation. Such events should be expected to have significant implications for river form processes (Kim et al., 2004). Wet conditions are known to increase the likelihood of landslips, whilst soil water content is a predictor of slope failure and is negatively associated with soil shear stress and soil penetrability (Osman and Barakbah, 2006). In addition, precipitation is known to increase the depth of the wetted band in soils, which is associated with increases in shallow slope failures (Guerra et al., 2017). Thus, it can be expected that ground conditions across study catchments during the summer of 2014 were ideal for slope and bank failures, as precipitation persisted for long periods from the onset of summer.

These wet conditions alone could drive bank failure (Kim et al., 2004). However, due to the decrease in soil shear stress, wetted soils can also be expected to increase the risk of bank erosion, due to hydraulic scouring along the wetted stream channel (Darby et al., 2007, Fox et al., 2016). Such erosion can act as an important sediment source, change the position of the wetted channel and act to recruit riparian wood to the stream channel (Abbe and Montgomery, 2003, Laubel et al., 2003). Further, discharges such as those recorded in LC are capable of mobilising bed sediments and driving bank migration in gravel bed rivers (Haschenburger and Wilcock, 2003, Mao and Surian, 2010, Chappell et al., 2003, Bertoldi et al., 2010), the implications of which will be analysed in Chapter 3. This capacity to drive physical change, alongside potential direct impacts of above average flows, may have significant implications for biotic communities in streams. However, there are few analyses of the impact of such high-frequency floods on biotic communities available in the literature (see Milner et al., 2018 for one example). This topic will be the primary focus of Chapters 4 and 5.

2.6 Conclusion

Overall, the results of these analyses suggest that trends in precipitation and stream discharge across southeast Alaska can be described at a regional scale. The summer of 2014 saw record breaking persistent and repeat precipitation events across the region, and more specifically in GBNP. Such events were associated with high stream discharges at gauged sites, with peak flows four times the median of the historic record. Elsewhere similar discharges have driven geomorphological change through bed sediment mobilisation and bank erosion. Further, given some individual high precipitation days, which occurred after prolonged wet periods and the general high precipitation trend (June to July), bank erosion is likely to have been extensive. Such erosion should be expected to have driven increased sediment inputs, instream wood recruitment, accumulation and channel migration. These impacts are the primary focus of the succeeding chapter (Chapter 3).

2.7 References

ABBE, T. B. & MONTGOMERY, D. R. 1996. Large woody debris dams, channel hydraulics and habitat formation in large rivers. *Regulated Rivers: Research & Management,* 12**,** 201-221.

ABBE, T. B. & MONTGOMERY, D. R. 2003. Patterns and processes of wood debris accumulation in the Queets river basin, Washington. *Geomorphology,* 51**,** 81-107.

BALLANTYNE, C. K. 2002. A general model of paraglacial landscape response. *The Holocene,* 12**,** 371-376.

BERTOLDI, W., ZANONI, L. & TUBINO, M. 2010. Assessment of morphological changes induced by flow and flood pulses in a gravel bed braided river: The Tagliamento River (Italy). *Geomorphology,* 114**,** 348-360.

BOGGS, K., KLEIN, S. C., GRUNBLATT, J., BOUCHER, T., KOLTUN, B., STURDY, M. & STREVELER, G. P. 2010. Alpine and Subalpine Vegetation Chronosequences following Deglaciation in Coastal Alaska. *Arctic Antarctic and Alpine Research,* 42**,** 385-395.

BOND, N. A., CRONIN, M. F., FREELAND, H. & MANTUA, N. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters,* 42**,** 3414-3420.

BORMANN, B. T. & SIDLE, R. C. 1990. Changes in Productivity and Distribution of Nutrients in a Chronosequence at Glacier Bay National Park, Alaska. *Journal of Ecology,* 78**,** 561-578.

BROWN, L. E., KHAMIS, K., WILKES, M., BLAEN, P., BRITTAIN, J. E., CARRIVICK, J. L., FELL, S., FRIBERG, N., FÜREDER, L., GISLASON, G. M., HAINIE, S., HANNAH, D. M., JAMES, W. H. M., LENCIONI, V., OLAFSSON, J. S., ROBINSON, C. T., SALTVEIT, S. J., THOMPSON, C. & MILNER, A. M. 2018. Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nature Ecology & Evolution,* 2**,** 325-333.

BROWN, L. E. & MILNER, A. M. 2012. Rapid loss of glacial ice reveals stream community assembly processes. *Global Change Biology,* 18**,** 2195-2204.

BUMA, B., BISBING, S., KRAPEK, J. & WRIGHT, G. 2017. A foundation of ecology rediscovered: 100 years of succession on the William S. Cooper plots in Glacier Bay, Alaska. *Ecology,* 98**,** 1513-1523.

CAVOLE, L. M., DEMKO, A. M., DINER, R. E., GIDDINGS, A., KOESTER, I., PAGNIELLO, C. M. L. S., PAULSEN, M.-L., RAMIREZ-VALDEZ, A., SCHWENCK, S. M., YEN, N. K., ZILL, M. E. & FRANKS, P. J. S. 2016. Biological Impacts of the 2013–2015 Warm-Water Anomaly in the Northeast Pacific Winners, Losers, and the Future. *Oceanography,* 29**,** 273-285.

ACRC Alaska Climate Research Center. 2014. Annual Rainfall statistics. Juneau, Alaska.

CHAPIN, F. S., WALKER, L. R., FASTIE, C. L. & SHARMAN, L. C. 1994. Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska. *Ecological Monographs,* 64**,** 149-175.

CHAPPELL, A., HERITAGE, G. L., FULLER, I. C., LARGE, A. R. G. & MILAN, D. J. 2003. Geostatistical analysis of ground-survey elevation data to elucidate spatial and temporal river channel change. *Earth Surface Processes and Landforms,* 28**,** 349-370.

CONGRESS, T. 1964. The Wilderness Act (Public Law 88-577). *In:* AMERICA, S. A. H. O. R. O. T. U. S. O. (ed.).

COOPER, W. S. 1923a. The Recent Ecological History of Glacier Bay, Alaska: Permanent Quadrats at Glacier Bay: An Initial Report upon a Long-Period Study. *Ecology,* 4**,** 355-365.

COOPER, W. S. 1923b. The Recent Ecological History of Glacier Bay, Alaska: The Interglacial Forests of Glacier Bay. *Ecology,* 4**,** 93-128.

COOPER, W. S. 1923c. The Recent Ecological History of Glacier Bay, Alaska: The Present Vegetation Cycle. *Ecology,* 4**,** 223-246.

COSTA, J. E. & O'CONNOR, J. E. 1995. Geomorphically Effective Floods. *Natural and Anthropogenic Influences in Fluvial Geomorphology.* American Geophysical Union.

CROCKER, R. L. & MAJOR, J. 1955. Soil Development in Relation to Vegetation and Surface Age at Glacier Bay, Alaska. *Journal of Ecology,* 43**,** 427-448.

DARBY, S. E., RINALDI, M. & DAPPORTO, S. 2007. Coupled simulations of fluvial erosion and mass wasting for cohesive river banks. *Journal of Geophysical Research: Earth Surface,* 112.

EICHEL, J., CORENBLIT, D. & DIKAU, R. 2016. Conditions for feedbacks between geomorphic and vegetation dynamics on lateral moraine slopes: a biogeomorphic feedback window. *Earth Surface Processes and Landforms,* 41**,** 406-419.

FASTIE, C. L. 1995. Causes and Ecosystem Consequences of Multiple Pathways of Primary Succession at Glacier Bay, Alaska. *Ecology,* 76**,** 1899-1916.

FETHERSTON, K. L., NAIMAN, R. J. & BILBY, R. E. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest A2 - Hupp, C.R. *In:* OSTERKAMP, W. R. & HOWARD, A. D. (eds.) *Biogeomorphology, Terrestrial and Freshwater Systems.* Amsterdam: Elsevier.

FIELD, W. O., JR. 1947. Glacier recession in the Muir Inlet, Glacier BAy, Alaska. *Geographical Review,* 37**,** 369-399.

FLORY, E. A. & MILNER, A. M. 2000. Macroinvertebrate community succession in Wolf Point Creek, Glacier Bay National Park, Alaska. *Freshwater Biology,* 44**,** 465-480.

FOSTER, B. L. & TILMAN, D. 2000. Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecology,* 146**,** 1-10.

FOX, G. A., PURVIS, R. A. & PENN, C. J. 2016. Streambanks: A net source of sediment and phosphorus to streams and rivers. *Journal of Environmental Management,* 181**,** 602-614.

FRITZ, S. C., ENGSTROM, D. R. & JUGGINS, S. 2004. Patterns of early lake evolution in boreal landscapes: a comparison of stratigraphic inferences with a modern chronosequence in Glacier Bay, Alaska. *Holocene,* 14**,** 828-840.

FRYIRS, K., LISENBY, P. & CROKE, J. 2015. Morphological and historical resilience to catastrophic flooding: The case of Lockyer Creek, SE Queensland, Australia. *Geomorphology,* 241**,** 55-71.

GOLDTHWAIT, R. P., LOEWE, F., UGOLINI, F. C., DECKER, H. F., DELONG, D. M., TRAUTMAN, M. B., GOOD, E. E., T. R. MERRELL, I. & RUDOLPH, E. D. 1966. Soil development and ecological succession in a deglaciated area of Muir Inlet, Southeast Alaska. *In:* MIRSKY, A. (ed.). Institute of Polar Studies.

GREGORY, K. J. & DAVIS, R. J. 1992. Coarse woody debris in stream channels in relation to river channel management in woodland areas. *Regulated Rivers: Research & Management,* 7**,** 117-136.

GUERRA, A. J. T., FULLEN, M. A., JORGE, M. D. C. O., BEZERRA, J. F. R. & SHOKR, M. S. 2017. Slope Processes, Mass Movement and Soil Erosion: A Review. *Pedosphere,* 27**,** 27-41.

GURNELL, A. M. & GREGORY, K. J. 1995. Interactions between semi-natural vegetation and hydrogeomorphological processes. *Geomorphology,* 13**,** 49-69.

HALL, D. K., BENSON, C. S. & FIELD, W. O. 1995. Changes of Glaciers in Glacier Bay, Alaska, Using Ground and Satellite Measurements. *Physical Geography,* 16**,** 27-41.

HASCHENBURGER, J. K. & WILCOCK, P. R. 2003. Partial transport in a natural gravel bed channel. *Water Resources Research,* 39**,** n/a-n/a.

HORNBECK, J. W., PIERCE, R. S. & FEDERER, C. A. 1970. Streamflow Changes after Forest Clearing in New England. *Water Resources Research,* 6**,** 1124-1132.

KIM, J., JEONG, S., PARK, S. & SHARMA, J. 2004. Influence of rainfall-induced wetting on the stability of slopes in weathered soils. *Engineering Geology,* 75**,** 251-262.

KLAAR, M. J. 2010. *The development of geomorphic and hydraulic complexity within streams and its influence on fish communities following glacial recession in Glacier Bay, Alaska.* PhD, University of Birmingham.

KLAAR, M. J., HILL, D. F., MADDOCK, I. & MILNER, A. M. 2011. Interactions between instream wood and hydrogeomorphic development within recently deglaciated streams in Glacier Bay National Park, Alaska. *Geomorphology,* 130**,** 208-220.

KLAAR, M. J., KIDD, C., MALONE, E., BARTLETT, R., PINAY, G., CHAPIN, F. S. & MILNER, A. 2015. Vegetation succession in deglaciated landscapes: implications for sediment and landscape stability. *Earth Surface Processes and Landforms,* 40**,** 1088-1100.

KLAAR, M. J., MADDOCK, I. & MILNER, A. M. 2009. The Development of Hydraulic and Geomorphic Complexity in Recently Formed Streams in Glacier Bay National Park, Alaska. *River Research and Applications,* 25**,** 1331-1338.

LAUBEL, A., KRONVANG, B., HALD, A. B. & JENSEN, C. 2003. Hydromorphological and biological factors influencing sediment and phosphorus loss via bank erosion in small lowland rural streams in Denmark. *Hydrological Processes,* 17**,** 3443-3463.

LAWRENCE, D. B., SCHOENIKE, R. E., QUISPEL, A. & BOND, G. 1967. The Role of Dryas Drummondii in Vegetation Development Following Ice Recession at Glacier Bay, Alaska, with Special Reference to Its Nitrogen Fixation by Root Nodules. *Journal of Ecology,* 55**,** 793-813.

LEOPOLD, L. B. & MADDOCK JR, T. 1953. The hydraulic geometry of stream channels and some physiographic implications. *Professional Paper.* Washington, D.C.

LOJKÁSEK, B., LUSK, S., HALAČKA, K., LUSKOVÁ, V. & DROZD, P. 2005. The Impact of the Extreme Floods in July 1997 on the Ichthyocenosis of the Oder Catchment Area (Czech Republic). *Hydrobiologia,* 548**,** 11-22.

MAO, L. & SURIAN, N. 2010. Observations on sediment mobility in a large gravel-bed river. *Geomorphology,* 114**,** 326-337.

MARSH, T. 2008. A hydrological overview of the summer 2007 floods in England and Wales. *Weather,* 63**,** 274-279.

MATTHEWS, W. J. 1986. Fish Faunal Structure in an Ozark Stream: Stability, Persistence and a Catastrophic Flood. *Copeia,* 1986**,** 388-397.

MIELKO, C. & WOO, M.-K. 2006. Snowmelt runoff processes in a headwater lake and its catchment, subarctic Canadian Shield. *Hydrological Processes,* 20**,** 987-1000.

MILAN, D. J. 2012. Geomorphic impact and system recovery following an extreme flood in an upland stream: Thinhope Burn, northern England, UK. *Geomorphology,* 138**,** 319-328.

MILNER, A. M. 1987. Colonization and ecological development of new streams in Glacier Bay National Park, Alaska. *Freshwater Biology,* 18**,** 53-70.

MILNER, A. M. & BAILEY, R. G. 1989. Salmonid colonization of new streams in Glacier Bay National Park Alaska USA. *Aquaculture and Fisheries Management,* 20**,** 179-192.

MILNER, A. M., FASTIE, C. L., CHAPIN, F. S., ENGSTROM, D. R. & SHARMAN, L. C. 2007. Interactions and linkages among ecosystems during landscape evolution. *Bioscience,* 57**,** 237-247.

MILNER, A. M. & GLOYNE-PHILLIPS, I. T. 2005. The role of riparian vegetation and woody debris in the development of macroinvertebrate assemblages in streams. *River Research and Applications,* 21**,** 403-420.

MILNER, A. M., KNUDSEN, E. E., SOISETH, C., ROBERTSON, A. L., SCHELL, D., PHILLIPS, I. T. & MAGNUSSON, K. 2000. Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences,* 57**,** 2319-2335.

MILNER, A. M., PICKEN, J. L., KLAAR, M. J., ROBERTSON, A. L., CLITHEROW, L. R., EAGLE, L. & BROWN, L. E. 2018. River ecosystem resilience to extreme flood events. *Ecology and Evolution,* 0.

MILNER, A. M., ROBERTSON, A. L., BROWN, L. E., SØNDERLAND, S. H., MCDERMOTT, M. & VEAL, A. J. 2011. Evolution of a stream ecosystem in recently deglaciated terrain. *Ecology,* 92**,** 1924-1935.

MILNER, A. M., ROBERTSON, A. L., MCDERMOTT, M. J., KLAAR, M. J. & BROWN, L. E. 2013. Major flood disturbance alters river ecosystem evolution. *Nature Climate Change,* 3**,** 137-141.

MILNER, A. M., ROBERTSON, A. L., MONAGHAN, K. A., VEAL, A. J. & FLORY, E. A. 2008. Colonization and development of an Alaskan stream community over 28 years. *Frontiers in Ecology and the Environment,* 6**,** 413-419.

MOLLES, M. C. 1985. Recovery of a Stream Invertebrate Community from Flash a Flash Flood in Tesuque Creek, New Mexico. *The Southwestern Naturalist,* 30**,** 279-287.

MONTGOMERY, D. R., BUFFINGTON, J. M., SMITH, R. D., SCHMIDT, K. M. & PESS, G. 1995. Pool Spacing in Forest Channels. *Water Resources Research,* 31**,** 1097-1105.

NOBLE, M. G., LAWRENCE, D. B. & STREVELER, G. P. 1984. Sphagnum invasion beneath an evergreen forest canopy in southeast Alaska. *Bryologist,* 87**,** 119-127.

OSMAN, N. & BARAKBAH, S. S. 2006. Parameters to predict slope stability—Soil water and root profiles. *Ecological Engineering,* 28**,** 90-95.

PEARSONS, T. N., LI, H. W. & LAMBERTI, G. A. 1992. Influence of Habitat Complexity on Resistance to Flooding and Resilience of Stream Fish Assemblages. *Transactions of the American Fisheries Society,* 121**,** 427-436.

POFF, N. L. 1997. Landscape Filters and Species Traits: Towards Mechanistic Understanding and Prediction in Stream Ecology. *Journal of the North American Benthological Society,* 16**,** 391-409.

REINERS, W. A., WORLEY, I. A. & LAWRENCE, D. B. 1971. Plant Diversity in a Chronosequence at Glacier Bay, Alaska. *Ecology,* 52**,** 55-69.

ROBERTSON, A. L., BROWN, L. E., KLAAR, M. J. & MILNER, A. M. 2015. Stream ecosystem responses to an extreme rainfall event across multiple catchments in southeast Alaska. *Freshwater Biology,* 60**,** 2523-2534.

ROGHAIR, C. N., DOLLOFF, C. A. & UNDERWOOD, M. K. 2002. Response of a Brook Trout Population and Instream Habitat to a Catastrophic Flood and Debris Flow. *Transactions of the American Fisheries Society,* 131**,** 718-730.

SCHWENDEL, A. C., FULLER, I. C. & DEATH, R. G. 2010. Morphological dynamics of upland headwater streams in the southern North Island of New Zealand. *New Zealand Geographer,* 66**,** 14-32.

SIDLE, R. C. & MILNER, A. M. 1989. Stream Development in Glacier Bay National Park, Alaska, U.S.A. *Arctic and Alpine Research,* 21**,** 350-363.

SWANK, W. T., SWIFT, L. W. & DOUGLASS, J. E. 1988. Streamflow Changes Associated with Forest Cutting, Species Conversions, and Natural Disturbances. *In:* SWANK, W. T. & CROSSLEY, D. A. (eds.) *Forest Hydrology and Ecology at Coweeta.* New York, NY: Springer New York.

TRIMBLE, S. W. 1997. Stream channel erosion and change resulting from riparian forests. *Geology,* 25**,** 467-469.

UGOLINI, F. C. 1968. Soil development and alder invasion in a recently deglaciated area of Glacier Bay, Alaska. *In:* TRAPPE, J. M., FRANKLIN, J. F., TARRANT, R. F. & HANSEN, G. M. (eds.) *Biology of alder. Proceedings of the Pacific Northwest Scientific Association Fortieth Annual Meeting.* Portland, Oregon, USA: Pacific Northwest Forest and Range Experiment Station.

USGS Data , 2019. https://nwis.waterdata.usgs.gov/nwis/inventory/?site_no=15057596&agency_cd=USGS

WALKER, L. R., CHAPINI, F. S. I., FASTIE, C. L. & SHARMAN, L. 1993. Mechanisms of primary succession at Glacier Bay, Alaska. *Bulletin of the Ecological Society of America,* 74**,** 475-475.

WALKER, L. R., WARDLE, D. A., BARDGETT, R. D. & CLARKSON, B. D. 2010. The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology,* 98**,** 725-736.

WEISHAMPEL, J. F. & SUGART, H. H. 1994. Spatial dynamics of primary forest succession along the Glacier Bay chronosequence. *Bulletin of the Ecological Society of America,* 75**,** 244-244.

WENZEL, R., REINHARDT-IMJELA, C., SCHULTE, A. & BÖLSCHER, J. 2014. The potential of in-channel large woody debris in transforming discharge hydrographs in headwater areas (Ore Mountains, Southeastern Germany). *Ecological Engineering,* 71**,** 1-9.

YARNELL, S. M., MOUNT, J. F. & LARSEN, E. W. 2006. The influence of relative sediment supply on riverine habitat heterogeneity. *Geomorphology,* 80**,** 310-324.

ZAIMES, G. N., SCHULTZ, R. C. & ISENHART, T. M. 2004. Stream bank erosion adjacent to riparian forest buffers, row-crop fields, and continuously-grazed pastures along Bear Creek in central Iowa. *Journal of Soil and Water Conservation,* 59**,** 19-27.

3. Geomorphological response of streams to extreme high-frequency floods

3.1 Introduction

Floods represent important disturbance events in lotic systems and are involved in numerous geomorphological and ecological processes (Poff, 2002, Poff et al., 1997). Predictable and smaller floods can: mobilise fine sediments from the stream bed (Malmon et al., 2004); drive localised geomorphological change (Montgomery et al., 2003); link rivers to their floodplains (Junk et al., 1989) and act as environmental filters of ecological community assembly (Poff, 1997). In contrast extreme flood events, which are defined here as rare or unusual weather or climatic driven events (as in Ledger and Milner, 2015), are unpredictable and generally have high-magnitude flows. Extreme floods can result in drastically different impacts depending upon the form of each flood and the catchment in which they occur (e.g. Milan, 2012, Thompson and Croke, 2013, Pasternack and Wyrick, 2017, Brogan et al., 2017, Tunnicliffe et al., 2017). Extreme flood events are capable of driving major geomorphological change, including channelization, reduced channel geomorphological complexity and mobilisation of otherwise immobile sediment clasts (Milan, 2012, Roghair et al., 2002, Hauer and Habersack, 2009, Thompson and Croke, 2013, Pasternack and Wyrick, 2017, Fryirs et al., 2015, Magilligan et al., 2015, Brogan et al., 2017). Crucially, extreme floods are increasing in occurrence globally (Wouter et al., 2017) and therefore their importance for the control of stream geomorphological conditions can only be expected to increase (Ledger and Milner, 2015).

The capacity of a given flood, extreme or otherwise, to drive geomorphological change has been described in an established theoretical framework that links flood duration and peak in stream power and the overall energy available for geomorphological change (Wolman and Miller, 1960, Costa and O'Connor, 1995). This theory demonstrates that increased levels of geomorphological change are linked to increased total energy available, rather than simply to peak flow magnitude. In a study of a small English upland stream, Chappell et al. (2003) provided evidence that both high-magnitude, low-frequency flood events and low-magnitude, high-frequency events can drive changes in river channel geomorphology. Despite the importance of low-magnitude, high-frequency floods, the literature continues to focus on high-magnitude, low-frequency floods (Milan, 2012, Hauer and Habersack, 2009, Thompson and Croke, 2013, Pasternack and Wyrick, 2017, Roghair et al., 2002, Fryirs et al., 2015, Magilligan et al., 2015, Brogan et al., 2017). In contrast, relatively little attention has been paid to the effects of low-magnitude, high-frequency floods, with the exception of studies by Mao and Surian (2010) and

Bertoldi et al. (2010) which identified the capacity of high-frequency floods to drive significant geomorphological change in large, braided, gravel bed rivers. However, small (1st, 2nd and 3rd order) and headwater streams also remain understudied, despite their importance for biodiversity regionally (Meyer et al., 2007) and their diverse physical (geomorphological and hydrological) and chemical environments, which enable the development of diverse ecosystems (Meyer et al., 2007). Understanding how floods can physically impact the geomorphological complexity and thus habitat heterogeneity of small streams is therefore a crucial aspect in understanding the ecological implications of changing future flood regimes (Pearsons et al., 1992, Yarnell et al., 2006).

As well as mobilising sediment through bed and bank erosion, floods facilitate the accumulation of instream wood (Steeb et al., 2017). Research in paraglacial systems has demonstrated a relationship between time since glacial retreat, increasing instream wood abundance and habitat heterogeneity (Klaar et al., 2009, Klaar et al., 2011). Instream wood has been shown to drive localised (10^1 m) changes to velocity profiles, sediment fining and the development of low velocity habitat types (Naiman et al., 1999, Klaar et al., 2011), as well as altering stream wide fluvial processes (Montgomery et al., 1995, Abbe and Montgomery, 1996, Wenzel et al., 2014). Therefore, where increased instream wood abundance occurs it can be expected to play an important geomorphological role in the development of instream habitat heterogeneity.

The physical impacts of flood events are associated with extrinsic thresholds in a system. These are the thresholds at which a system significantly responds to an external or abnormal influence (Schumm, 1979). In a sensitive system, extrinsic thresholds are crossed during a disturbance event and the system is considered to have low resilience to the given disturbance (Fryirs, 2017, Downs and Gregory, 1993, Downs and Gregory, 2004). When extrinsic thresholds are crossed directional changes in riverform (the physical form of the river or stream channel) occur in response to driving variables such as energy for geomorphological change (e.g. a significant flood) or sediment input (e.g. mass wasting event; Miller, 1990, Phillips, 2009, Werritty and Leys, 2001). In an insensitive system (Fryirs, 2017), extrinsic thresholds are not crossed during a flood and subsequently no major changes in riverform are observed and resistance is considered to be high. Intrinsic thresholds (thresholds which when crossed wholescale changes to geomorphological form do not occur) can however be crossed, resulting in small scale changes in riverform composition, such as small-scale sediment mobilisation or bank erosion. Factors which could decrease the sensitivity of a river system include the dominance of large (cobbles and boulders) or very fine (silts and clays) bed sediment sizes, bed armouring, and bank stabilisation through riparian vegetation (Brunsden, 1993, Fryirs, 2017).

Resistance is the capacity of physical features or habitat types to persist through floods and is one component of overall resilience. The other component is the ability of physical features or habitat types to recover/respond during the post-flood period. This metric has been adopted from the ecological literature (Holling, 1973, Milner et al., 2018) and will be used in both physical and ecological discussion throughout this thesis (Chapters 3, 4 and 5). Importantly, the capacity of a stream to resist the physical impacts of floods could have major ecological implications including: the convergence of benthic macroinvertebrate community composition between streams post-flood; shifts in community trait composition, and changes to habitat availability (Pearsons et al., 1992, Robertson et al., 2015, Poff et al., 2018).

In addition to initial impacts, floods can decrease the stability or persistence of geomorphological conditions post-flood (Dean and Schmidt, 2013). Such a decrease in the stability of geomorphological conditions has the potential to influence long term ecological recovery through changes in the available niche space (Roghair et al., 2002, Tunnicliffe et al., 2017). This period of instability is known as the post-flood relaxation stage (Milan, 2012). During this stage, sediments mobilised during floods or mass wasting events, alongside newly accumulated or exposed roughness elements such as instream wood and boulders, drive ongoing geomorphological change (Tunnicliffe et al., 2017). Roughness elements reduce local bed and water surface gradients and facilitate lateral channel movement in proportion to element size (Brummer et al., 2006) as a result of increased local erosion rates around roughness elements (Lester and Wright, 2009). The duration of this relaxation stage is related to the sensitivity of a system; a sensitive system takes longer to recover from a disturbance than a robust system (Brunsden and Thornes, 1979). As a result of this lower capacity to recover post-disturbance, sensitive systems can be considered to have lower resilience to flooding than robust systems.

Instability of geomorphological conditions is similarly observed in recently deglaciated landscapes (Ballantyne, 2002, Carrivick et al., 2013). The processes associated with the release of land from historic glaciation, such as the decreasing availability of glacial sediment over time, are known as paraglacial processes (Church and Ryder, 1972). The concept of paraglacial processes has been applied widely to the sediment dynamics of hillslopes and fluvial systems (Curry, 1999, Church and Ryder, 1972, Carrivick et al., 2013, Legg et al., 2014). Under the paraglacial processes model a catchment’s relative sediment supply begins high as a result of sediment deposition by receding glaciers and decreases with increasing age following an asymptotic curve towards non-glaciated catchments conditions (Ballantyne, 2002). Variation in the relative sediment supply to a fluvial system has been directly related to instream habitat heterogeneity, with a peak in habitat heterogeneity predicted at intermediate relative sediment supplies (Yarnell et al., 2006). This relationship has been observed in Glacier Bay National Park (GBNP), in a study of five small coastal streams with ages ranging from 60 to 200 years since deglaciation (Klaar et al., 2009). Young catchments, with abundant unconsolidated glacial sediment (McColl, 2012), demonstrate high terrestrial landform erosion rates and high sediment availability (Klaar et al., 2015). Such catchments are very sensitive to changing environmental conditions (Ballantyne, 2002, Carrivick and Heckmann, 2017), and thus can be expected to have low physical resilience. Through time, the total sediment availability decreases as vegetation establishes (Eichel, 2019, Eichel et al., 2016) and soil organic matter increases (Sidle and Milner, 1989, Egli et al., 2006, Klaar et al., 2015). This decrease in sediment availability lowers system sensitivity, and results in an increase in physical resilience of older catchments to hydrological variation. Extreme disturbance events, however, such as heavy precipitation and floods, have the capacity to mobilise large amounts of sediment (Zonta et al., 2005, Stocker-Waldhuber et al., 2017).

Riverforms and geomorphological processes are known to vary across multiple spatial scales, and consequently a hierarchical approach to understanding freshwater geomorphology has been established (Pasternack and Wyrick, 2017, Frissell et al., 1986, Beechie et al., 2010). Importantly, biota respond to riverforms and processes at varying spatial scales (e.g. Lammert and Allan, 1999). Benthic macroinvertebrates demonstrate niche differentiation (Reice, 1980), and their life histories are typically associated with CGU scale (10^1 m^2) geomorphological conditions (Blettler et al., 2016). Generally, benthic macroinvertebrate communities are most diverse and abundant in large gravel and cobble substrates, free from fine sediment accumulations (Larsen and Omerod, 2010, Culp et al., 1983). During high flow events, the presence of low velocity habitat units such as backwaters, main channel pools and regions behind very large sediment clasts (e.g. boulders) can confer ecological resistance to stream benthic macroinvertebrate communities, through the dissipation and deflection of the full force of flows creating flow refugia, where peak flow rates remain lower than other areas of the stream channel (Sedell et al., 1990, Masanao et al., 2014, Bogan et al., 2017). Therefore, macroinvertebrate communities in streams with higher hydrogeomorphological complexity may demonstrate higher ecological resistance than communities in streams which support little low velocity habitat, such as streams with high anthropogenic influence (Laub et al., 2012). Fish, including juvenile salmon, are more dynamic in their utilisation of the riverscape than benthic macroinvertebrates, and respond to fluctuations in flow velocities by migrating through the riverscape (Lencioni and Rossaro, 2005, Beechie et al., 2005). Increased geomorphological complexity can, however, enhance the habitat availability for both fry and parr (of varying sizes) particularly through the winter when flows are often high (Johnson et al., 2016). Indeed, the availability of suitable habitat for stream dwelling life stages has been identified as a limiting factor in Pacific northwest coastal stream salmon production (Nickelson et al., 1992).

In this chapter, two spatial scales were selected for analysis. The segment scale (10^3 m) was chosen to assess changes in river planform and geomorphological composition and complexity, and the pool/riffle scale (10^1 m; here the Channel Geomorphological Unit (CGU) scale) was selected to assess localised changes in river geomorphology. The main aim of this chapter is to identify the capacity of extreme high-frequency floods to drive geomorphological change in stream channels and identify the implications of such change for habitat heterogeneity post-flood. To do this four main hypotheses will be tested:

> H1 Extreme high-frequency floods will drive a decrease in river channel positional persistence and drive changes to stream channel form at the segment scale, as a result of significant bank erosion (Pasternack and Wyrick, 2017) and the accumulation of instream wood (Ruiz-Villanueva et al., 2016);
>
> H2 Extreme high-frequency floods will drive increases to geomorphological and habitat complexity at the segment scale, due to the accumulation of instream wood (Klaar et al., 2009, Klaar et al., 2011);
>
> H3 Resilience of habitat heterogeneity will be higher at streams with higher pre-flood geomorphological complexity at both the segment and CGU scales;
>
> H4 Pre-flood trends in CGU scale hydraulic and geomorphological habitat conditions, both within and between streams, will persist post-flood.

3.2 Methods

3.2.1 Study site

Glacier Bay National Park and Preserve, in southeast Alaska (58°10′–59°15′ N; 135°15′–138°10′ W) is dominated by a ‘Y’ shaped tidal fjord, 150 km long and 20 km wide (Figure 3.1). The park covers an area of 11,030 km^2 and has a maritime climate with a mean annual precipitation of 1400 mm. Since the year ~1700, a Neoglacial ice sheet covered the majority of the region which surrounds the now exposed tidal fjord. The rate of retreat of this Neoglacial ice sheet is one of the most rapid in modern global conditions (Chapin et al., 1994).

Fluvial systems establish following glacial retreat and can be aged based upon the time since the glacier retreated from the river mouth based on historic records and imagery (Milner et al., 2000). This ability to age streams allows for a space-for-time substitution approach to be applied in studies of their physical and ecological succession (Milner, 1987, Milner and Bailey, 1989, Sidle and Milner, 1989, Milner et al., 2000, Milner et al., 2008, Klaar et al., 2009, Klaar et al., 2011). In this chapter, four catchments with long term ecological and geomorphological records were selected (Table 1), representing a 141-year age range of catchment and riverine development. Importantly, these streams are a subset of the streams studied in Klaar et al. (2009), Klaar et al. (2011) and Klaar et al. (2015), which allows direct comparisons of findings of previous studies of stream catchment hydrogeomorphology. These second and third order streams were chosen based on the similarities of their catchments and geology (Milner et al., 2000, Klaar et al., 2009, Klaar et al., 2011).

Table 3.1 Physical characteristics of study streams. Catchment size calculated from 2014 southeast Alaska 5 m DEM. Adapted from Klaar et al. (2009).

Site	Stream age (years)	Stream length (km)	Catchment size (km^2)	Average discharge (m^3/s)	Stream order	Dominant substrate type	Average gradient (%)	Dominant riparian vegetation
WPC	70	5.6	29.8	2.29	2	Boulder	1.14	Alder
IVS	146	8.3	19.2	3.02	2	Cobble	0.98	Alder/ Cottonwood
BBS	186	7.2	27.3	4.95	3	Gravel	0.80	Sitka spruce
RPC	211	6.6	26.3	7.51	2	Gravel	0.88	Sitka spruce

The summer of 2014 was characterised by recurrent precipitation from June to August, with more than 100 mm of precipitation falling in three weeks through the summer (one in July and two in August). These persistent precipitation fronts resulted in the summer of 2014 being recorded as the wettest in a 30 year record (Chapter 2) and was associated with the Pacific warm surface water anomaly (Bond et al., 2015). This persistent precipitation drove flooding across the region of southeast Alaska (as described in Chapter 2), including floods with peak discharges four times greater than the median in a local gauged stream (Figure 3.2).

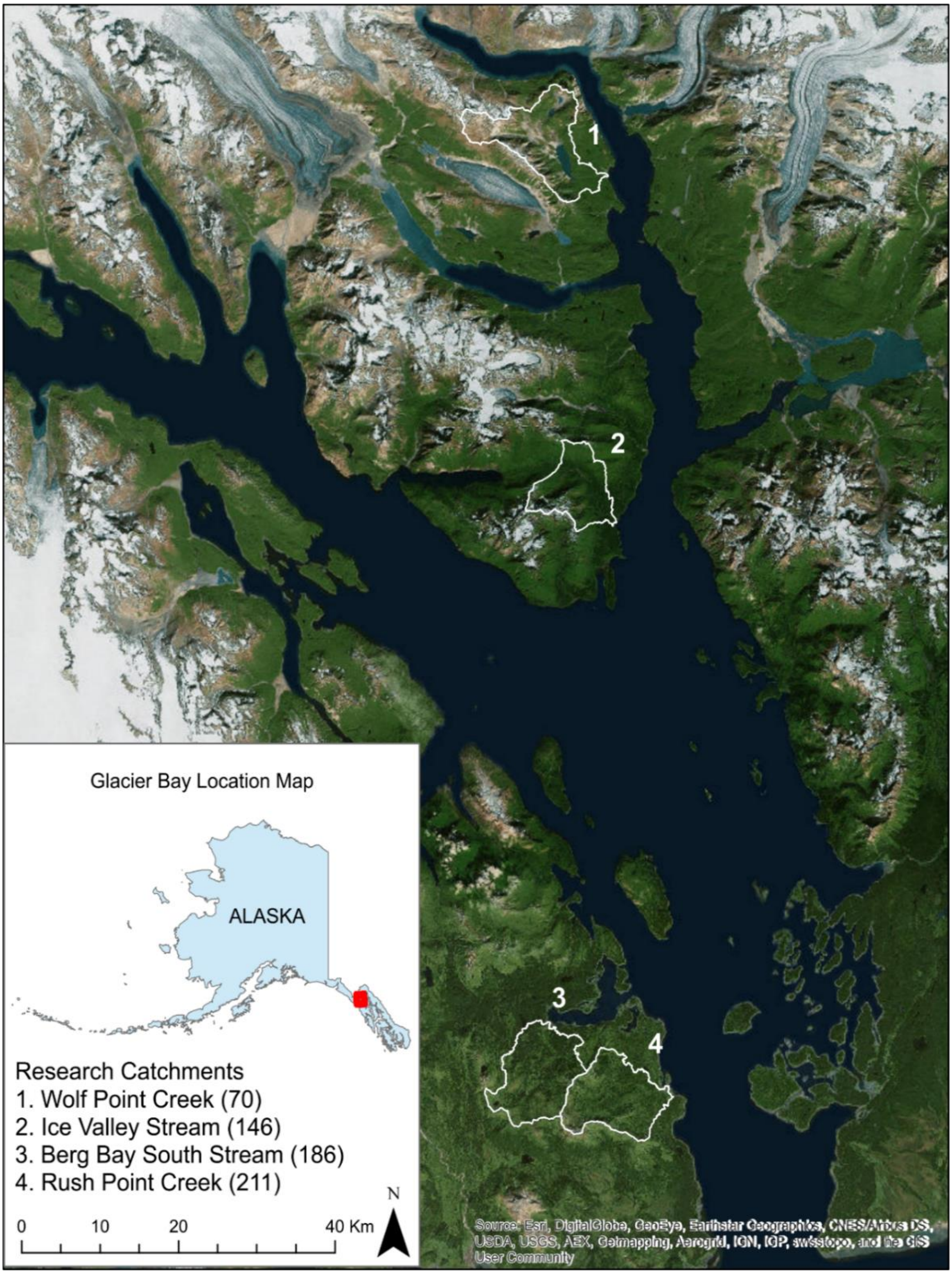


Figure 3.1 Map of Glacier Bay, Alaska. Study catchments outlined in white.

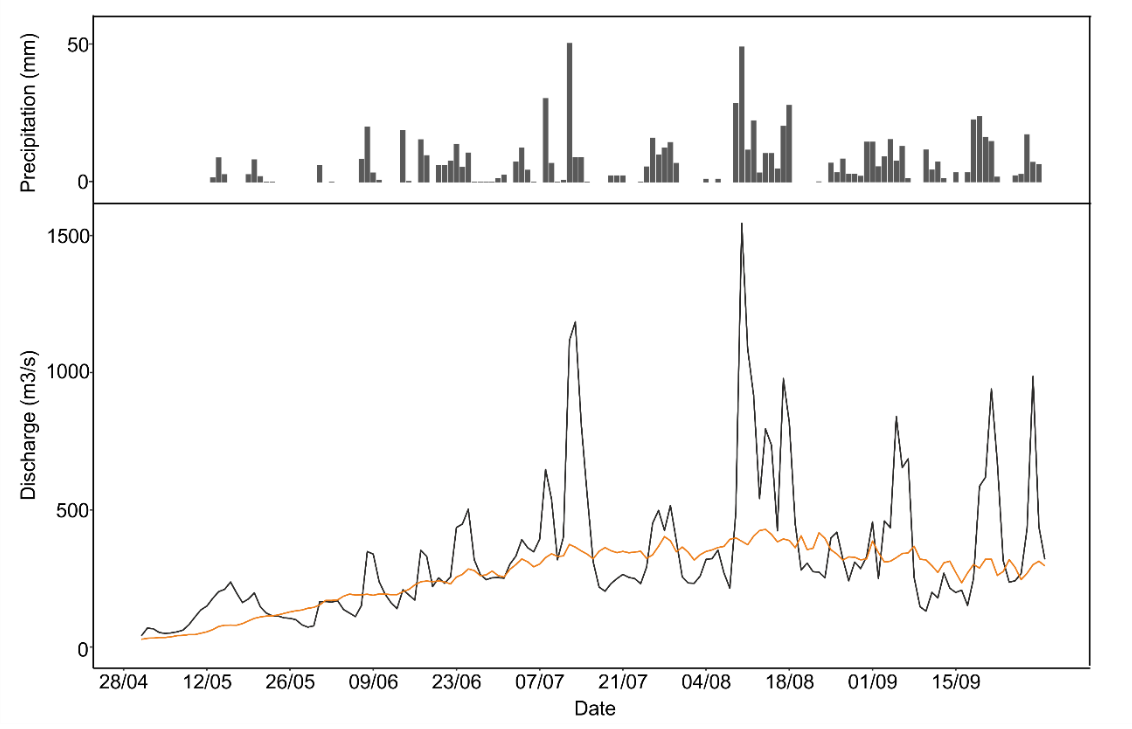


Figure 3.2. Daily precipitation totals (mm) in Bartlett Cove (grey bars). Summer 2014 hydrograph for local stream Lemon Creek (black). Lemon Creek median daily discharge over 33 years (orange).

3.2.2 Segment scale data analysis

Ground based surveys of river planform were undertaken in two pre-flood (2007, 2010) and two post-flood (2016, 2017) years, and river channel position was mapped over a minimum of 1.3 km, starting at the tidal limit of the stream. Mapping was completed to ~ 1 metre accuracy using mapping grade GPS devices, Thales Promark 3 (Magellan, California) and Trimble GeoXT (Trimble Navigation Limited, Westminster, Colorado), and associated Mobile Mapper and Pathfinder software. Subsequent spatial analysis of mapped data was completed in ESRI software ArcMap 10.4.1 and summary metrics, outlined below, were calculated in Microsoft Excel 2013, R Studio version 1. 1. 456 and R version 3. 5. 1 (R-Core-Team, 2017)

Sinuosity of a river channel was calculated using Equation 1, where sinuosity equals the total wetted length of the stream channel divided by the downstream valley length (see Figure 3.3 for example).

$$Sinuosity = \frac{total\ wetted\ channel\ length\ (m)}{downstream\ valley\ length\ (m)}$$ Equation 1

Given the presence of braided sections in each river, sinuosity provides information on the meandering and braided nature of the river concurrently. In this chapter it was not possible to distinguish the main river channel from mapped secondary channels. Therefore, it was not possible to calculate a main channel sinuosity score in this analysis, as argued for by Egozi and Ashmore (2008). To assist in the differentiation of changes in braiding and true sinuosity in this chapter, a braiding index was also calculated (Equation 2). This braiding index score equals the sum of all wetted channels counted in *n* cross sections of river bed divided by *n* (Egozi and Ashmore, 2008).

$$Braiding = \frac{\sum number\ of\ wetted\ channels\ per\ cross\ section}{n} \qquad \text{Equation 2}$$

A percentage metric of wetted channel positional persistence (*persistence*) was also calculated (Equation 3). The metric is based on the persistence of occupied raster cells between two surveys namely either before, before and after or after the floods (Figure 3.3). GPS line maps were converted to raster layers with 5m resolution, and the raster calculator tool in ArcMap was then used to create a new raster layer containing all cells occupied in both surveys. The number of cells occupied in this new raster layer was divided by the total number of unique cells occupied across both surveys (i.e. sum of both raster layers cell counts minus number of shared cells). This was multiplied by 100 to create a percentage score, in which, a score of 100 means the wetted stream channel was identical in both surveys (i.e. no grid cells representing a wetted channel were lost or formed). A score of 0 means no part of a wetted stream channel was shared between the two surveys (no grid cells representing a wetted channel were shared). No survey was available for RPC in 2016 and the subsequent flood comparison analyses used the 2017 survey instead. As such, no further post-flood comparisons were possible (Table 2.1Table 3.2).

$$Persistence = \left(\frac{number\ of\ raster\ cells\ occupied\ in\ both\ layers}{\begin{array}{c}\sum\ number\ of\ unique\ raster\ cells\ occupied\ in\ each\ layer - \\ number\ of\ raster\ cells\ occupied\ in\ both\ layers\end{array}} \right) x\ 100 \qquad \text{Equation 3}$$

The relationship between number of years between surveys and the persistence of wetted channel position was tested using a Generalised Linear Model (GLM) with a gaussian error distribution to identify if differences in the number of years between surveys was a significant predictor of extent of change. If a significant relationship was observed this metric would not have been used to interpret response to the 2014 floods. The model took the form: Persistence = α + β * years between surveys. GLM demonstrated no significant relationship between persistence and years between samples (Figure 9.1), and as such this metric was taken as a true measure of channel persistence.

The locations of instream wood dams and pieces were recorded during surveys. Instream wood was defined as pieces with widest trunk diameters > 10 cm and lengths > 1 m. This was then used to calculate instream wood abundance per 100 m channel length in each survey (Equation 4), by:

$$Instream\ wood\ abundance\ per\ 100m\ = \left(\frac{total\ number\ of\ instream\ wood\ pieces}{total\ wetted\ channel\ length}\right) x\ 100$$

Equation 4

Cross sections established by Sidle and Milner (1989) were surveyed in a number of years pre- and post-flood (years varied with sites, see Figure 3.5). Elevation was measured at 0.5 m intervals across the stream using a dumpy level (Topcon, Tokyo, Japan) mounted on an adjustable tripod. Mapping of river channel geomorphology and hydraulics were undertaken using a CGU approach, first established in GBNP by Klaar et al. (2009). CGUs were mapped using the same approach as for river planform surveys, described in the previous section, along the same survey stretches. During CGU surveys the thalweg length of each CGU was recorded moving downstream based upon a hierarchical visual approach (Hawkins et al., 1993, Klaar et al., 2009). To ensure consistency in the allocation of CGUs to CGU types across years, training was given to new surveyors by previous survey personnel. Surveys were completed at base flow each year. GPS maps were checked for GPS accuracy errors and then lengths of all CGUs were extracted in ArcMap 10.4.1.

Habitat diversity and evenness metrics were calculated for each CGU survey using the software package FRAGSTATS (McGarigal et al., 2012). This program is designed to compute landscape metrics from categorical grid maps. GeoTiff files created from original GPS surveys of stream segments were subsequently analysed to compute Shannon’s and Simpson’s metrics of habitat diversity and habitat evenness.

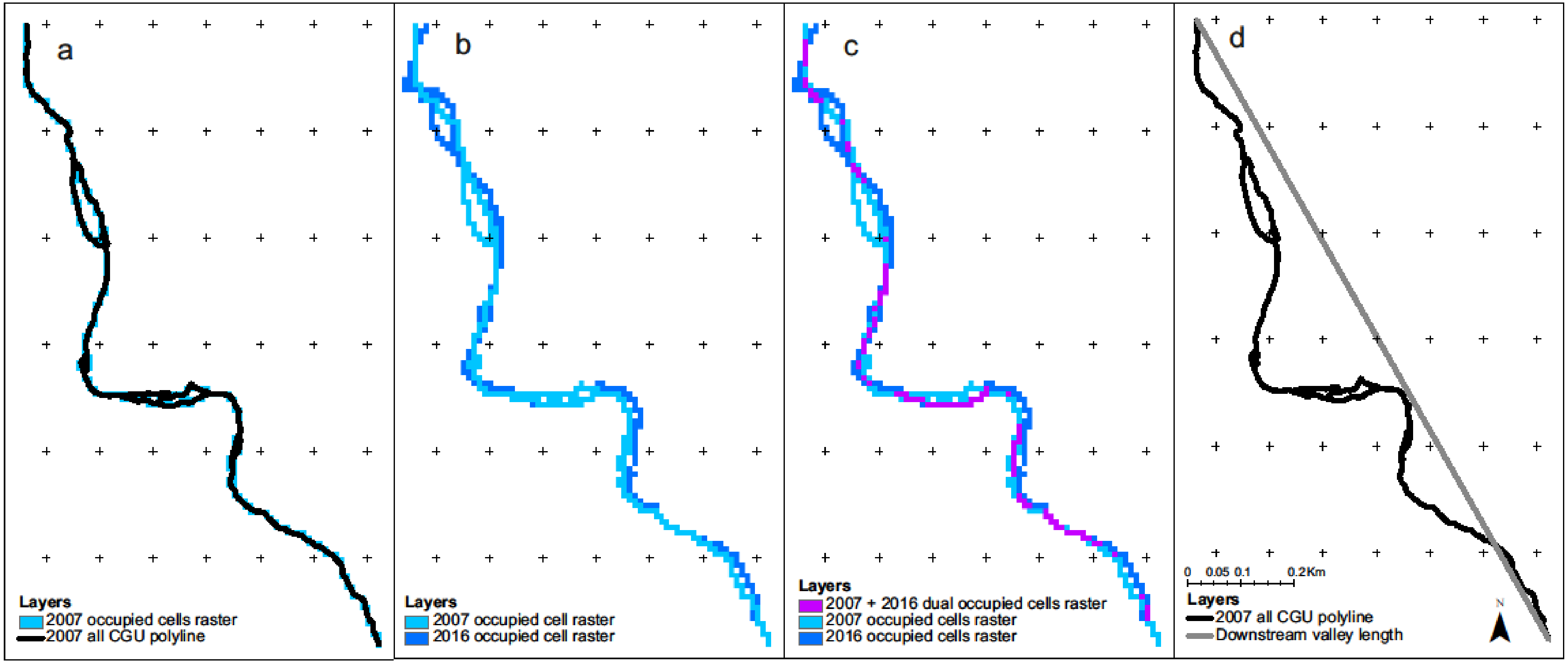


Figure 3.3. Persistence and sinuosity metric calculation steps. Persistence metric score calculation processing steps, showing a) the conversion of polyline shape file (black) to raster (light blue) (GeoTiff), b) overlaying newly created rasters for each pair of years at each site (here BBS 2007 (light blue) and 2016 (dark blue), c) a new raster layer being created containing only cells occupied in both surveys (purple). Sinuosity (d) was calculated by dividing total channel length (black) (here BBS2007) by the downstream valley distance (grey) (distance from most upstream to most downstream points) of each survey.

Shannon’s Diversity Index (SHDI) was calculated using the formula in Equation 5. SHDI increases from 0 to 1 as habitat type richness increases and/or as the proportional contribution of habitat types becomes more equitable. When compared to Simpson’s Diversity Indices (SIDI), SHDI is more sensitive to rare habitat types. SIDI is calculated using Equation 6, and as scores increase from 0 there is an increased likelihood that two cells chosen at random will be of different habitat types. In both indices P_i equals the proportion of landscape occupied by habitat type *i*.

$$SHDI = -\sum_{i=1}^{m}(P_i * lnP_i) \quad \text{Equation 5}$$

$$SIDI = 1 - \sum_{i=1}^{m}(P_i^2) \quad \text{Equation 6}$$

Shannons Evenness Index (SHEI; Equation 7) equals 1 when the distribution of area between patches is even and decreases as the distribution of area between patches becomes more uneven. SHEI equals zero when there is only one patch. The expression of SHEI means that a completely even distribution of area between patches results in a maximum evenness score. Simpsons Evenness Index (SIEI) describes evenness in the same manner as SHEI but based on its associated SIDI scores and as such is less sensitive to rare habitat types than SHEI.

$$SHEI = \frac{-\sum_{i=1}^{m}(P_i * lnP_i)}{\ln(m)} \quad \text{Equation 7}$$

$$SIEI = \frac{1 - \sum_{i=1}^{m}(P_i^2)}{1 - \left(\frac{1}{m}\right)} \quad \text{Equation 8}$$

3.2.3 CGU scale data analysis

In 2017, detailed hydraulic surveys were completed to assess differences in post-flood hydraulic conditions. These surveys were undertaken in all CGU types present at each stream. A minimum of 20 water velocity measurements (at 0.6 m depth using a SonTek FlowTracker2 (FT2) handheld Acoustic Doppler Velocimeter (ADV®)) and 20 total depth measurements were taken across two cross sections at representative locations in each CGU (Casado, 2006). Whilst efforts were made to survey at base flow, one of the two days surveying at RPC is thought to have been at slightly above base flow. On this day riffles and runs were predominantly surveyed.

Depth and velocity data were further assessed using Hydrosignature (Le Coarer, 2005) which classifies surface depth and velocity data into classified grids, providing percentages of surface depth and velocities per 0.2 m^2 grid cell. This grid describes the hydraulic diversity of a dataset as a two-dimensional depth/velocity plane, referred to as a hydrosignature (Le Coarer, 2005).

Hydrosignatures were created based on each CGU unit by inputting data using the NOXY2 method, which assimilates measurements using pseudo-spatialization based on a Froude number. Froude numbers were calculated using Equation 9, where velocity is divided by gravitational acceleration multiplied by channel depth.

$$Froude\ number\ = \frac{velocity\ (\frac{m}{s})}{gravity\ \left(\frac{m}{s^2}\right) * water\ depth\ (m)} \qquad \text{Equation 9}$$

The NOXY2 method allows multiple cross sections to be combined (Scharl and Coarer, 2005). Plotting hydraulic conditions in two dimensions in this way has been shown to allow for greater differentiation between CGUs than using standard statistical approaches and individual hydraulic parameters (Moir and Pasternack, 2008). After creating hydrosignatures for individual CGUs, a built-in Hydrosignature Comparison Index (HSC) was used to compare between hydrosignatures. The HSC approach uses a spatial analysis filtering technique with the aim of producing a comparison matrix for two (or two sets of) hydrosignatures. Subsequently, Hydrosignature produces a single HSC total score of between 0 and 100 for the comparison. A score of 0 implies two hydrosignatures are completely homogenous and therefore identical, whereas a score of 100 suggests the two are completely heterogeneous and therefore unique from one another.

HSC was applied in two ways. Firstly, at each stream a comparison was made between all CGUs of the same type, hereafter referred to as intra-stream comparisons. Such comparisons of all CGUs of one type, within a stream, provides an understanding of consistency of conditions within a CGU type. Secondly, each CGU type was compared across streams, hereafter referred to as inter-stream comparisons. This approach facilitates an understanding of variation in hydraulic conditions between sites of different ages.

In addition to the analysis of CGU hydrosignatures, single dimensional comparisons of velocity, depth and Froude numbers were made for each CGU type across streams. In CGUs where hydraulic surveying took place, sediment surveys were completed to assess substrate compositional change associated with the flood time period. Sediment was sampled using a modified Wolman walk where individual pieces of sediment were selected at random within each CGU (Wolman, 1954, Bevenger and King, 1995). In 2008, a minimum of 30 and in 2017, a minimum of 200 sediment β axis lengths were measured in each CGU surveyed. Median particle size (D_{50}) was calculated and cumulative frequency curves were plotted for each stream overall and for each CGU type in each stream. Full stream cumulative frequencies were compared between years at each site using Kolmogorov – Smirnov tests (Holm adjusted p values).

3.3 Results

3.3.1 Segment scale

Differences in the *persistence* of the wetted stream channel were observed across the geomorphological complexity gradient during pre-flood and post-flood time periods (Table 3.2). During the pre-flood period (2007-2010) *persistence* of the location of the stream channel was high (>50 %) across all sites. The highest pre-flood score was recorded at the oldest site (RPC – 66 % persistence) (Table 3.2. Persistence scores for pre-, flood and post-flood periods. These values are percentages where 100 indicates no change in stream channel position and 0 indicates complete change of position.Table 3.2.; Figure 3.4d), whilst the lowest score was recorded at the intermediate age site (IVS – 52 %; Figure 3.4b). The range of *persistence* scores across streams was lower during the pre-flood period (14 %), than subsequent flood (26 %) and post-flood (34 %) time periods. During the flood time period, *persistence* declined at all sites, with the youngest site (Figure 3.4a) demonstrating the highest *persistence* (51 %), followed by the intermediate aged site (44 %) and with the oldest sites having the lowest persistence scores (RPC – 42 % and BBS – 25 %). The same relationship between sites was identified during the post-flood period. However, at all sites scores were higher post-flood than during the flood period. Post-flood, WPC had the highest score recorded during any period, with 73 % of the wetted river channel remaining in the same position between surveys. IVS had a score of 48 % persistence (similar to its pre-flood and flood period scores), whilst BBS (Figure 3.4c) post-flood had the second lowest *persistence* score recorded at any time (39 %).

Table 3.2. Persistence scores for pre-, flood and post-flood periods. These values are percentages where 100 indicates no change in stream channel position and 0 indicates complete change of position.

Period	WPC	IVS	BBS	RPC
Pre-flood (2007 v 2010)	58	52	-	66
Flood (2010 v 2016 (2017 at RPC))	51	44	25	42
Post-flood (2016 v 2017)	73	48	39	-

Stream channels varied between years and streams as illustrated in the stream segment planform maps (Figure 3.4). Pre- and post-flood sinuosity and braiding index scores varied across the chronosequence (Table 3.3). At the youngest site (WPC), sinuosity decreased (1.7 to 1.6) to the lowest observed sinuosity score in this chapter, whilst the braiding index score remained consistent (1.2) and was joint lowest post-flood (with the oldest site RPC). The intermediate site

(IVS) had the highest pre- and post-flood sinuosity score, however the score declined from 2.2 to 2.0 after flooding, and conversely the braiding index increased from 1.2 to 1.4 post-flood. The oldest sites (BBS and RPC) displayed consistent increases in braiding and sinuosity scores with small increases in both following flooding. Pre-flood, instream wood abundance varied with increasing stream age (Table 3.3). This relationship changed dramatically post-flood. The youngest stream (WPC) demonstrated a loss of wood (1.3 to 0.8 pieces/100 m), whereas all other streams accumulated large amounts of wood, with IVS almost doubling its instream wood abundance (1.3 to 2.5 pieces/100 m) and large increases were recorded at BBS (1.4 to 2.4 pieces/100 m) and RPC (1.8 to 2.4 pieces/100 m).

During the pre-flood time period, cross sections across all the study streams demonstrated relatively consistent wetted channel position and structure (Figure 3.5a and Figure 3.5b). Whilst channel migration was recorded at some sites, the rate of movement was typically low. Generally, thalweg position moved <1 m between any pair of surveys, and the scour or deposition of large amounts of sediment was uncommon.

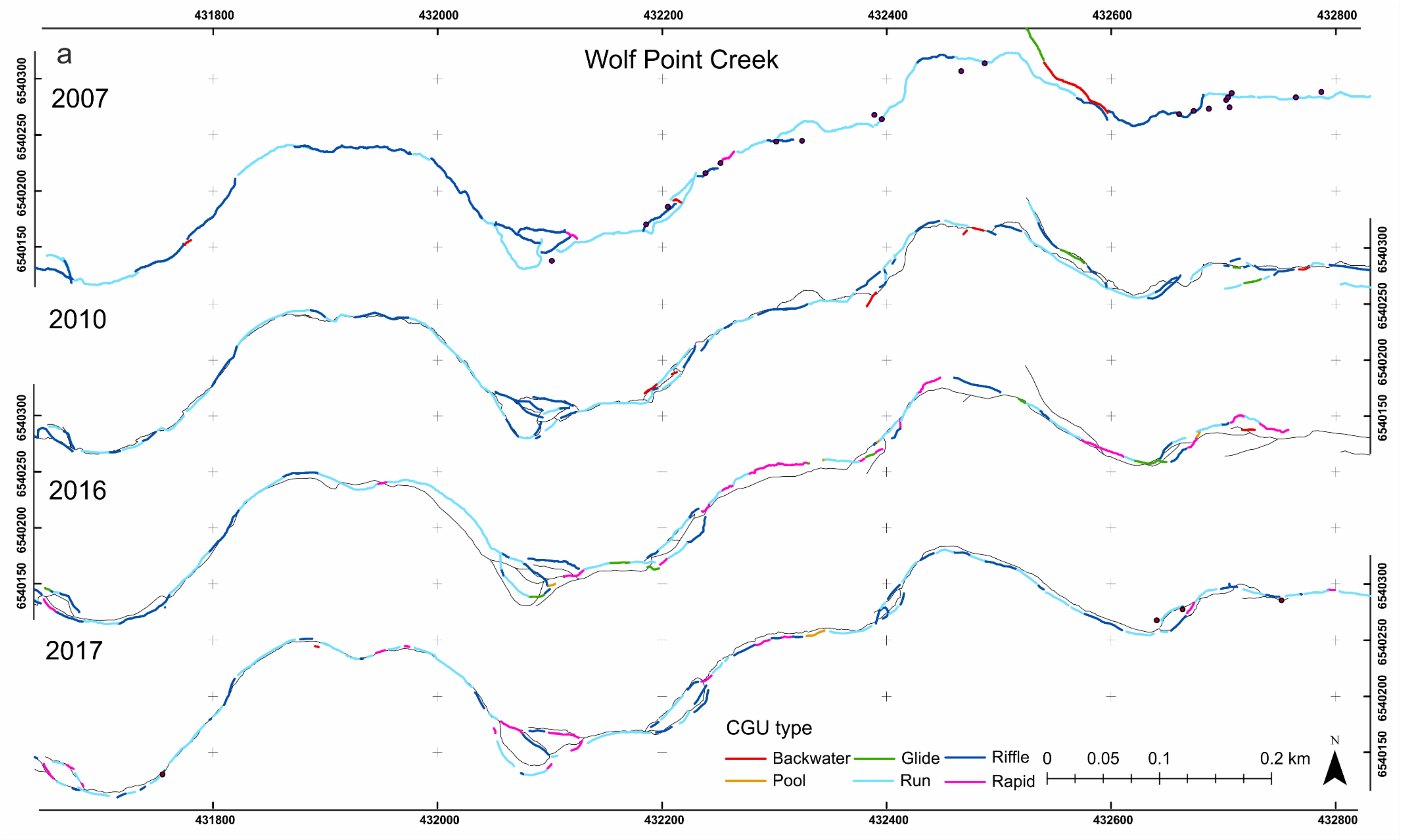
Table 3.3. Summary metrics for river planform surveys in pre (2010 (Instream wood abundance (2008)) and post-flood years (2016).

Metric	Period	WPC	IVS	BBS	RPC
Sinuosity	Pre	1.7	2.2	1.8	1.6
	Post	1.6	2.0	1.9	1.7
Braiding	Pre	1.2	1.2	1.4	1.1
	Post	1.2	1.4	1.5	1.2
Instream wood abundance pieces/100m	Pre	1.3	1.3	1.4	1.8
	Post	0.8	2.5	2.4	2.4

At WPC, both cross sections' wetted channel positions remained consistent in the pre-flood period, following a deepening of the wetted channel between 2007 and 2008 surveys. This consistency remained in post-flood surveys with little change in channel depth and position following flooding. Post-flood, a small movement toward the left-hand bank was recorded in the position of the lower cross section channel thalweg (<2 m).

At IVS, the upper cross section was very consistent in all pre-flood surveys. Post-flood surveys showed limited initial response to flooding, then changes in wetted channel position by 2016, and subsequently by the final survey (2017) 0.8 m of sediment had accumulated in the pre-flood wetted channel, while the wetted channel position had migrated by 10 m to the right (Figure 3.5c). The lower site cross section illustrated a more dynamic channel which migrated through time. Post-flood surveys recorded a shift in channel position of up to 8 m per year (Figure 3.5d). By the final survey almost 1 m of sediment had been scoured from the new wetted channel.

At the BBS upper cross section, two wetted channels were recorded from 2007 to 2010 (see Figure 3.5e and Figure 3.5f for 2010 positions). These channels were replaced in 2011 by a single wider wetted channel, which occupied both previously wetted channels and the space between them. This new wetted channel narrowed post-flood and two backwater channels were established. During the final two surveys (2016 and 2017) the main channel had shifted to the far left of the channel, occupying the position of a backwater recorded in 2015. At the lower cross section, a main wetted channel and a small <2 m wide backwater were consistently recorded pre-flood. Post-flood (2015; Figure 5f), the main channel had migrated 14 m and an additional small channel had been established. During the final post-flood survey, the main channel migrated an additional 10 m leaving the formerly wetted channel dry. A large upstream wood dam facilitated sediment deposition in the former channel upstream of the cross section and was likely to have been associated with wetted channel migration.


a
Wolf Point Creek
2007
2010
2016
2017
431800
432000
432200
432400
432600
432800
6540150
6540200
6540250
6540300
CGU type
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Riffle
Pool
Run
Rapid
0
0.05
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0.2 km
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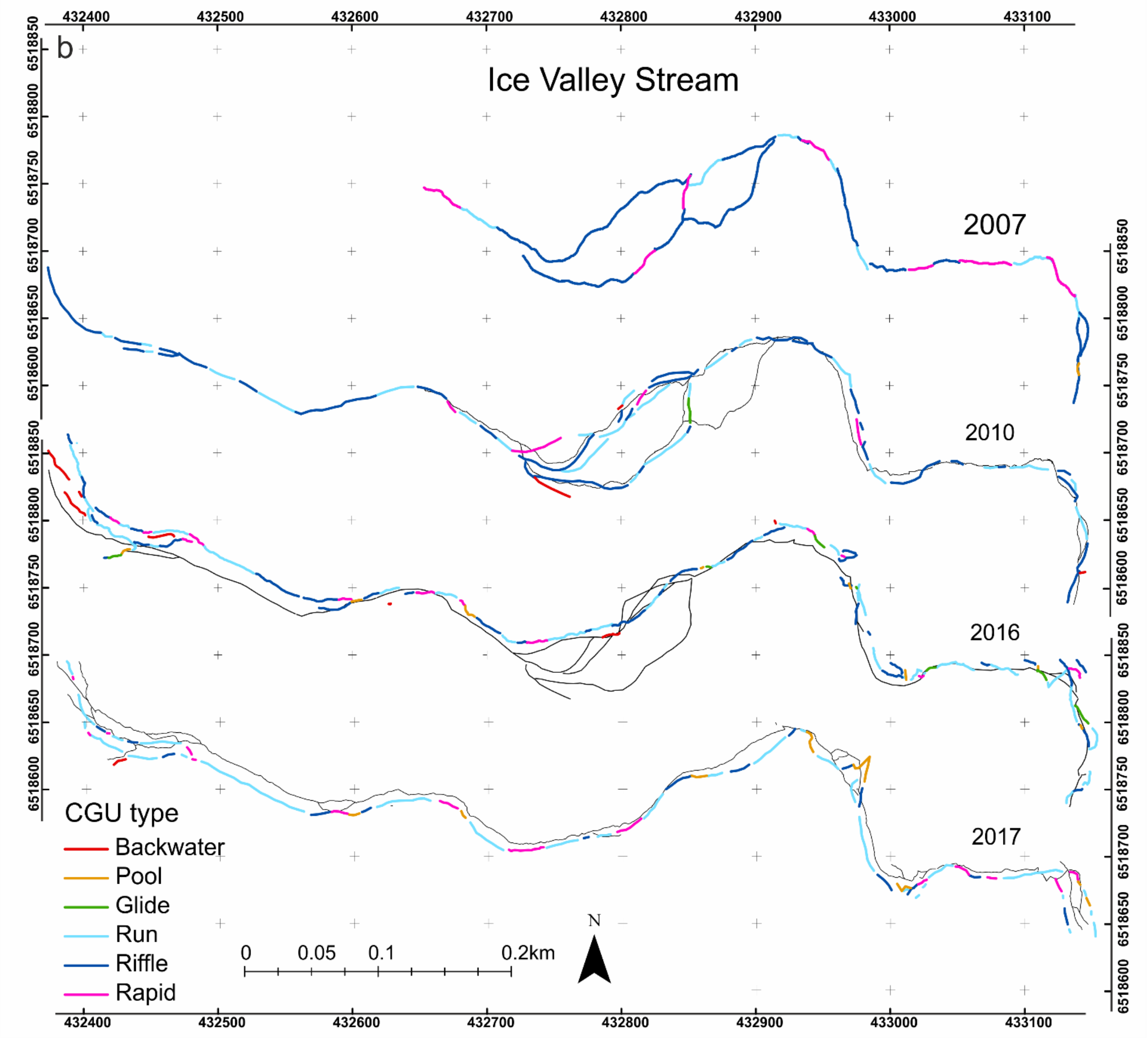
b
Ice Valley Stream
2007
2010
2016
2017
CGU type
Backwater
Pool
Glide
Run
Riffle
Rapid
0
0.05
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432400
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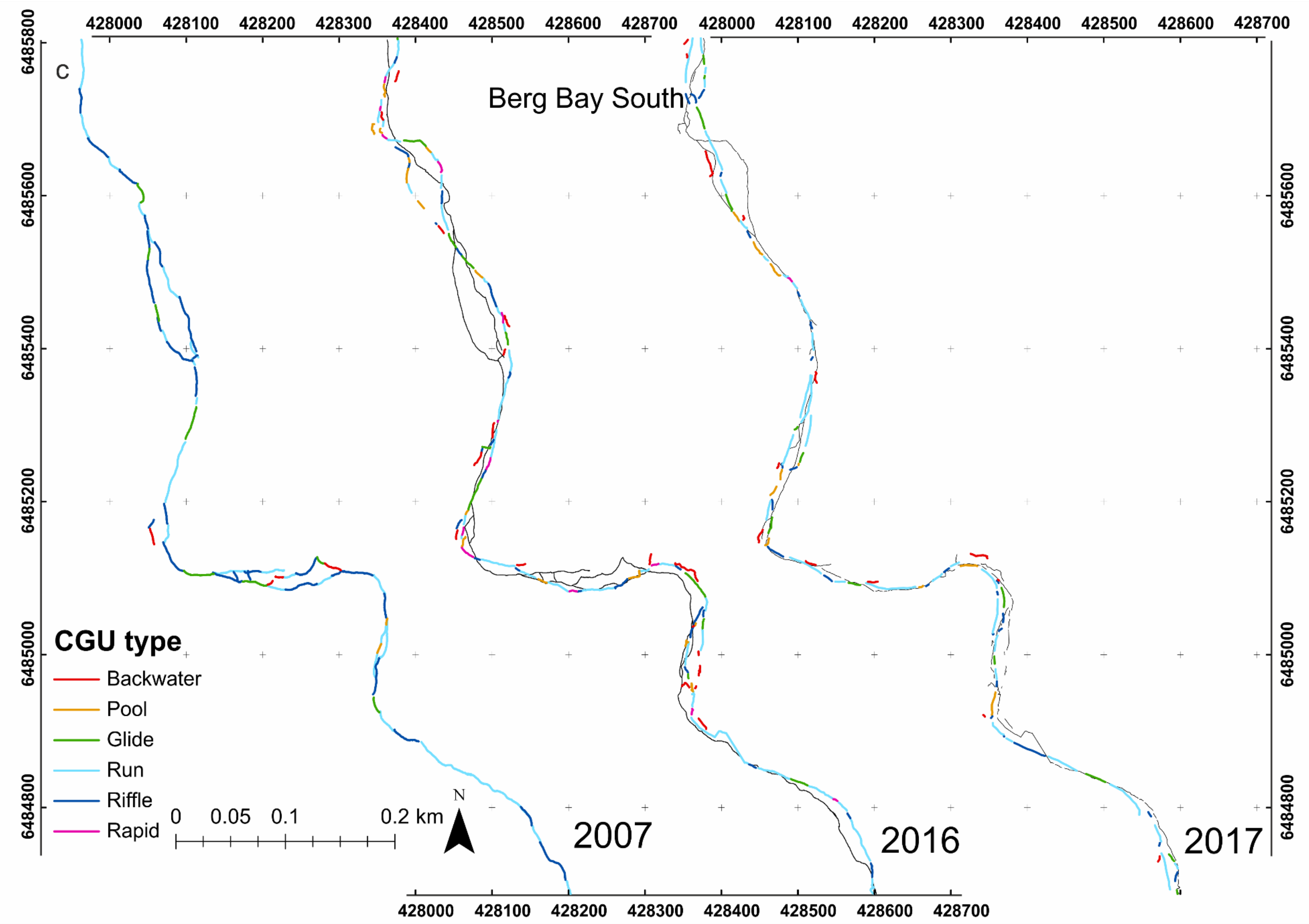
c
Berg Bay South
CGU type
Backwater
Pool
Glide
Run
Riffle
Rapid
0
0.05
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2007
2016
2017
428000
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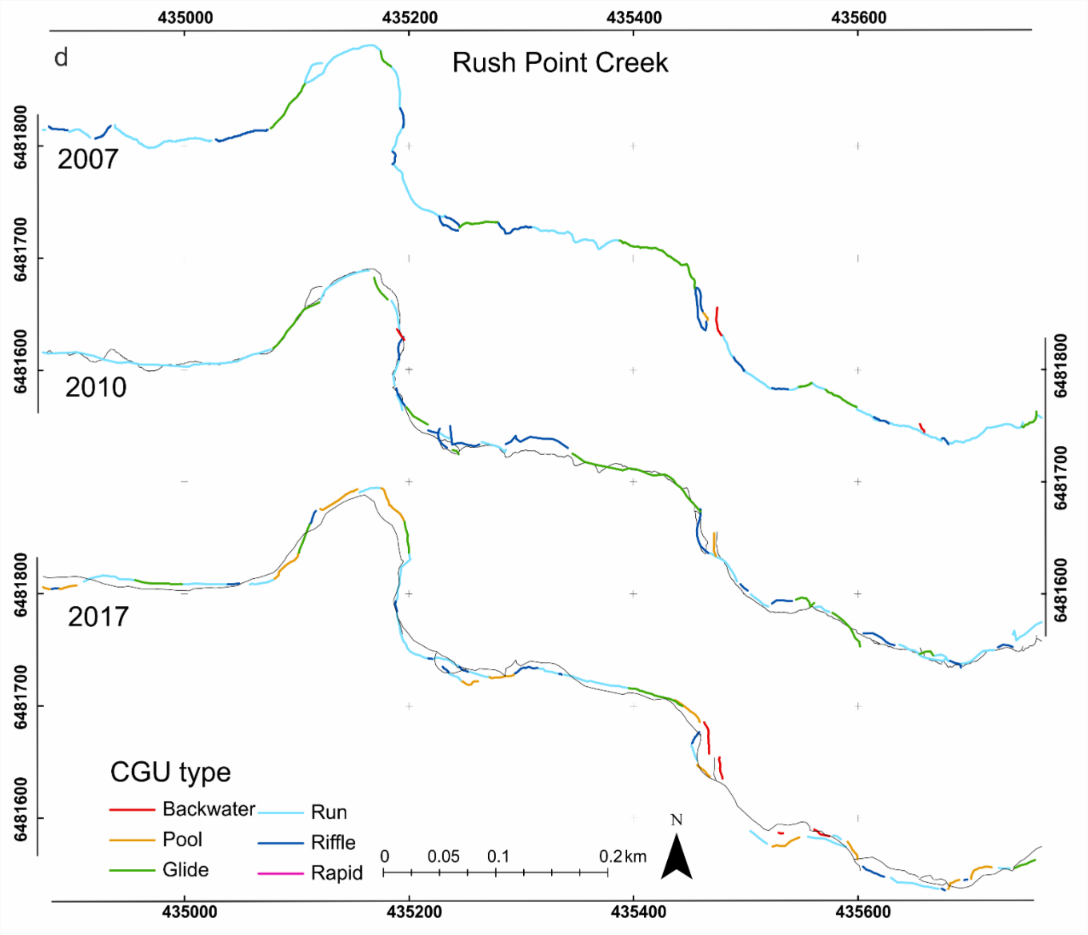

Figure 3.4. Stream planform CGU maps for all survey years. Black line – previous survey position

The oldest site, RPC, demonstrated a varied response across post-flood surveys at the two cross sections. The upper cross section wetted channel position remained relatively consistent throughout all surveys, being comprised of a main channel and small backwater (Figure 3.5g). However, in post-flood surveys the backwater showed fluctuations in width and depth. At the lower cross section pre-flood wood accumulated in the channel due to bank erosion. Following flooding this part of the cross section saw the deposition of large amounts of sediment (>1 m) which was then scoured before the final survey (2017; Figure 3.5h).

Pre-flood trends in sediment β axis cumulative length frequency curves persisted following flooding, with older sites (BBS D_{50} = 31 mm, RPC D_{50} = 37 mm) having finer sediments than younger sites (IVS D_{50} = 76 mm, WPC D_{50} = 84 mm; Figure 3.6). Significant difference in sediment cumulative length frequency was identified at RPC (Table 3.4), with post-flood curve dominated by finer sediments. Contrastingly, at BBS a loss of fine sediments was identified following flooding, associated with statistically significant changes in cumulative length frequency curves (Table 3.4) between initial and post-flood surveys.

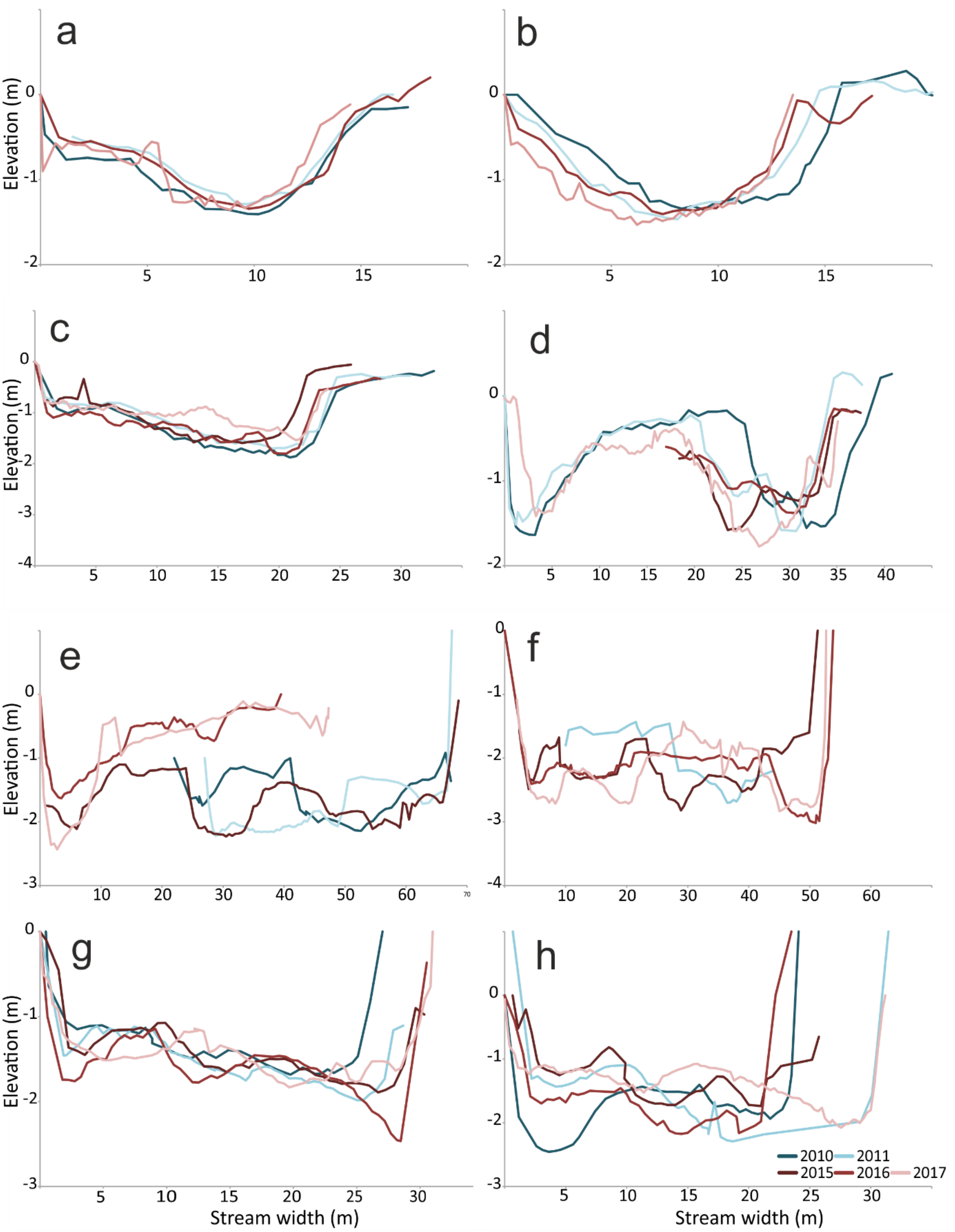

Figure 3.5. Stream bed profiles at upper and lower cross section sites for all sites in pre- and post-flood years. See legend for individual years. a – WPC upper, b – WPC lower, c – IVS upper, d – IVS lower, e – BBS upper, f – BBS lower, g – RPC upper, h – RPC lower.

Table 3.4.. Kolmogorov - Smirnov tests p values (Bonferroni adjusted) for comparison of sediment size between years and across streams.

	IVS 08	**BBS 08**	**RPC 08**
IVS 17	0.391	<0.001	<0.001
BBS 17	<0.001	<0.001	<0.001
RPC 17	<0.001	0.063	<0.001

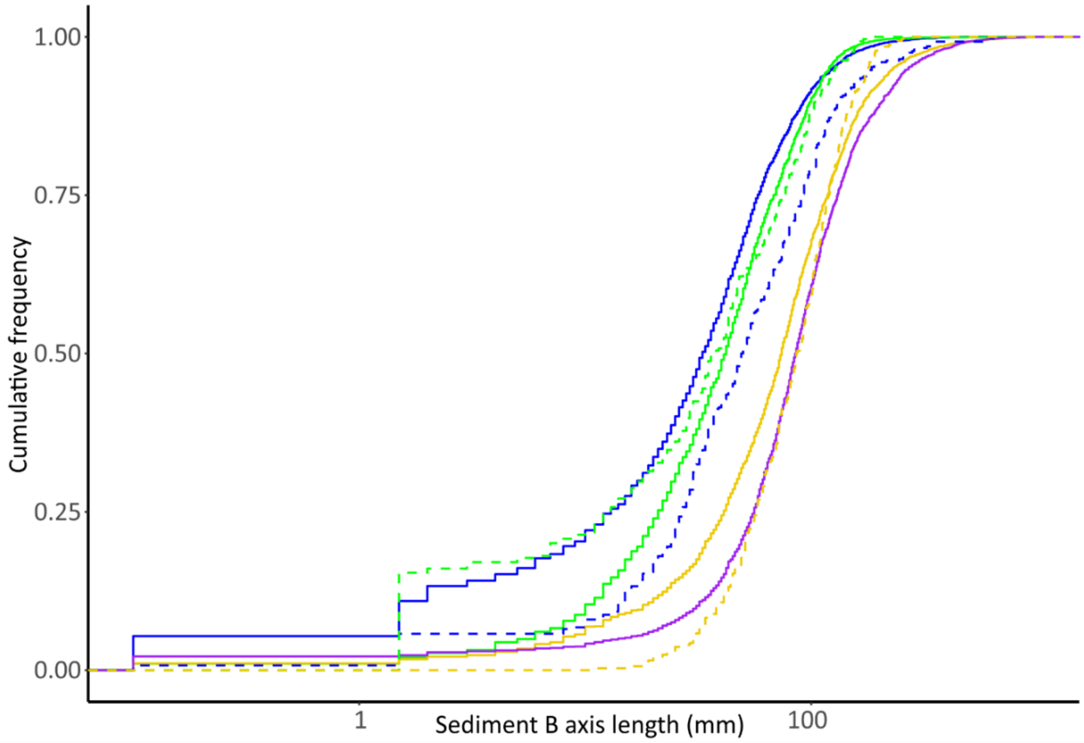

Figure 3.6. Full stream segment sediment b axis length cumulative frequency curves solid lines 2017 dashed lines 2008. WPC – purple, IVS – red, BBS - green, RPC - blue.

Pre-flood CGU composition was consistent between years across the geomorphological gradient, with CGU diversity increasing as streams increased in age (Figure 3.7.), consistent with the findings reported in Klaar et al. (2009) for the same GBNP streams. This general relationship remained consistent following flooding. However, CGU compositional change varied through time at each site during the post-flood time period. WPC demonstrated limited change in overall CGU composition following flooding, although an increase in the proportional contribution of rapids was identified, as well as a small loss of slower flowing CGUs. The major response observed at IVS was a shift in dominant CGU types from riffles to runs, as well as year-on-year increases in slow flowing CGU types (particularly pools) post-flood. The post-flood responses at the two oldest sites (BBS and RPC) contrasted. At the highly dynamic BBS the establishment of pools was recorded in the first post-flood survey (2015), which persisted during the subsequent surveys. The initial response at RPC differed from BBS with a loss of pools post-flood, which subsequently re-established by 2017. All streams but WPC (the youngest site) demonstrated increased abundance of slow flowing CGUs by the final survey (2017) compared to pre-flood surveys. Equally all sites, except WPC, showed greater evenness and diversity scores for CGU type contributions in post-flood than were recorded pre-flood (Figure 3.8.).

When compared across the geomorphological gradient, trends in sediment composition observed at the segment scale were mirrored in CGU specific cumulative length frequency curves. Older sites typically had finer sediments than younger sites across all CGU types. Fine sediments were more abundant in slower flowing CGU types (pools and glides) whilst larger sediment sizes were typically found in faster and more turbulent flow CGU types (rapids and riffles). These relationships persisted following flooding with a general trend for fining of sediment post-flood (Figure 3.8., Table 3.5.). The exceptions to this trend were in rapids at IVS and in runs and glides at BBS, which saw coarsening of sediments following flooding (Figure 3.9., Table 3.5.).

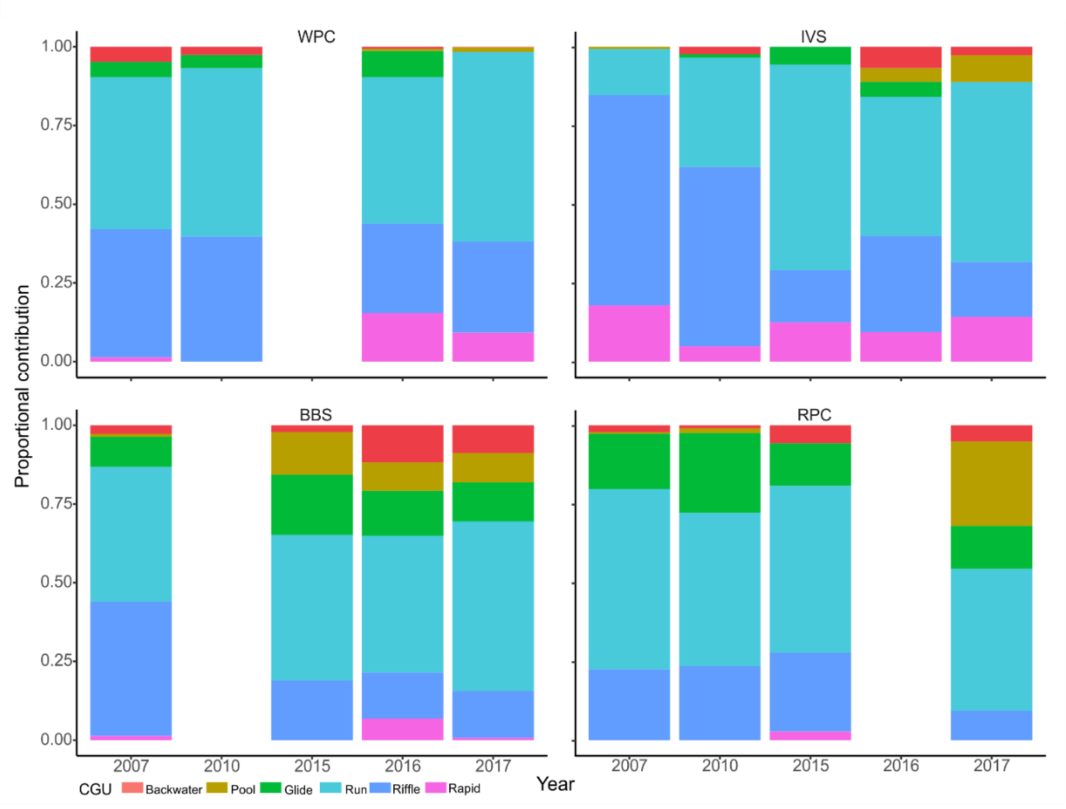

Figure 3.7. Cumulative proportion bar charts for all streams study segments in all years.

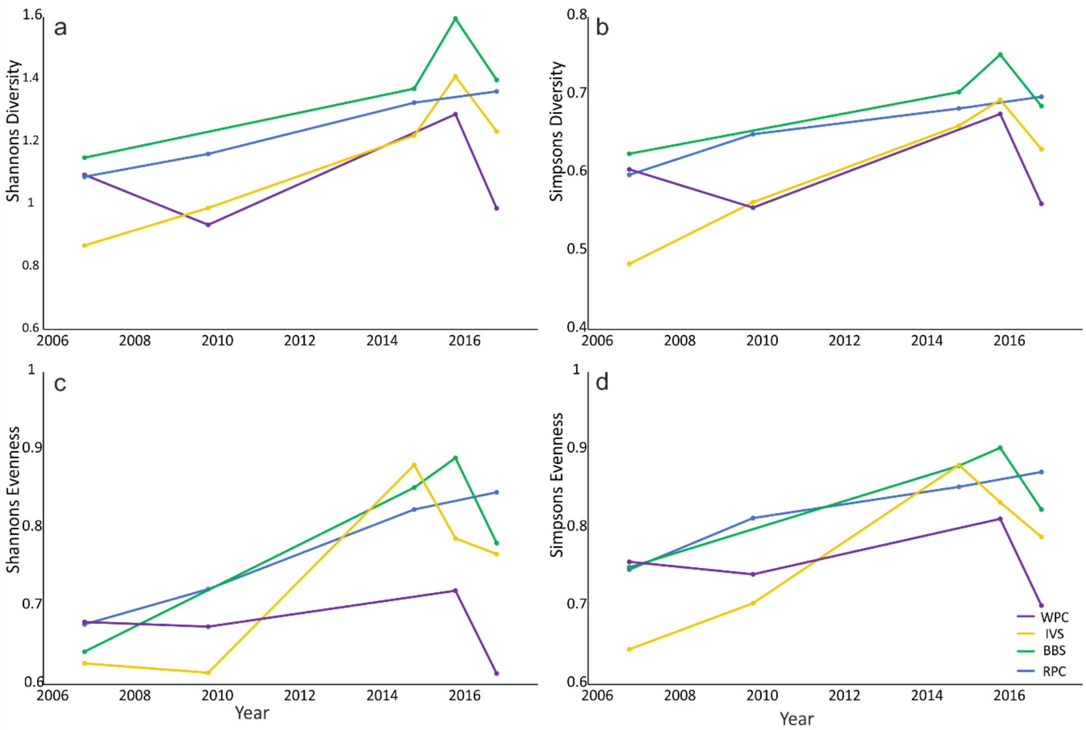

Figure 3.8. Diversity and evenness metrics for all streams in all survey years. a) Shannon's diversity, b) Simpson's diversity, c) Shannon's evenness, d) Simpson's evenness

Table 3.5. Pre- and post-flood sediment b axis D50 (mm) values for all CGU types at each stream. A '–' indicates that the CGU type was not present at a given stream in that year. No sediment data is available for WPC in 2008

Site	Year	Rapid D_{50} (mm)	Riffle D_{50} (mm)	Run D_{50} (mm)	Glide D_{50} (mm)	Pool D_{50} (mm)
WPC	2008					
	2017	128	86	83	-	46
IVS	2008	94	85	88	70	-
	2017	109	84	69	-	24
BBS	2008	-	68	41	11	75
	2017	85	55	44	32	22
RPC	2008	-	93	38	40	37
	2017	-	74	37	26	18

Intra-stream CGU consistency of HSCs varied greatly between CGU types and across the geomorphological gradient (Table 3.6.). Slow flow CGUs had both the lowest and highest HSC scores across intra-stream comparisons. Glides demonstrated consistently low (hydraulically similar) HSC scores across sites (14-20) whilst pools demonstrated consistently high (dissimilar) HSC scores (30-41). In fast flowing CGU types both riffles (20-33) and rapids (18-35) displayed relatively low HSC scores across streams, whilst runs showed the widest range of intra-stream CGU HSC scores (12-43). In the intra-stream CGU comparisons, the youngest (WPC) and oldest (RPC) sites generally demonstrated higher HSC scores and therefore greater diversity in hydrosignatures than IVS and BBS.

In inter-stream CGU comparisons, HSC scores were highest (most dissimilar) in comparisons involving WPC, and these scores were typically higher than intra-stream scores for individual sites involved in the inter-stream comparison (Table 3.6). Inter-stream HSC scores in WPC comparisons were on occasions up to three times higher than the individual site's intra-stream scores. This differed markedly to inter-stream CGU comparisons between the old and intermediate age sites' HSC scores, which were often consistent with the variation found during intra-stream analyses HSC scores. Inter-stream comparisons between IVS and BBS resulted in the lowest HSC scores for all CGU types compared.

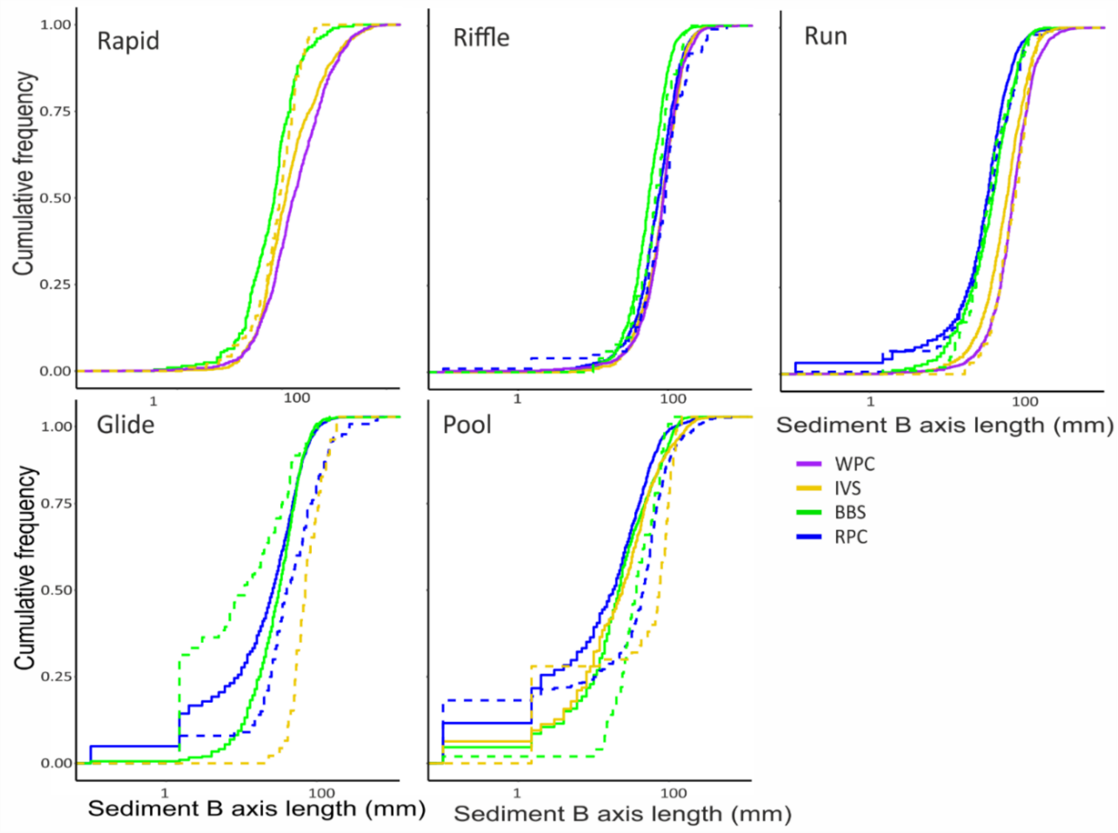

Figure 3.9. CGU specific sediment β axis length cumulative frequency curves solid lines for 2008 (dashed lines) and 2017 (solid lines).

In addition to HSC comparisons, tests for differences in depth, velocity and Froude numbers between sites showed significant differences across the age gradient (Figure 3.10.). Mean depths of CGU types at WPC were generally similar, whilst a broad range of mean velocities were observed across CGU types. The widest range of mean depths was observed at the older streams (BBS and RPC). These sites generally had lower velocities than WPC and were also more consistent across CGU types. IVS demonstrated an intermediate range of mean depths and velocities across CGU types.

Table 3.6. Hydrosignature comparisons (HSC) of CGUs within each site to assess internal consistency and CGUs between sites to access variation across the geomorphological complexity gradient post-flood. 0-10 no colour, 10-20, 20-30, 30-40, 40-50, 50-60, 60+. Dash indicates insufficient data was available for comparisons

CGU	**WPC**	**IVS**	**BBS**	**RPC**
Pool	41	33	30	35
Glide	-	-	20	14
Run	32	12	21	43
Riffle	22	29	20	33
Rapid	35	18	21	-

Pool

Site	**WPC**	**IVS**	**BBS**	**RPC**
WPC				
IVS	42			
BBS	49	33		
RPC	50	39	35	

Glide

Site	**WPC**	**IVS**	**BBS**	**RPC**
WPC				
IVS	-			
BBS	-	-		
RPC	-	-	35	

Run

Site	**WPC**	**IVS**	**BBS**	**RPC**
WPC				
IVS	49			
BBS	48	17		
RPC	47	37	39	

Riffle

Site	**WPC**	**IVS**	**BBS**	**RPC**
WPC				
IVS	42			
BBS	47	29		
RPC	30	36	36	

Rapid

Site	**WPC**	**IVS**	**BBS**	**RPC**
WPC				
IVS	55			
BBS	61	24		
RPC	-	-	-	

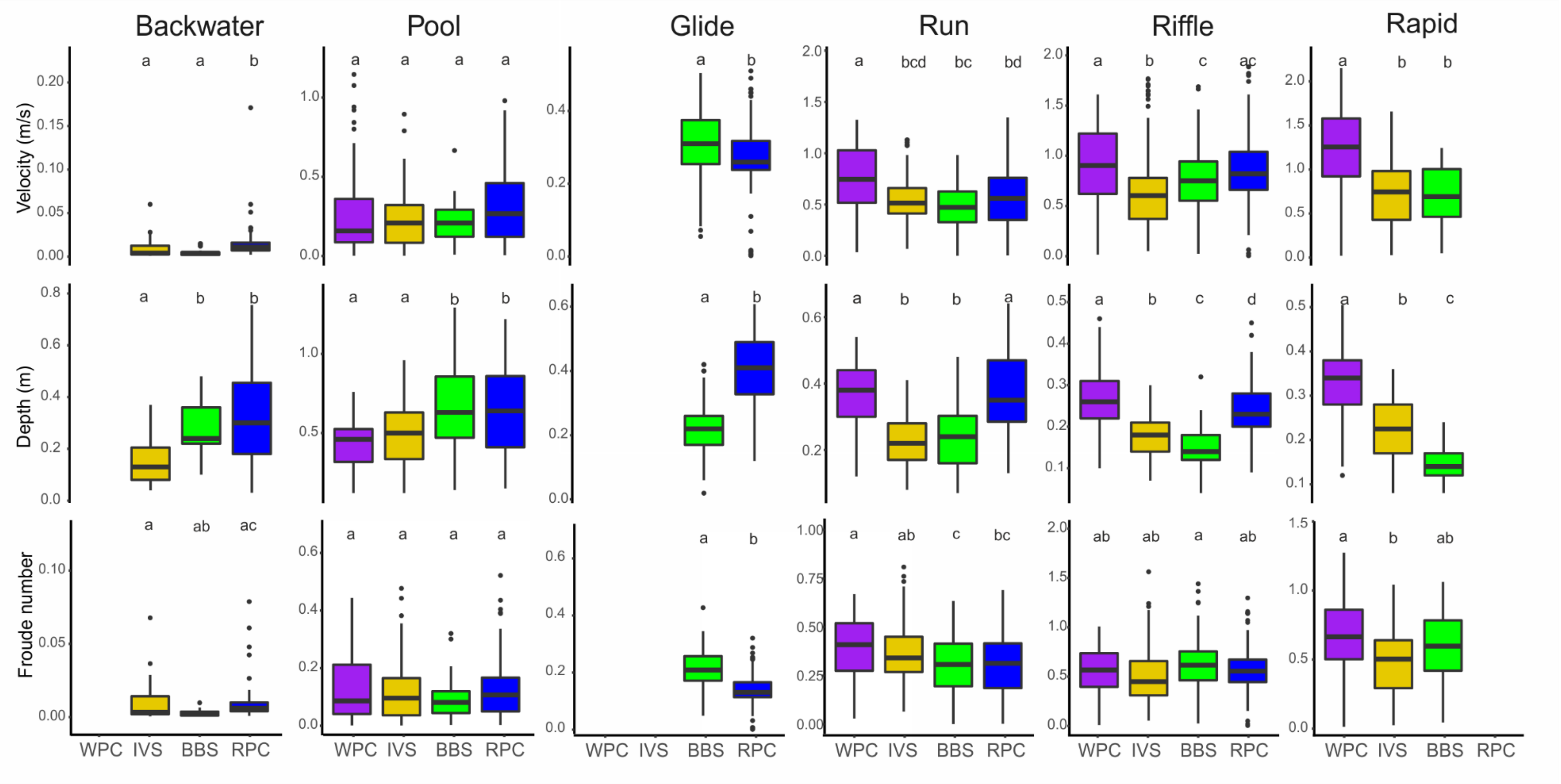

Figure 3.10. CGU type specific Velocity (m/s), Depth (m) and Froude number at each stream from CGU specific surveys. Different letters above streams boxes indicate significantly different values in a given pairwise comparison. Test types and results are reported in the appendices.

3.4 Discussion

This study has provided four valuable insights into the capacity of extreme high-frequency floods, occurring during a particularly wet summer (Chapter 2), to drive geomorphological and associated habitat change across streams of varying age. Firstly, high-frequency floods altered channel position and form at all streams, highlighting the capacity of high-frequency floods to drive major geomorphological change in small streams, a result previously reported in large gravel bed rivers (Mao and Surian, 2010, Bertoldi et al., 2010). Secondly, this study identified variation in the resilience of habitat heterogeneity across a geomorphological complexity gradient. Thirdly, this study identified consistent hydraulic habitat conditions pre- and post-flood across all streams no matter their geomorphological complexity. Fourthly, the study highlights the role of high-frequency floods in driving the ongoing development of habitat heterogeneity across streams of varying ages.

3.4.1 Geomorphological change and relative sediment supply

An important and novel contribution of this chapter is the extensive high-frequency flood-driven geomorphological and channel planform changes in support of H_1, which stated that high-frequency floods will drive a decrease in river channel persistence and changes to stream channel form at the segment scale. Indeed, all streams analysed in this chapter demonstrated decreased persistence in wetted channel position during flooding, alongside contrasting changes in sinuosity, braiding and abundance of instream wood between streams. These changes to channel geomorphology were similar to those reported for high-magnitude floods in small streams (e.g. Milan, 2012, Rickenmann and Koschni, 2010). Evidence presented in this chapter further supports the theoretical framework that repeat low-magnitude floods, such as those identified in summer 2014 in GBNP (Chapter 2), have the capacity to drive substantial geomorphological change (Costa and O'Connor, 1995). To date there is only one example in the literature which identifies a role for multiple low-magnitude flood events in driving geomorphological change in a relatively small (catchment size <30 km^2) river (Chappell et al., 2003). Chappell et al. (2003) argued that low-magnitude high-frequency floods played a role in smoothing the physical changes caused by larger events and, in doing so, caused large amounts of cumulative geomorphological change. Whilst such smoothing represents one role of low-magnitude floods, the present analyses indicate that high-frequency floods also drive large scale geomorphological change, resulting in a 75 % change in the wetted channel position at BBS. This has important implications for ecological communities as, for example, biota in heavily disturbed channels may have less access to refugia during extreme floods as a higher proportion of the channel is physically altered. Therefore, such communities may demonstrate lower resilience than the ecological communities at sites experiencing lower rates of geomorphological change.

The impacts of the floods varied across the four streams. At the youngest stream where (WPC), the channel became straighter and less braided following flooding. This homogenisation of the stream channel could possibly be due in part to the low abundance of instream wood, which is known to act as an important localised point of channel change during floods (Gregory and Davis, 1992). However, this straightening may also be associated with its higher average gradient. The effect of the floods at the youngest stream could act to delay future geomorphological development following extreme floods. Importantly, due to the lack of data regarding variations in bank stability, stream power, bed imbrication amongst other variables it is not possible to confidently relate the differences in response across the stream of varying age to any individual factor. Although it is possible that extensive change observed at older streams was in part the result of higher pre-flood instream wood load (particularly BBS and RPC), although this was not explored statistically. These differences in the geomorphological impact of floods across streams can be expected to play an important role in the post-flood sediment dynamics. Streams that experienced lower *persistence* (IVS, BBS and RPC) are likely to have experienced greater increases in post-flood sediment load, compared to streams where little bank erosion occurs. Such increased sediment availability may reinitiate paraglacial adjustment processes and their associated feedback mechanisms (Eichel et al., 2016), that were otherwise stabilised through time and vegetative development. As such extreme high-flow events may represent a crucial driver of the ongoing development of geomorphology in older catchments. These differences in post-flood sediment load could drive differences in future habitat development across streams post-flood, following the model of Yarnell et al. (2006).

Statistically significant bed sediment fining was observed post-flood at RPC, with a similar fining across all streams in pools, glides and runs. This trend for sediment fining, may be the result of increased sediment availability post-flood driven by bank erosion, and precipitation driven mass wasting events along stream channels and in high relief areas (Miller et al., 2014, Fox et al., 2016). Such inputs provide an important sediment source for deposition during the falling flood hydrograph and subsequent high flow events. Indeed, a trend of bed sediment fining has been reported in both experimental and observational work following increased sediment inputs (Recking, 2012, Hassan and Church, 2000). The accumulation of fine sediments can reduce habitat quality for benthic macroinvertebrate communities which are normally most diverse in habitat free from fine sediments (Larsen and Omerod, 2010, Culp et al., 1983). Such sediment fining following high-frequency floods in streams is a novel contribution to the literature and further highlights one potential pathway through which high-frequency floods could impact biotic communities. Such sediment fining could represent a press effect on instream habitat which alters the available niche space (Chapter 4 and 6) for benthic macroinvertebrate communities post-flood.

3.4.2 Role of instream wood in geomorphological response

The extent of instream wood recruitment associated with the floods and observed in post-flood surveys varied with increasing stream age. This variation is based upon differences in the characteristics of riparian vegetation resulting from terrestrial succession and the extent of bank erosion. At WPC riparian vegetation was predominantly Sitka alder *Alnus viridis*, which has generally thin trunks (often <10 cm diameter) and an open structure, and bank erosion was relatively low. IVS (intermediate age) was dominated by cottonwoods *Populus trichocarpa* which have much wider trunks (>15 cm) than alder and a cluster of branches near their top. The dominant riparian tree species at both BBS and RPC was Sitka spruce *Picea sitchensis*, which can have trunks with diameters >60 cm and dense branches along their length. Therefore, with increasing stream age, an increase was observed in the capacity of riparian tree species to act as barriers to flow, once recruited into the stream channel. This relationship has been shown to increase the magnitude of hydraulic and geomorphological alterations immediately surrounding and further downstream of an instream wood piece (Gurnell et al., 2002, Klaar et al., 2011).

These factors suggest that at older streams, individual wood pieces are more effective drivers of channel positional change than at younger streams. The increased importance of larger instream wood pieces in controlling geomorphic and hydraulic processes may further explain the increased levels of channel change observed at older sites in this chapter (Klaar et al., 2011). Indeed, this may represent a positive feedback loop, whereby streams with larger instream wood pieces pre-flood exhibit greater levels of localised bank erosion during high flow periods due to wood-flow interactions (Wohl et al., 2016). With higher rates of bank erosion, greater rates of riparian vegetation recruitment occur, which drives further bank erosion. Such systems suggest low geomorphological resilience with stream channel form and position changing markedly pre- to post-flood.

In contrast, at young streams where vegetation is almost exclusively alder (Klaar et al., 2011), characterised by small multi-trunked trees, even low magnitude floods could displace wood accumulated within the channel during flood free periods. Whilst some bank erosion will occur due to the energy available to drive geomorphological change, no riparian wood is of sufficient size to persist within the wetted channel once it has been recruited. An exception to this could occur where alder re-roots within the channel, although their more open structure and smaller size make them a less significant roughness element than larger and more densely formed instream wood (Wohl and Goode, 2008), such as larger cottonwoods and Sitka spruce which are dominant at the older sites in GBNP. Indeed, in such channels with limited instream wood, an extreme high-magnitude flood has been shown to drive bed scour rather than lateral bed migration (Milner et al., 2013). The current chapter is the first contribution of a similar finding for high-frequency floods. This observation suggests that young systems can be expected to become more resilient to flood disturbance as channels become increasingly channelized and constrained with each subsequent extreme flood event (Fryirs, 2017). This increasing resilience has major implications for heavily managed river channels in less remote regions of the world. In channels which are actively straightened, instream wood is removed and are constrained by stabilised banks, as is often observed in more urban systems as discussed by Gregory (2006). Reductions in channel geomorphological complexity and therefore habitat availability should be expected following extreme high-frequency floods. This directional response and increased resilience should also be expected to make future restoration efforts of such channels increasingly challenging.

3.4.3 Post-flood geomorphological and habitat response

Post-flood geomorphological response was linked to changing relative sediment availability with increasingly dynamic post-flood cross sections and lower channel *persistence* scores observed at older streams, a finding consistent with the post-flood response of upland streams to high-magnitude floods (Milan, 2012). It is suggested that variation in geomorphological resilience across streams was linked to the pre-flood stream paraglacial condition, specifically the sediment availability and terrestrial vegetative cover (Ballantyne, 2002, Eichel, 2019, Carrivick and Heckmann, 2017, Carrivick et al., 2013). Reduced sediment availability in older catchments limits the capacity for continued geomorphological development (Klaar et al., 2015), because sediment becomes stored in increasingly deep organic matter rich soils, and stabilised by the root structures of first pioneer species and subsequently coniferous trees (Eichel, 2019, Sidle and Milner, 1989, Klaar et al., 2015). However, it appears that the significant erosive action of the high-frequency floods and associated precipitation driven mass wasting events (Miller, 1990, Darby et al., 2007, Guerra et al., 2017), altered this relationship between sediment availability and stream age in the short-term. This alteration is thought to have led to greater increases in relative sediment supply at older streams and to have facilitated a short-term boost in the development of geomorphological complexity in older streams, which otherwise would be expected to demonstrate relatively low rates of geomorphological development (Yarnell et al., 2006). This contrasting response of geomorphological complexity between older and younger streams suggests a lack of support for H_2; that the floods will drive increases to complexity at the segment scale at all streams. Rather given older streams' greater post-flood response these streams can be considered more geomorphologically sensitive to extreme high-frequency floods than younger streams. This finding is the first demonstration of the significance of extreme high-frequency floods to ongoing paraglacial processes. In addition, it provides further evidence for the importance of extreme disturbance events within the paraglacial adjustment theory (Ballantyne, 2002, Eichel, 2019, Carrivick and Heckmann, 2017), and as such warrants further attention within the literature.

The response of habitat heterogeneity (namely proportional contribution of habitat types and associated instream depth and velocity) contrasts with the highly dynamic geomorphological response. High rates of channel change have been reported in field and in modelling studies of extreme high-magnitude floods (Staines and Carrivick, 2015, Staines et al., 2015). Initial resistance to change of habitat heterogeneity was observed at all streams. However, differences in post-flood geomorphological stability have important implications for the continued development and resilience of habitat heterogeneity. At sensitive streams, a greater response in habitat heterogeneity was observed due to increased sediment availability for stream channel restructuring (Yarnell et al., 2006), in spite of ongoing changes to channel position and form. Development of habitat evenness and diversity at sensitive streams post-flood, was driven by a larger contribution of low velocity CGU types. The pattern of increased habitat heterogeneity which persists during the relaxation stage is similar to the temporal trend of developing habitat heterogeneity with increasing time since deglaciation, which is already reported for GBNP streams (Klaar et al., 2009). Increasing habitat heterogeneity during the relaxation stage suggests an important role for floods in the process of stream habitat development in GBNP, and other streams undergoing paraglacial adjustment. Specifically, floods facilitate this habitat development through the accumulation of instream wood and increased post-flood sediment availability, allowing a short-term boost to habitat development.

In contrast, WPC (the youngest stream) demonstrated low post-flood habitat resilience with habitat heterogeneity declining through the post-flood relaxation stage. This finding offers support to H_3, that the resilience of habitat heterogeneity will be higher at streams with higher pre-flood geomorphological complexity. This decline in habitat heterogeneity was driven by the disappearance of low velocity habitat types, resulting from instream wood loss. This pattern has been reported previously, following the active removal of instream wood across North America (Mellina and Hinch, 2009). Following the floods, WPC straightened and saw increased bed scour which homogenised channel geomorphology potentially further limiting the channel's capacity to maintain high habitat heterogeneity consistent with modelling studies of response to series of extreme events (Guan et al., 2016). Furthermore, the larger bed sediment size clasts found at WPC were less likely to be mobilised by post-flood flow events than finer sediments at older sites (Wilcock, 1993). Increased sediment sizes are likely to reduce bed mobilisation in future events and thus may decrease the likelihood of response to subsequent high-flow events (Guan et al., 2016). Together, these factors indicate that extreme high-frequency flood events can act to reduce habitat development at young sites in GBNP, as they reduced the diversity of channel geomorphology in the short-term.

Overall, atypical heavy precipitation and associated high-frequency flooding have an important role in driving the ongoing development of habitat heterogeneity in unmanaged streams, such as those in GBNP. As streams age over decades to centuries following glacial retreat, without extreme flood events streams experience significant declines in the availability of sediment as banks become stabilised by riparian forests (Ballantyne, 2002, Sidle and Milner, 1989, Klaar et al., 2009). As such, the potential for future geomorphological development can be expected to decline (Ballantyne, 2002, Yarnell et al., 2006). However, floods have the capacity to alter short term (<10 years) sediment dynamics by mobilising bank and bed sediment and consequently increase relative sediment supply to streams. Further, where stream power is insufficient to wash out instream wood, floods have the capacity to recruit additional wood into a stream channel (Wohl et al., 2016). This recruitment enhances the stream channel's capacity for habitat heterogeneity. These two factors combined can lead to the rapid development of instream habitat heterogeneity where conditions are suitable, as observed at IVS, BBS and RPC.

3.4.4 Hydraulic and geomorphological habitat variation across streams post-flood.

In this chapter the general trends observed in CGU type hydraulic and geomorphological conditions both pre- and post-flood were broadly consistent with those reported pre-flood (Klaar et al., 2009). In the hydraulic surveys, minor increases in the intra-stream variation were observed (Table 3.6). Small observed changes were thought to be associated with variations in pre-flood bed gradient and sediment size ranges, which are important factors in controlling allocation of riverine habitat to CGU classes (Hawkins et al., 1993). The greatest changes in CGU hydraulic characteristics were identified in pools and rapids, both of which are associated with instream roughness elements such as instream wood (Bilby and Ward, 1991, Hawkins et al., 1993). Instream roughness elements can drive pool formation and control pool type, depending on the position and complexity of the structures (Abbe and Montgomery, 1996, Klaar et al., 2011). High intra-stream variation (HSC scores) in pools observed at all streams in this chapter may be linked to differences in instream wood form. The lowest pool HSC score found at WPC (42), was likely explained by the presence of pools formed by instream alder and one by a boulder (>2000 cm diameter). Such pools are shallower and faster flowing than pools associated with large instream wood (Abbe and Montgomery, 1996). In spite of the capacity for large boulders to drive pool formation, the general absence of boulders from the study streams in this thesis limits their importance to GBNP streams' hydrogeomorphological regimes, compared to abundant and more mobile instream wood.

The form of instream wood pieces and their position are known to control the extent of sediment scour and deposition (Gomi et al., 2001, Klaar et al., 2011), a pattern also observed in experimental studies (Mutz et al., 2007). Consistent with this, pools at older sites were deeper than at younger sites. However, these inter-stream differences were small when compared to those observed in pre-flood analyses (Klaar et al., 2009). This suggests that the hydraulic conditions of pools may become more uniform across streams following flooding. Unfortunately, no intra-stream comparisons of pools were made in historic analyses at these streams (Klaar et al., 2009) and therefore a comparison to pre-flood scores, as reported for other CGU types, is not possible. The contribution of inter- and intra-stream pool hydraulic comparisons made in the current chapter therefore represent a valuable new insight which can now be incorporated into future syntheses of GBNP stream hydrogeomorphology.

In contrast, riffles and runs (the most abundant CGU types at all streams) showed highly consistent characteristics both within and between streams and when compared to reported pre-flood conditions (Klaar et al, 2009), in support of H_4 that CGU hydraulic habitat conditions would persist post-flood. As regions of high and consistent flow velocity and gradient (Frissell et al., 1986, Hawkins et al., 1993), these CGUs can be expected to respond in a similar manner to drivers of change during floods wherever they are found because they are not controlled by barriers to flow. Similar consistency between pre- and post-flood conditions in high velocity CGUs has been observed elsewhere (Roghair et al., 2002). Significantly, changing sediment size distributions within riffles and runs may impact local instream habitat conditions and thus benthic macroinvertebrates (Jowett, 2003). The observed trend of post-flood sediment fining

(Figure 3.9) can be expected to reduce instream habitat availability for pre-disturbance benthic macroinvertebrate communities as reported by Wood and Armitage (1997) and Von Bertrab et al. (2013). Fine sediment deposition alters carbon and nitrogen dynamics, reduces bed roughness and the availability of interstitial space necessary for the survival of a broad a range of common species and functional groups of benthic invertebrates (Quinn and Hickey, 1990, Culp et al., 1983). Specific impacts can be expected to vary on an individual basis depending on the niche space associated with a given taxa.

In contrast to benthic macroinvertebrates' localised habitat use, juvenile salmonids have a greater capacity to migrate through the riverscape in response to local hydraulic conditions (Nickelson et al., 1992, Bramblett et al., 2002). As such, the persistence of juvenile salmonids following flooding within a given stream can be expected to vary more with changes in the overall availability of necessary habitat types more so than precise variations in local hydraulic conditions. Interestingly, the post-flood recovery of another juvenile salmonid population (brook trout *Salvelinus fontinalis*) has been reported in the literature following the recovery of suitable habitat (Roghair et al., 2002). A range of adult salmon return to streams in GBNP each year to spawn, and to do this successfully, they are dependent upon coarse gravels and cobbles free from fine sediments for spawning success (Riebe et al., 2014). Whilst the floods in this chapter facilitated an overall fining of sediments across CGU types, there was no evidence for large accumulations of fine sediment in riffles and runs that could reduce salmon spawning success post-flood.

3.5 Conclusion

This chapter has quantified and explored the capacity of extreme high-frequency flood events to drive geomorphological change within streams of varying catchment age, riparian vegetation characteristics and instream geomorphological complexity. The floods decreased channel *persistence* to as low as 25% (BBS), and drove divergent responses in sinuosity, braiding and instream wood abundance across streams. Such an extensive geomorphological response to high-frequency floods has previously only been reported in large gravel bed rivers (Mao and Surian, 2010, Bertoldi et al., 2010), and as such these findings of geomorphological responsiveness of stream channels to high-frequency low magnitude floods represent an important contribution to the literature. These changes are thought to be linked to changing relative sediment supply from pre- to post-flood, and the development of habitat heterogeneity has been tied to established principles of paraglacial adjustment processes. Habitat heterogeneity was resistant and resilient to high-frequency floods at the segment scale.

However, whilst this pattern was evident in habitat diversity and evenness metrics at streams of intermediate to old age (IVS, BBS and RPC), habitat resilience was low at the youngest and least complex stream (WPC). This variation in habitat resilience of streams during the post-flood relaxation stage represents a novel contribution to both ecological and geomorphological literatures. The floods had a varying effect on the CGU- specific hydraulic conditions across the age gradient. Increased variation in HSC comparisons between and within streams were identified in pools, to as high as 50 (WPC to RPC), whilst differences in HSC of riffle and runs remained notably low. Changes in habitat heterogeneity associated with changing geomorphological complexity at the segment and CGU scales may have implications for biotic and ecosystem scale responses following the summer of 2014. These implications are expected to be dependent upon the spatial scales pertinent to individual taxa and will be explored in the subsequent chapters (Chapters 4, 5 and 6) of this thesis.

3.6 References

ABBE, T. B. & MONTGOMERY, D. R. 1996. Large woody debris dams, channel hydraulics and habitat formation in large rivers. *Regulated Rivers: Research & Management,* 12**,** 201-221.

BALLANTYNE, C. K. 2002. A general model of paraglacial landscape response. *The Holocene,* 12**,** 371-376.

BEECHIE, T. J., LIERMANN, M., BEAMER, E. M. & HENDERSON, R. 2005. A Classification of Habitat Types in a Large River and Their Use by Juvenile Salmonids. *Transactions of the American Fisheries Society,* 134**,** 717-729.

BEECHIE, T. J., SEAR, D. A., OLDEN, J. D., PESS, G. R., BUFFINGTON, J. M., MOIR, H., RONI, P. & POLLOCK, M. M. 2010. Process-based Principles for Restoring River Ecosystems. *BioScience,* 60**,** 209-222.

BERTOLDI, W., ZANONI, L. & TUBINO, M. 2010. Assessment of morphological changes induced by flow and flood pulses in a gravel bed braided river: The Tagliamento River (Italy). *Geomorphology,* 114**,** 348-360.

BEVENGER, G. S. & KING, R. M. 1995. *A pebble count procedure for assessing watershed cumulative effects.* , Fort Collins, CO, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

BILBY, R. E. & WARD, J. W. 1991. Characteristics and Function of Large Woody Debris in Streams Draining Old-Growth, Clear-Cut, and Second-Growth Forests in Southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences,* 48**,** 2499-2508.

BLETTLER, M. C. M., AMSLER, M. L., EBERLE, E. G., SZUPIANY, R., LATOSINSKI, F. G., ABRIAL, E., OBERHOLSTER, P. J., ESPINOLA, L. A., PAIRA, A., POZA, A. & RODRIGUES CAPÍTULO, A. 2016. Linking hydro-morphology with invertebrate ecology in diverse morphological units of a large river-floodplain system. *Water Resources Research,* 52**,** 9495-9510.

BOGAN, M. T., HWAN, J. L., CERVANTES-YOSHIDA, K., PONCE, J. & CARLSON, S. M. 2017. Aquatic invertebrate communities exhibit both resistance and resilience to seasonal drying in an intermittent coastal stream. *Hydrobiologia,* 799**,** 123-133.

BOND, N. A., CRONIN, M. F., FREELAND, H. & MANTUA, N. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters,* 42**,** 3414-3420.

BRAMBLETT, R. G., BRYANT, M. D., WRIGHT, B. E. & WHITE, R. G. 2002. Seasonal Use of Small Tributary and Main-Stem Habitats by Juvenile Steelhead, Coho Salmon, and Dolly Varden in a Southeastern Alaska Drainage Basin. *Transactions of the American Fisheries Society,* 131**,** 498-506.

BROGAN, D. J., NELSON, P. A. & MACDONALD, L. H. 2017. Reconstructing extreme post-wildfire floods: a comparison of convective and mesoscale events. *Earth Surface Processes and Landforms,* 42**,** 2505-2522.

BRUMMER, C. J., ABBE, T. B., SAMPSON, J. R. & MONTGOMERY, D. R. 2006. Influence of vertical channel change associated with wood accumulations on delineating channel migration zones, Washington, USA. *Geomorphology,* 80**,** 295-309.

BRUNSDEN, D. 1993. Barriers to geomorphological change. *In:* THOMAS, D. & ALLISON, R. (eds.) *Landscape Sensitivity.* Chichester: John Wiley &Sons.

BRUNSDEN, D. & THORNES, J. B. 1979. Landscape Sensitivity and Change. *Transactions of the Institute of British Geographers,* 4**,** 463-484.

CARRIVICK, J. L., GEILHAUSEN, M., WARBURTON, J., DICKSON, N. E., CARVER, S. J., EVANS, A. J. & BROWN, L. E. 2013. Contemporary geomorphological activity throughout the proglacial area of an alpine catchment. *Geomorphology,* 188**,** 83-95.

CARRIVICK, J. L. & HECKMANN, T. 2017. Short-term geomorphological evolution of proglacial systems. *Geomorphology,* 287**,** 3-28.

CASADO, M. R. 2006. *The use of geostatistics for hydromorphological assessment in rivers.* PhD, Cranfield University.

CHAPIN, F. S., WALKER, L. R., FASTIE, C. L. & SHARMAN, L. C. 1994. Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska. *Ecological Monographs,* 64**,** 149-175.

CHAPPELL, A., HERITAGE, G. L., FULLER, I. C., LARGE, A. R. G. & MILAN, D. J. 2003. Geostatistical analysis of ground-survey elevation data to elucidate spatial and temporal river channel change. *Earth Surface Processes and Landforms,* 28**,** 349-370.

CHURCH, M. & RYDER, J. M. 1972. Paraglacial Sedimentation: A Consideration of Fluvial Processes Conditioned by Glaciation. *GSA Bulletin,* 83**,** 3059-3072.

COSTA, J. E. & O'CONNOR, J. E. 1995. Geomorphically Effective Floods. *Natural and Anthropogenic Influences in Fluvial Geomorphology.* American Geophysical Union.

CULP, J. M., WALDE, S. J. & DAVIES, R. W. 1983. Relative Importance of Substrate Particle Size and Detritus to Stream Benthic Macroinvertebrate Microdistribution. *Canadian Journal of Fisheries and Aquatic Sciences,* 40**,** 1568-1574.

CURRY, A. M. 1999. Paraglacial modification of slope form. *Earth Surface Processes and Landforms,* 24**,** 1213-1228.

DARBY, S. E., RINALDI, M. & DAPPORTO, S. 2007. Coupled simulations of fluvial erosion and mass wasting for cohesive river banks. *Journal of Geophysical Research: Earth Surface,* 112.

DEAN, D. J. & SCHMIDT, J. C. 2013. The geomorphic effectiveness of a large flood on the Rio Grande in the Big Bend region: Insights on geomorphic controls and post-flood geomorphic response. *Geomorphology,* 201**,** 183-198.

DOWNS, P. & GREGORY, K. 1993. *The sensitivity of river channels in the landscape system*.

DOWNS, P. & GREGORY, K. 2004. *River Channel Management:Towards Sustainable Catchment Hydrosystems.,* London, Arnold.

EGLI, M., WERNLI, M., KNEISEL, C. & HAEBERLI, W. 2006. Melting Glaciers and Soil Development in the Proglacial Area Morteratsch (Swiss Alps): I. Soil Type Chronosequence. *Arctic, Antarctic, and Alpine Research,* 38**,** 499-509.

EGOZI, R. & ASHMORE, P. 2008. Defining and measuring braiding intensity. *Earth Surface Processes and Landforms,* 33**,** 2121-2138.

EICHEL, J. 2019. Vegetation Succession and Biogeomorphic Interactions in Glacier Forelands: Landform and Sediment Dynamics in Recently Deglaciated Alpine Landscapes.

EICHEL, J., CORENBLIT, D. & DIKAU, R. 2016. Conditions for feedbacks between geomorphic and vegetation dynamics on lateral moraine slopes: a biogeomorphic feedback window. *Earth Surface Processes and Landforms,* 41**,** 406-419.

FOX, G. A., PURVIS, R. A. & PENN, C. J. 2016. Streambanks: A net source of sediment and phosphorus to streams and rivers. *Journal of Environmental Management,* 181**,** 602-614.

FRISSELL, C. A., LISS, W. J., WARREN, C. E. & HURLEY, M. D. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management,* 10**,** 199-214.

FRYIRS, K., LISENBY, P. & CROKE, J. 2015. Morphological and historical resilience to catastrophic flooding: The case of Lockyer Creek, SE Queensland, Australia. *Geomorphology,* 241**,** 55-71.

FRYIRS, K. A. 2017. River sensitivity: a lost foundation concept in fluvial geomorphology. *Earth Surface Processes and Landforms,* 42**,** 55-70.

GOMI, T., SIDLE, R. C., BRYANT, M. D. & WOODSMITH, R. D. 2001. The characteristics of woody debris and sediment distribution in headwater streams, southeastern Alaska. *Canadian Journal of Forest Research,* 31**,** 1386-1399.

GREGORY, K. J. 2006. The human role in changing river channels. *Geomorphology,* 79**,** 172-191.

GREGORY, K. J. & DAVIS, R. J. 1992. Coarse woody debris in stream channels in relation to river channel management in woodland areas. *Regulated Rivers: Research & Management,* 7**,** 117-136.

GUAN, M., CARRIVICK, J., WRIGHT, N., SLEIGH, A. & E.H. STAINES, K. 2016. *Quantifying the combined effects of multiple extreme floods on river channel geometry and on flood hazards*.

GUERRA, A. J. T., FULLEN, M. A., JORGE, M. D. C. O., BEZERRA, J. F. R. & SHOKR, M. S. 2017. Slope Processes, Mass Movement and Soil Erosion: A Review. *Pedosphere,* 27**,** 27-41.

GURNELL, A. M., PIEGAY, H., SWANSON, F. J. & GREGORY, S. V. 2002. Large wood and fluvial processes. *Freshwater Biology,* 47**,** 601-619.

HASSAN, M. A. & CHURCH, M. 2000. Experiments on surface structure and partial sediment transport on a gravel bed. *Water Resources Research,* 36**,** 1885-1895.

HAUER, C. & HABERSACK, H. 2009. Morphodynamics of a 1000-year flood in the Kamp River, Austria, and impacts on floodplain morphology. *Earth Surface Processes and Landforms,* 34**,** 654-682.

HAWKINS, C. P., KERSHNER, J. L., BISSON, P. A., BRYANT, M. D., DECKER, L. M., GREGORY, S. V., MCCULLOUGH, D. A., OVERTON, C. K., REEVES, G. H., STEEDMAN, R. J. & YOUNG, M. K. 1993. A Hierarchical Approach to Classifying Stream Habitat Features. *Fisheries,* 18**,** 3-12.

HOLLING, C. S. 1973. Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics,* 4**,** 1-23.

JOHNSON, J. H., ABBETT, R., CHALUPNICKI, M. A. & VERDOLIVA, F. 2016. Seasonal habitat use of brook trout and juvenile steelhead in a Lake Ontario tributary. *Journal of Freshwater Ecology,* 31**,** 239-249.

JOWETT, I. G. 2003. Hydraulic constraints on habitat suitability for benthic invertebrates in gravel-bed rivers. *River Research and Applications,* 19**,** 495-507.

JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E. 1989. The Flood Pulse Concept in River-Floodplain Systems. *Canadian Special Publication of Fisheries and Aquatic Science,* 106**,** 110 - 127.

KLAAR, M. J., HILL, D. F., MADDOCK, I. & MILNER, A. M. 2011. Interactions between instream wood and hydrogeomorphic development within recently deglaciated streams in Glacier Bay National Park, Alaska. *Geomorphology,* 130**,** 208-220.

KLAAR, M. J., KIDD, C., MALONE, E., BARTLETT, R., PINAY, G., CHAPIN, F. S. & MILNER, A. 2015. Vegetation succession in deglaciated landscapes: implications for sediment and landscape stability. *Earth Surface Processes and Landforms,* 40**,** 1088-1100.

KLAAR, M. J., MADDOCK, I. & MILNER, A. M. 2009. The Development of Hydraulic and Geomorphic Complexity in Recently Formed Streams in Glacier Bay National Park, Alaska. *River Research and Applications,* 25**,** 1331-1338.

LAMMERT, M. & ALLAN, J. D. 1999. Assessing Biotic Integrity of Streams: Effects of Scale in Measuring the Influence of Land Use/Cover and Habitat Structure on Fish and Macroinvertebrates. *Environmental Management,* 23**,** 257-270.

LARSEN, S. & OMEROD, S. J. 2010. Low-level effects of inert sediments on temperate stream invertebrates. *Freshwater Biology,* 55**,** 476-486.

LAUB, B. G., BAKER, D. W., BLEDSOE, B. P. & PALMER, M. A. 2012. Range of variability of channel complexity in urban, restored and forested reference streams. *Freshwater Biology,* 57**,** 1076-1095.

LE COARER, Y. 2005. *HydroSignature Software for Hydraulic Quantification,* Silkeborg: Denmark.

LEDGER, M. E. & MILNER, A. M. 2015. Extreme events in running waters. *Freshwater Biology,* 60**,** 2455-2460.

LEGG, N. T., MEIGS, A. J., GRANT, G. E. & KENNARD, P. 2014. Debris flow initiation in proglacial gullies on Mount Rainier, Washington. *Geomorphology,* 226**,** 249-260.

LENCIONI, V. & ROSSARO, B. 2005. Microdistribution of chironomids (Diptera: Chironomidae) in Alpine streams: an autoecological perspective. *Hydrobiologia,* 533**,** 61-76.

LESTER, R. E. & WRIGHT, W. 2009. Reintroducing wood to streams in agricultural landscapes: changes in velocity profile, stage and erosion rates. *River Research and Applications,* 25**,** 376-392.

MAGILLIGAN, F. J., BURAAS, E. M. & RENSHAW, C. E. 2015. The efficacy of stream power and flow duration on geomorphic responses to catastrophic flooding. *Geomorphology,* 228**,** 175-188.

MALMON, D. V., RENEAU, S. L. & DUNNE, T. 2004. Sediment sorting and transport by flash floods. *Journal of Geophysical Research: Earth Surface,* 109.

MAO, L. & SURIAN, N. 2010. Observations on sediment mobility in a large gravel-bed river. *Geomorphology,* 114**,** 326-337.

MASANAO, S., DAISUKE, N. & FUTOSHI, N. 2014. The relative contributions of refugium types to the persistence of benthic invertebrates in a seasonal snowmelt flood. *Freshwater Biology,* 59**,** 257-271.

MCCOLL, S. T. 2012. Paraglacial rock-slope stability. *Geomorphology,* 153-154**,** 1-16.

MCGARIGAL, K., CUSHMAN, S. & ENE E 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Amherst: University of Massachusetts.

MELLINA, E. & HINCH, S. G. 2009. Influences of riparian logging and in-stream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. *Canadian Journal of Forest Research,* 39**,** 1280-1301.

MEYER, J. L., STRAYER, D. L., WALLACE, J. B., EGGERT, S. L., HELFMAN, G. S. & LEONARD, N. E. 2007. The Contribution of Headwater Streams to Biodiversity in River Networks1. *JAWRA Journal of the American Water Resources Association,* 43**,** 86-103.

MILAN, D. J. 2012. Geomorphic impact and system recovery following an extreme flood in an upland stream: Thinhope Burn, northern England, UK. *Geomorphology,* 138**,** 319-328.

MILLER, A. J. 1990. Fluvial response to debris associated with mass wasting during extreme floods. *Geology,* 18**,** 599-602.

MILLER, R. B., FOX, G. A., PENN, C. J., WILSON, S., PARNELL, A., PURVIS, R. A. & CRISWELL, K. 2014. Estimating sediment and phosphorus loads from streambanks with and without riparian protection. *Agriculture, Ecosystems & Environment,* 189**,** 70-81.

MILNER, A. M. 1987. Colonization and ecological development of new streams in Glacier Bay National Park, Alaska. *Freshwater Biology,* 18**,** 53-70.

MILNER, A. M. & BAILEY, R. G. 1989. Salmonid colonization of new streams in Glacier Bay National Park Alaska USA. *Aquaculture and Fisheries Management,* 20**,** 179-192.

MILNER, A. M., KNUDSEN, E. E., SOISETH, C., ROBERTSON, A. L., SCHELL, D., PHILLIPS, I. T. & MAGNUSSON, K. 2000. Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences,* 57**,** 2319-2335.

MILNER, A. M., PICKEN, J. L., KLAAR, M. J., ROBERTSON, A. L., CLITHEROW, L. R., EAGLE, L. & BROWN, L. E. 2018. River ecosystem resilience to extreme flood events. *Ecology and Evolution,* 0.

MILNER, A. M., ROBERTSON, A. L., MCDERMOTT, M. J., KLAAR, M. J. & BROWN, L. E. 2013. Major flood disturbance alters river ecosystem evolution. *Nature Climate Change,* 3**,** 137-141.

MILNER, A. M., ROBERTSON, A. L., MONAGHAN, K. A., VEAL, A. J. & FLORY, E. A. 2008. Colonization and development of an Alaskan stream community over 28 years. *Frontiers in Ecology and the Environment,* 6**,** 413-419.

MOIR, H. J. & PASTERNACK, G. B. 2008. Relationships between mesoscale morphological units, stream hydraulics and Chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat on the Lower Yuba River, California. *Geomorphology,* 100**,** 527-548.

MONTGOMERY, D. R., BUFFINGTON, J. M., SMITH, R. D., SCHMIDT, K. M. & PESS, G. 1995. Pool Spacing in Forest Channels. *Water Resources Research,* 31**,** 1097-1105.

MONTGOMERY, D. R., COLLINS, B. D., BUFFINGTON, J. M. & ABBE, T. B. 2003. Geomorphic Effects of Geomorphic Effects of Geomorphic Effects of Wood in Ri ood in Ri ood in Rivers. *American Fisheries Society Symposium*.

MUTZ, M., KALBUS, E. & MEINECKE, S. 2007. Effect of instream wood on vertical water flux in low-energy sand bed flume experiments. *Water Resources Research,* 43.

NAIMAN, R. J., BALIAN, E. V., BARTZ, K. K., BILBY, R. E. & LATTERELL, J. J. 1999. Dead Wood Dynamics in Stream Ecosystems. *Symposium on the Ecology and Management of Dead Wood in Western Forests*.

NICKELSON, T. E., RODGERS, J. D., JOHNSON, S. L. & SOLAZZI, M. F. 1992. Seasonal Changes in Habitat Use by Juvenile Coho Salmon (Oncorhynchus kisutch) in Oregon Coastal Streams. *Canadian Journal of Fisheries and Aquatic Sciences,* 49**,** 783-789.

PASTERNACK, G. B. & WYRICK, J. R. 2017. Flood-driven topographic changes in a gravel-cobble river over segment, reach, and morphological unit scales. *Earth Surface Processes and Landforms,* 42**,** 487-502.

PEARSONS, T. N., LI, H. W. & LAMBERTI, G. A. 1992. Influence of Habitat Complexity on Resistance to Flooding and Resilience of Stream Fish Assemblages. *Transactions of the American Fisheries Society,* 121**,** 427-436.

PHILLIPS, J. D. 2009. Changes, perturbations, and responses in geomorphic systems. *Progress in Physical Geography: Earth and Environment,* 33**,** 17-30.

POFF, N. L. 1997. Landscape Filters and Species Traits: Towards Mechanistic Understanding and Prediction in Stream Ecology. *Journal of the North American Benthological Society,* 16**,** 391-409.

POFF, N. L. 2002. Ecological response to and management of increased flooding caused by climate change. *Philosophical Transactions of the Royal Society of London. Series A: Mathematical, Physical and Engineering Sciences,* 360**,** 1497-1510.

POFF, N. L., ALLAN, J. D., BAIN, M. B., KARR, J. R., PRESTEGAARD, K. L., RICHTER, B. D., SPARKS, R. E. & STROMBERG, J. C. 1997. The Natural Flow Regime. *BioScience,* 47**,** 769-784.

POFF, N. L., LARSON, E. I., SALERNO, P. E., MORTON, S. G., KONDRATIEFF, B. C., FLECKER, A. S., ZAMUDIO, K. R. & FUNK, W. C. 2018. Extreme streams: species persistence and genomic change in montane insect populations across a flooding gradient. *Ecology Letters,* 21**,** 525-535.

QUINN, J. M. & HICKEY, C. W. 1990. Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research,* 24**,** 411-427.

R-CORE-TEAM 2017. R: A language and environment for statistical computing. . Vienna, Austria.: R Foundation for Statistical Computing.

RECKING, A. 2012. Influence of sediment supply on mountain streams bedload transport. *Geomorphology,* 175-176**,** 139-150.

REICE, S. R. 1980. The Role of Substratum in Benthic Macroinvertebrate Microdistribution and Litter Decomposition in a Woodland Stream. *Ecology,* 61**,** 580-590.

RICKENMANN, D. & KOSCHNI, A. 2010. Sediment loads due to fluvial transport and debris flows during the 2005 flood events in Switzerland. *Hydrological Processes,* 24**,** 993-1007.

RIEBE, C. S., SKLA, R. L. S., OVERSTREET, B. T. & WOOSTER, J. K. 2014. Optimal reproduction in salmon spawning substrates linked to grain size and fish length. *Water Resources Research,* 50**,** 898-918.

ROBERTSON, A. L., BROWN, L. E., KLAAR, M. J. & MILNER, A. M. 2015. Stream ecosystem responses to an extreme rainfall event across multiple catchments in southeast Alaska. *Freshwater Biology,* 60**,** 2523-2534.

ROGHAIR, C. N., DOLLOFF, C. A. & UNDERWOOD, M. K. 2002. Response of a Brook Trout Population and Instream Habitat to a Catastrophic Flood and Debris Flow. *Transactions of the American Fisheries Society,* 131**,** 718-730.

RUIZ-VILLANUEVA, V., WYŻGA, B., MIKUŚ, P., HAJDUKIEWICZ, H. & STOFFEL, M. 2016. The role of flood hydrograph in the remobilization of large wood in a wide mountain river. *Journal of Hydrology,* 541**,** 330-343.

SCHARL, A. & COARER, Y. L. 2005. *Morphohydraulic Quantification of Non Spatialized Datasets With the HydroSignature Software,* Silkeborg: Denmark.

SCHUMM, S. A. 1979. Geomorphic Thresholds: The Concept and Its Applications. *Transactions of the Institute of British Geographers,* 4**,** 485-515.

SEDELL, J. R., REEVES, G. H., HAUER, F. R., STANFORD, J. A. & HAWKINS, C. P. 1990. Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. *Environmental Management,* 14**,** 711-724.

SIDLE, R. C. & MILNER, A. M. 1989. Stream Development in Glacier Bay National Park, Alaska, U.S.A. *Arctic and Alpine Research,* 21**,** 350-363.

STAINES, K. E. H. & CARRIVICK, J. L. 2015. Geomorphological impact and morphodynamic effects on flow conveyance of the 1999 jökulhlaup at sólheimajökull, Iceland. *Earth Surface Processes and Landforms,* 40**,** 1401-1416.

STAINES, K. E. H., CARRIVICK, J. L., TWEED, F. S., EVANS, A. J., RUSSELL, A. J., JÓHANNESSON, T. & ROBERTS, M. 2015. A multi-dimensional analysis of pro-glacial landscape change at Sólheimajökull, southern Iceland. *Earth Surface Processes and Landforms,* 40**,** 809-822.

STEEB, N., RICKENMANN, D., BADOUX, A., RICKLI, C. & WALDNER, P. 2017. Large wood recruitment processes and transported volumes in Swiss mountain streams during the extreme flood of August 2005. *Geomorphology,* 279**,** 112-127.

STOCKER-WALDHUBER, M., FISCHER, A., KELLER, L., MORCHE, D. & KUHN, M. 2017. Funnel-shaped surface depressions — Indicator or accelerant of rapid glacier disintegration? A case study in the Tyrolean Alps. *Geomorphology,* 287**,** 58-72.

THOMPSON, C. & CROKE, J. 2013. Geomorphic effects, flood power, and channel competence of a catastrophic flood in confined and unconfined reaches of the upper Lockyer valley, southeast Queensland, Australia. *Geomorphology,* 197**,** 156-169.

TUNNICLIFFE, J., BRIERLEY, G., FULLER, I. C., LEENMAN, A., MARDEN, M. & PEACOCK, D. 2017. Reaction and relaxation in a coarse-grained fluvial system following catchment-wide disturbance. *Geomorphology*.

VON BERTRAB, M. G., KREIN, A., STENDERA, S., THIELEN, F. & HERING, D. 2013. Is fine sediment deposition a main driver for the composition of benthic macroinvertebrate assemblages? *Ecological Indicators,* 24**,** 589-598.

WENZEL, R., REINHARDT-IMJELA, C., SCHULTE, A. & BÖLSCHER, J. 2014. The potential of in-channel large woody debris in transforming discharge hydrographs in headwater areas (Ore Mountains, Southeastern Germany). *Ecological Engineering,* 71**,** 1-9.

WERRITTY, A. & LEYS, K. F. 2001. The sensitivity of Scottish rivers and upland valley floors to recent environmental change. *CATENA,* 42**,** 251-273.

WILCOCK, P. R. 1993. Critical Shear Stress of Natural Sediments. *Journal of Hydraulic Engineering,* 119**,** 491-505.

WOHL, E., BLEDSOE, B. P., FAUSCH, K. D., KRAMER, N., BESTGEN, K. R. & GOOSEFF, M. N. 2016. Management of Large Wood in Streams: An Overview and Proposed Framework for Hazard Evaluation. *JAWRA Journal of the American Water Resources Association,* 52**,** 315-335.

WOHL, E. & GOODE, J. R. 2008. Wood dynamics in headwater streams of the Colorado Rocky Mountains. *Water Resources Research,* 44.

WOLMAN, M. G. 1954. A method of sampling coarse river-bed material. *Eos, Transactions American Geophysical Union,* 35**,** 951-956.

WOLMAN, M. G. & MILLER, J. P. 1960. Magnitude and Frequency of Forces in Geomorphic Processes. *The Journal of Geology,* 68**,** 54-74.

WOOD, P. J. & ARMITAGE, P. D. 1997. Biological Effects of Fine Sediment in the Lotic Environment. *Environmental Management,* 21**,** 203-217.

WOUTER, R. B., EMMA, E. A., JOSHUA, R. L., RALPH, T. & ROSS, A. W. 2017. Recent changes in extreme floods across multiple continents. *Environmental Research Letters,* 12**,** 114035.

YARNELL, S. M., MOUNT, J. F. & LARSEN, E. W. 2006. The influence of relative sediment supply on riverine habitat heterogeneity. *Geomorphology,* 80**,** 310-324.

ZONTA, R., COLLAVINI, F., ZAGGIA, L. & ZULIANI, A. 2005. The effect of floods on the transport of suspended sediments and contaminants: A case study from the estuary of the Dese River (Venice Lagoon, Italy). *Environment International,* 31**,** 948-958.

4. Low ecological resilience drives convergence of stream macroinvertebrate communities following high-frequency summer floods

4.1 Introduction

Increased frequency and magnitude of extreme flood events, defined here as rare or unusual weather or climatic driven flood occurrences (sensu Ledger and Milner, 2015), are becoming more common (Wouter et al., 2017). Two crucial drivers of changing stream flood regimes are increased magnitude and duration of precipitation events, linked to temperature dependence in the hydrological cycle (Trenberth, 2011). Floods represent an important natural aspect of stream flow regimes and are characterised by five critical components; magnitude, frequency, duration, timing, and rate of change of hydrologic conditions (Poff et al., 1997). All five components can be important in geomorphological and ecological response to both extreme and more regularly observed flood events (Lytle and Poff, 2004, Poff et al., 1997), but major questions revolve around how changes in these components in future extreme events will modify ecosystems.

Smaller magnitude, predictable floods can facilitate the persistence of ecosystems in their current state by acting as environmental filters of community composition (Poff, 1997), facilitating the completion of life cycles and enabling the influx of nutrients from headwaters and floodplains (Junk et al., 1989). In contrast extreme floods, which often have high magnitudes and are unpredictable or unseasonal in timing, can drive marked changes to fluvial system geomorphology (Pasternack and Wyrick, 2017) and alter local ecology (Milner et al., 2013). Further, extreme floods have the potential to exacerbate the impact and extent of other stressors, such as non-native species (Diez et al., 2012). Importantly, the effect of extreme high-frequency floods (defined here as floods, each with >1-in-1 year return intervals, which occur repeatedly over short time-scales), have only been explored in highly altered ecosystems below dams (e.g. Robinson, 2012a, Robinson and Uehlinger, 2008, Uehlinger et al., 2003, Robinson et al., 2018). Even though this work was limited to highly modified systems, these studies provided evidence that the restoration of former flood regimes reduced fine sediment loads and shifted community composition. Specifically, a shift from Chironomidae and Gammaridae dominated systems towards communities supporting a greater diversity Ephemeroptera and Plecoptera taxa was reported, showing the importance high-frequency flood events can have for ecological systems. The response of ‘natural’ ecosystems to high-frequency floods has also not been thoroughly explored, except by a single study of one stream within Glacier Bay National Park, Alaska, USA (GBNP; Milner et al., 2018). Significantly, Milner et al. (2018) demonstrated the capacity of both extreme high-magnitude and high-frequency floods to shift ecosystems to alternative stable states immediately post-flood. However, the long-term recovery of natural aquatic ecosystems from extreme high-frequency floods has yet to be explored.

Debate surrounds the relative importance of a single extreme, high-magnitude event and multiple high-frequency lower-magnitude events in driving change to fluvial systems (Wolman and Miller, 1960, Costa and O'Connor, 1995, Magilligan et al., 2015, Milner et al., 2018). Chappell et al. (2003) demonstrated the capacity of high-frequency, low-magnitude floods to drive significant geomorphological change, a result supported in Chapter 3. Ecological theory suggests that floods can be viewed as pulse disturbances for the majority of benthic macroinvertebrate communities (Lake, 2000), in which the environmental pressure of altered flow acts over a short temporal scale. Lake (2000) has also suggested that biotic responses to disturbance can also take the form of either a pulse, press or ramp, depending on the extent and rate of recovery observed in the biological variable of interest. When a flood significantly alters community composition, the shift in the stream environment post-flood can be viewed as a press. In a press response persistent changes to communities are observed due to alterations to the processes of (re)assembly. Contrastingly, lower magnitude floods are predicted to cause a pulse biological response, whereby composition and subsequent (re)assembly are altered but recovery of a community can be observed post-flood over a given time period. There is now evidence to suggest that high-frequency smaller pulse disturbances can lead to a press biological response, where niche space and/or dispersal and thus (re)assembly is altered more permanently, even where initial disturbances alone are not sufficient to elicit a permanent ecological response (Villnäs et al., 2013). This conceptual approach to defining disturbances and responses is explored further in Chapter 8.

The impact of a flood on a riverine community is influenced by the life history traits of the individual taxa present (Townsend and Hildrew, 1994) and thus communities may respond differently to the same flood depending upon: pre-flood composition (Robertson et al., 2015), legacy effects of taxa which survive (Ledger et al., 2006) and priority effects of taxa which recolonise most rapidly following floods (Fraser et al., 2015). Even though extreme floods can reduce total macroinvertebrate abundance by an order of magnitude more than lower magnitude floods, post-flood recovery of total abundance is generally rapid (Mundahl and Hunt, 2011, Woodward et al., 2015). This suggests persistent changes in community composition are linked primarily to taxonomic change post-flood (Milner et al., 2013). Importantly, such changes in taxonomic composition have been reported in studies of both extreme high-magnitude and high-frequency floods (Mundahl and Hunt, 2011, Rader et al., 2008, Robertson et al., 2015, Milner et al., 2018).

Changes to community composition may be associated with shifts in the relative dominance of taxa within the community. For low flow disturbances, Lu et al. (2016) demonstrated that taxa which were previously at the core of food webs occupied the periphery of disturbance impacted food webs and vice versa. Similar patterns in the relative dominance of individual taxa may be observed in the benthic macroinvertebrate community's response to floods. Taxa capable of exploiting disturbance conditions would be expected to become more dominant post-flood, whilst intolerant taxa would become rarer or indeed be lost from the community.

Alongside direct impacts on biota, floods drive changes to stream channel form and localised bed sediment dynamics (Chapter 3). Such changes to the habitat template have three major implications for macroinvertebrates; (1) changes in habitat heterogeneity at the section/reach scale influences habitat availability and distribution, including refugia to future disturbance events (Sedell et al., 1990), (2) patterns of fine sediment deposition and scour within habitat patches can alter the quality of available habitat (Mathers et al., 2017), and (3) floods can facilitate the recruitment of instream wood (Hering et al., 2004) increasing geomorphological complexity and providing localised sites for the accumulation of fine sediments (Wohl, 2011, Klaar et al., 2011) improving the availability and quality of habitat. Additionally, instream wood can drive the development of slower flowing habitats including main channel and backwater pools (Abbe and Montgomery, 1996), which may represent suitable refugia in future floods.

As well as changing the habitat template, the physical impacts of floods may have additional indirect effects on benthic macroinvertebrate communities. Bed disturbance can reduce autochthonous resource availability, including epilithic diatoms (Power and Stewart, 1987, Bergey and Resh, 2006). Diatoms typically represent the most significant basal resource in GBNP stream food webs (Clitherow, 2016). Decreased autochthonous resource availability can lead to increased proportional utilisation of allochthonous resources (Larson et al., 2018). Whilst decreased instream primary resource availability may only persist for a limited time period, benthic macroinvertebrates can be significantly impacted, particularly herbivores which rely on biofilms and algae (Larson et al., 2018). Floods may also release benthic macroinvertebrate communities from top down pressure, due to decreased density of predators (Roghair et al., 2002, Milner et al., 2013, George et al., 2015, Robertson et al., 2015). In spite of the potential influences of these biotic interactions, benthic macroinvertebrate community assembly is thought to be tied to temporal dynamics of disturbance (Poff, 2002) and dispersal limitation (Brown et al., 2018).

The response of communities following a flood depends upon their ecological resilience, here defined under Holling (1973)'s model. Ecological resilience consists of two components, (1) resistance - the capacity of biota to survive at a site throughout the duration of a flood and (2) the ability to re-establish pre-flood levels of abundance through reproduction of resistant individuals and recolonization through time post-flood. Resistance in fluvial systems is linked to the availability of flow refugia at a site (Sedell et al., 1990, Negishi et al., 2002) and the traits of taxa present in the pre-flood community (e.g. small size, streamlined bodies and high mobility; Townsend et al., 1997b, Poff et al., 2018). The capacity of taxa to recolonise is dependent upon the presence of source populations (including resistant individuals which persist within the stream channel post-flood), dispersal capacity (Sundermann et al., 2011, Brown et al., 2018) and the availability of suitable instream habitat post-flood (Jowett and Richardson, 1989).

In spite of the increased occurrence of extreme floods under climate change, the climate change literature has generally focused upon responses to incremental change, such as average temperature or acidification (Ledger and Milner, 2015). This is largely because of the unpredictable nature of floods, forcing research to be undertaken opportunistically. One challenge this presents is capturing the response of ecosystems to different types of floods across fluvial systems with varying forms (e.g. underlying geology, catchment land cover, channel complexities, anthropogenic impacts etc). Crucially fluvial systems with contrasting geomorphological complexities have different capacities to hold water during high flow events (Wenzel et al., 2014), whilst the position of a stream within its catchment can influence the severity of a given flood (Lake, 2008). This spatial variation in the action of floods could lead to markedly different levels of ecological resilience following floods between different streams and throughout a stream network. These potential differences in ecological resilience indicate the need for comparative work both within and between streams to fully elucidate processes that link flood severity and ecological resilience.

Glacier Bay National Park and Preserve (GBNP) in southeast Alaska experienced the wettest summer in a 30-year record in 2014 (averaging 189 mm of precipitation per month for three months in contrast to the average of 110 mm per month). During the summer of 2014 three weeks were recorded with approximately 100 mm of precipitation falling in each week (three of the ten wettest summer weeks on record; Chapter 2). This precipitation was consistent across southeast Alaska, and was potentially caused by the presence of elevated Pacific ocean surface water temperatures in the 'Pacific blob' (Bond et al., 2015). In 2014 the wettest June and July on record resulted in saturated soils and high-frequency high stream flows. These were followed by a two-week period, beginning on the 10th August, where approximately 200 mm of rain fell leading to repeated floods, observed at gauged sites across southeast Alaska. For example, in a long-term discharge record (33 years) for Lemon Creek, Juneau, a stream proximal to the National Park (80 km southeast; Chapter 2), discharge repeatedly reached 4x the historic daily median (Chapter 2). In GBNP streams the 2014 floods have been shown to drive major geomorphological change (e.g. Milner et al., 2018, Chapter 2). Herein these floods will be referred to as extreme high-frequency summer floods, high-frequency floods or simply 'the floods'. The term high frequency floods recognises that each individual flood (driven by a recorded precipitation event) is not in of itself the magnitude which would be generally be considered extreme in the wider flood literature (see Rickenmann and Koschni (2010), Milly et al. (2002), Milly et al. (2005), Milner et al. (2013) for examples). Rather, it is the series of floods driven by repeated precipitation events falling on saturated soils, which together were unique and extreme. The floods' form provides an opportunity to enhance our understanding of benthic macroinvertebrate community resilience to floods and compare this community resilience with that observed to other forms and timed floods in the literature.

This chapter aimed to test three main hypotheses:

> H_1 High-frequency summer floods will result in declines in benthic macroinvertebrate taxonomic richness and density one year post-flood across all streams, driven by the loss of flood sensitive taxa (Herbst and Cooper, 2010) such as non-insects and large immobile dipteran larvae;
>
> H_2 Community composition of benthic macroinvertebrates will be significantly altered and become dominated post-flood by Chironomidae (Anderson and Ferrington, 2013) and small Ephemeroptera (Herbst and Cooper, 2010), which can rapidly exploit opportunities in disturbed ecosystems (Poff et al., 2018)
>
> H_3 Benthic macroinvertebrate communities in higher geomorphological complexity streams will demonstrate higher resilience to floods than communities in lower complexity streams, as a result of more diverse local species pool and increased availability of instream refugia.

4.2 Methods

4.2.1 Study site

GBNP (58°10′–59°15′ N.; 135°15′–138°10′ W.) spans an area of 11, 030 km^2 and was covered by a Neoglacial ice sheet as recently as 1700. This ice sheet has since retreated markedly and persists now as a number of remnants and smaller active icefields, of which the Brady icefield is the largest (Field, 1947, Hall et al., 1995). The retreat of ice following the Neoglacial maximum exposed a large tidal fjord and surrounding terrestrial landscapes. These recently exposed landscapes become available for colonisation by terrestrial biota which develop through time under the pathways of primary succession (Fastie, 1995, Crocker and Major, 1955, Lawrence et al., 1967, Chapin et al., 1994). Freshwater environments also establish on the landscape following glacial retreat (Milner et al., 2007, Klaar et al., 2009). These aquatic environments including lakes (Fritz et al., 2004, Engstrom and Fritz, 2006), streams and rivers (Milner et al., 2000, Milner et al., 2008, Milner et al., 2011) demonstrate similar pathways of succession.

In GBNP, long term stream ecological monitoring has been in place since the 1970s (Milner, 1987, Milner and Bailey, 1989). The temporal development of freshwater environments in GBNP results in a spatial gradient of habitats ages and geomorphological complexity (Klaar et al., 2009). This gradient allows the pursuit of research focused on the role of geomorphological complexity and associated habitat heterogeneity in ecological processes (Flory and Milner, 1999, Milner et al., 2007, Robertson et al., 2015). Following the extreme high-frequency floods of summer 2014, GBNP streams provide an opportunity to identify the role of geomorphological complexity in determining ecological resilience to floods. Such an opportunity has not previously been rigorously explored. In this study, four streams were selected with different ages and geomorphological complexity across a 140-year gradient (Milner et al., 2000, Klaar et al., 2009, Klaar et al., 2011).

4.2.2 Sampling and identification

In each of the four study streams, macroinvertebrate sampling was undertaken at a single study reach of ~25 m which has previously been selected for long-term (up to >40 years) study as a representative reach of the wider river network (Milner et al., 2000). A minimum of five benthic macroinvertebrate samples were collected annually (in August or early September) from 2012 to 2017 in each study reach using a modified Surber sampler (0.092 m^2 area; 330 µm mesh). These samples were preserved onsite using 70% ethanol and subsequently sorted and identified, under a binocular microscope to the lowest possible taxonomic level, using the keys available for North America (Merritt and Cummins, 1996, Thorp and Covich, 2009). Oligochaeta were identified to class. Chironomidae larvae were identified to species groups using Brooks et al. (2008) and Andersen et al. (2017), after being mounted in Euparal on slides and observed under a light microscope (Leica LMS 2000) at 1000x magnification.

4.2.3 Data analysis:

All statistical analyses were undertaken in R studio version 1. 1. 456 (R version 3. 5. 1; R-Core-Team, 2017). After exploratory analyses the 2014 summer samples were excluded from subsequent analyses, as due to the timing of 2014 sampling (during August) it was not possible to ensure samples from all streams were collected after the same number of flood events. A nested analytical approach was used to assess the role of high-frequency floods inclusively across all streams (hereafter ‘overall’ analyses) and at individual streams of varying geomorphological complexity (hereafter ‘individual’ analyses). This nested approach allows the identification of potentially contrasting responses of streams based upon their geomorphological complexity. Within this nested design, analysis was undertaken at four levels of community organisation:

(1) **Macroinvertebrate community level** based upon the following metrics - (i) taxonomic richness, (ii) Shannon diversity, (iii) total macroinvertebrate density (total individuals/m^2), (iv) beta-diversity amongst replicates for a given year (intra-year), (v) beta-diversity comparisons between the first study year (2012) and all subsequent years (vi) and persistence between replicates of sequential pairs of years. Beta-diversity and persistence analyses were undertaken on binary presence absence data. Intra-year beta-diversity, 2012 to subsequent year beta-diversity and persistence were partitioned into turnover and nestedness elements which capture the extent of replacement and net loss/gain of taxa respectively (Baselga, 2010);

(2) **Order level** density was calculated for the Ephemeroptera. This order is particularly abundant in GBNP stream macroinvertebrate communities (Milner et al., 2000);

(3) **Family level** density was calculated for Heptageniidae and Chironomidae. Chironomidae was selected as this family has the highest density of individuals in many local streams (Milner et al., 2000). Heptageniidae were selected based upon traits (small size, high mobility and streamlined body shape) perceived as conferring resilience to disturbance (Poff et al., 2006).

(4) **Species level** density of *Orthocladius S* type and *Eukiefferiella claripennis* within the Chironomidae were calculated, based on their differential abundance across the stream development gradient in GBNP (Milner, unpublished data), and their life history traits (small size, high dispersal capacity and fecundity) which are expected to demonstrate high resilience following disturbance (Poff et al., 2006). *Cinygmula* sp. (Heptageniidae) was selected due to its presence across all streams pre-flood and its traits as a heptagenid.

The nested approach of overall and individual stream analysis was also applied to non-metric multidimensional scaling (NMDS) and PERMANOVA of $\log_{10}(x+1)$ macroinvertebrate density data for replicates at all sites in all years. NMDS plots were produced for samples, species and 95% confidence ellipsoids of year group centroids, to visually describe changes, in both overall and individual stream community composition using the vegan R package (Oksanen et al., 2018). PERMANOVA was used to test for differences in community composition between sequential pairs of sampling years and for overall differences between all year groups at both overall and individual stream scales. A balanced testing design was applied to PERMANOVA, with even numbers of replicates per year used in the analyses, because a balanced PERMANOVA design is robust to differences within group dispersion (Anderson, 2014), which are expected under the GBNP succession model (Milner et al., 2008). Pairwise PERMANOVA were also undertaken using the vegan package. Pairwise p values were corrected for multiple testing using the Holm adjustment (Aickin and Gensler, 1996).

Shannon diversity was calculated for all Surber sample replicates using the diversity function in the vegan package. This metric is preferred to other diversity metrics, such as Simpsons diversity, due to its sensitivity to rare species (observed at all sites), and evidence from previous work which has identified the capacity of rare taxa to capitalise on disturbance in GBNP streams (Milner et al., 2018). Pairwise between stream beta-diversity was calculated using Jaccard's Dissimilarity which is calculated as 1- Jaccards index of similarity (Jaccard, 1912), which is used to describe changes in GBNP regional beta-diversity visually. Persistence was calculated using Jaccard's index of similarity (Jaccard, 1912) to allow direct comparisons to previous studies in GBNP (Milner et al., 2018). Beta-diversity and persistence measures were calculated using the betapart R package (Baselga et al., 2018).

Rank proportional abundance curves were plotted for 2013 (Flood-1), 2015 (Flood+1) and 2017 (Flood+3) for all streams to visually display relative taxon densities through time and space. Taxa were classified as a dominant member or rare member of a community based on the total cumulative density of individuals at a site in a given year. A boundary for delineating the core of communities from the taxa at their periphery was set as the 90th percentile of total density as described in Flather and Sieg (2007) based on the argument of Gaston (1994). This allowed observations to be made about changes to the relative importance of taxa which remained in, returned to or joined communities after the floods.

Generalized linear models (GLM) and generalized linear mixed effects models (GLMM) were used to test for an initial effect of the high-frequency summer floods and subsequent Post-flood response. To achieve this, years were combined into three categorical time periods; (1) Years 2012 & 2013 “Pre-flood” (Pre-flood), (2) Year 2015 “Immediate Post-flood” (Immediate Post-flood) and (3) Years 2016 & 2017 “Post-flood Response” (Response). Persistence values were compared statistically between pairs of persistence values each initially calculated from sequential pairs of years. At the individual stream scale, the categorical grouping or pairwise persistence scores were used as the explanatory variable in GLMs. In GLMMs they were used as fixed effects alongside one random effect ‘replicate’ which relates a given sample to the position upstream it was collected within the riffle. Akaike Information Criterion (AIC) was used to compare the fit of prospective models and for individual stream models GLM fit better than GLMM in all but one case, thus for consistency in approach GLMs were taken forward for all individual stream models. At the overall level, more complex mixed effects models were built. Here the random effect of ‘stream’ was applied to identify differing responses across the geomorphological complexity gradient whilst ‘replicate’ was nested within ‘stream’. Final model type is recorded in Chapter 4

Table 9.7.

For taxonomic richness, Shannon diversity, beta-diversity and persistence metrics, a model fitting approach was taken to identify the distribution of errors from a number of candidate error fits using the MASS package (Venables and Ripley, 2002). This approach identified a normal error distribution as the best fit to the data in all cases. For density data, which stems from counts of individuals, a model fitting approach was undertaken beginning with a Poisson error distribution using the glm function in base R. Where overdispersion was identified, negative binomial models were applied to count data using glm.nb in the MASS package. Negative binomial models were preferred to quasiPoisson because of the ability to compare models using AIC. Where taxa were relatively rare and there was an unexpectedly large count of zeros, zero-inflated negative binomial models were produced (using the pscl package; (Jackman, 2017, Zeileis et al., 2008)). The fit of these models was compared to other potential models. Where a zero count parameter was not significant in the zero-inflated model and a chi squared goodness of fit test indicated the negative binomial model fit the data well, the negative binomial approach was taken forward. The temporal autocorrelation of model residuals was tested using the acf function in R. Where temporal autocorrelation was identified, modelling approaches which allow for the incorporation of a correlation structure were applied. For Poisson type GLM models this required a generalised estimating equation approach to be taken. In generalised estimating equation approaches a type of quasi glm is undertaken. This approach allows for testing of differences between groups within the geepack package (Hajsgaard et al., 2006), but does not allow a true AIC to be produced. Goodness of fit tests based on model residuals and degrees of freedom were used to identify when a model was produced which fit the data.

In overall models the same approach was undertaken in GLMM construction. GLMMs were fit in the lme4 (negative binomial family models; Bates et al., 2015) and nlme (normal family models; Pinheiro et al., 2018) packages. The function lme in nlme has the capacity to handle correlation structure, including temporal autocorrelation of model residuals. Further it allows for an ANOVA and post hoc testing type approach. In negative binomial family models, the glmmPQL function in MASS was used to construct models incorporating temporal autocorrelation structure. These models do not allow an ANOVA of model outcomes. However marginal (Welch) tests for intercepts of groups compared to a reference group in the categorical grouping variable (here pre-flood in the time period grouping variable) are possible. The type of model applied to each metric is recorded in Appendix Table 9.7.

4.3 Results

4.3.1 Individual stream analysis

Significant shifts in community composition were observed following the floods (Figure 4.1) in PERMANOVA analyses, a pattern that was observed across all four study streams (Figure 4.2; Table 4.1). Chironomidae density generally declined at all streams in the Immediate Post-flood time period, to a low as 10% of Pre-flood density (Figure 4.3, Table 4.2). During the Response time period the Chironomidae recovered to Pre-flood levels at all streams apart from IVS. Similarly, Chironomidae species groups generally recovered to Pre-flood densities by the Response time period, except *E. claripennis* at IVS, where density rose from zero to greater than 10 ind m^{-2}. Across the streams Heptageniidae density demonstrated an Immediate Post-flood increase (significant change at all streams apart from IVS), but through time declined at the youngest sites (WPC and IVS). At WPC only, a single replicate during the Response time period contained Heptageniidae.

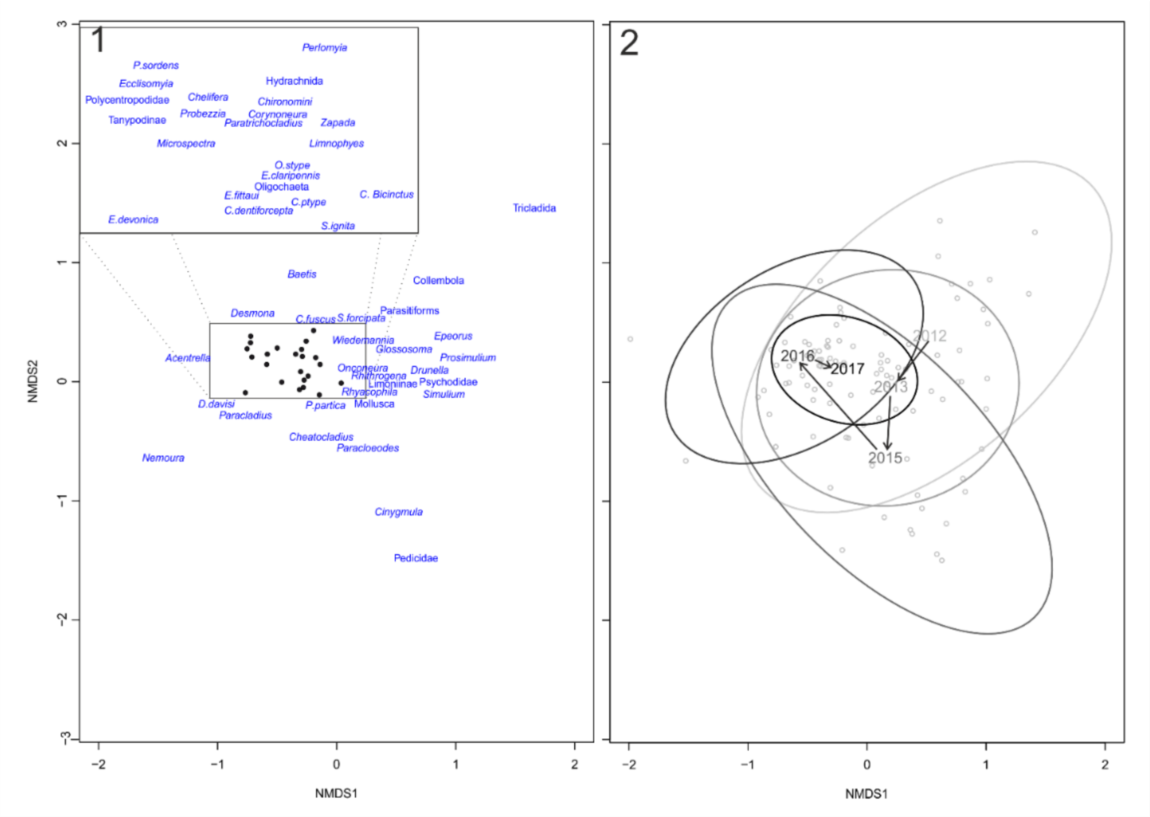

Figure 4.1. NMDS plots of (1) taxa and (2) year groups (all streams combined) 95% confidence ellipsoids of the group centroid plotted. Solid black arrows represent steps between years where PERMANOVA identified significant difference in communities

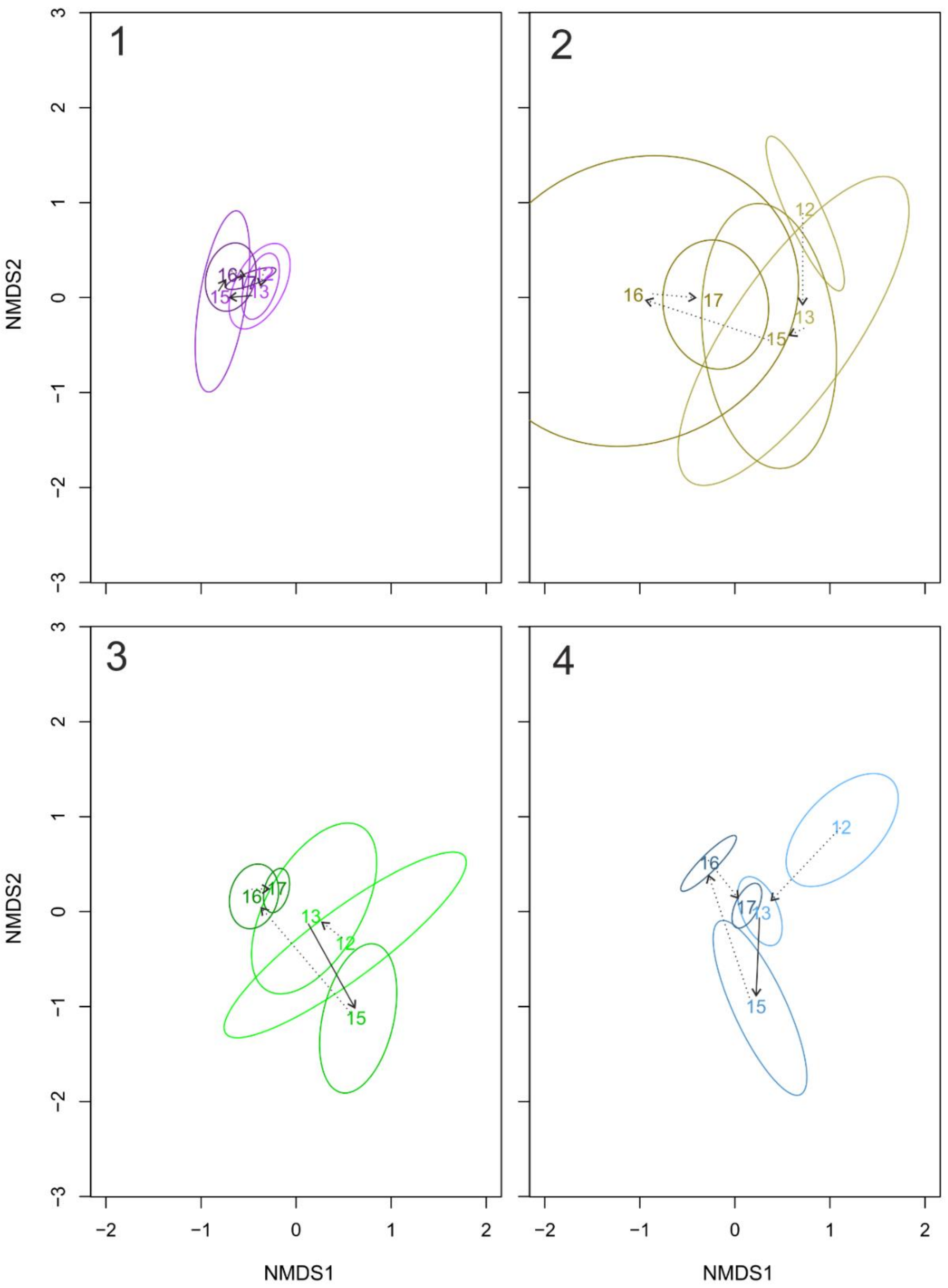

Figure 4.2. NMDS plots with year groups (individual streams) 95% confidence ellipsoids of the group centroid plotted. Purple (1) = WPC, gold (2) = IVS, green (3) = BBS, blue (4) = RPC. Solid black arrows represent sequential years where PERMANOVA identified a significant difference between community composition, dashed lines equal non-significant change

Table 4.1. PERMANOVA results for overall and individual stream community change between all pairwise sets of years.

	All			**WPC**			**IVS**			**BBS**			**RPC**		
Comparison	**F**	**r^2**	**p**	**F**	**r^2**	**p**	**F**	**r^2**	**p**	**F**	**r^2**	**p**	**F**	**r^2**	**p**
All Years	7.34	0.24	<0.001	7.06	0.40	<0.001	6.63	0.58	<0.001	11.44	0.70	<0.001	9.19	0.66	<0.001
	t	**r^2**	**p adj**	**t**	**r^2**	**p adj**	**t**	**r^2**	**p adj**	**t**	**r^2**	**p adj**	**t**	**r^2**	**p adj**
17 to 16	2.19	0.11	0.002	1.12	0.07	0.219	2.47	0.43	0.067	2.62	0.46	0.060	2.98	0.53	0.059
17 to 15	3.52	0.25	0.002	3.06	0.34	0.003	2.66	0.47	0.067	4.77	0.74	0.060	3.03	0.53	0.059
17 to 13	2.73	0.16	0.002	2.68	0.28	0.004	2.25	0.39	0.067	3.12	0.55	0.060	2.82	0.50	0.059
17 to 12	3.34	0.23	0.002	2.10	0.20	0.020	4.06	0.67	0.067	2.84	0.50	0.060	4.73	0.74	0.059
16 to 15	2.97	0.19	0.002	3.24	0.37	0.001	2.24	0.39	0.067	4.43	0.71	0.060	3.03	0.53	0.059
16 to 13	2.48	0.14	0.002	2.69	0.29	0.005	2.14	0.36	0.067	3.28	0.57	0.060	2.82	0.50	0.059
16 to 12	2.79	0.17	0.002	2.12	0.20	0.021	3.11	0.55	0.067	2.82	0.50	0.060	3.96	0.66	0.059
15 to 13	2.22	0.12	<0.001	3.61	0.42	<0.001	1.45	0.34	0.067	2.86	0.67	0.0072	2.29	0.57	0.007
15 to 12	2.62	0.15	<0.001	2.83	0.31	0.002	2.10	0.52	0.0165	2.03	0.51	0.0086	2.67	0.64	0.007
13 to 12	1.92	0.09	0.003	1.52	0.11	0.157	2.16	0.37	0.067	2.67	0.47	0.060	3.88	0.65	0.059

Individual stream trends in taxonomic richness, Shannon diversity and total density were typically consistent across the four streams. Significant differences in total density were observed between time periods with declines of between 30 to 50% Pre-flood to Immediate Post-flood at all sites except Ice Valley Stream (IVS; Figure 4.3; Table 4.2). The largest decrease was observed at the lowest complexity site Wolf Point Creek (WPC; 6586 ± 5168 to 1808 ± 541 ind m^{-2}). At higher complexity streams (Rush Point Creek (RPC) and Berg Bay South Stream (BBS)) total macroinvertebrate density recovered to Pre-flood levels (1017 ± 313 and 1157 ± 611 ind m^{-2}) by 2017; such a recovery was not evident at WPC. Statistically significant differences in taxonomic richness were observed between time periods (Table 4.2). Pre-flood taxonomic richness declined as compared to Immediate Post-flood at WPC (10.5 ± 1.8 to 8.6 ± 1.1 taxa), BBS (11.5 ± 4.6 to 4.4 ± 2.8 taxa) and RPC (10.7 ± 5.1 to 3.8 ± 0.8 taxa), but not at IVS. During the Response time taxonomic richness reached significantly higher levels than previously recorded at WPC (12.6 ± 2.1 taxa) and BBS (14.5 ± 3.6 taxa).

Intra-year beta-diversity demonstrated significant differences between time periods. An increase Immediate Post-flood at RPC (0.56 ± 0.11 to 0.74 ± 0.17; Figure 4.4), with the exception of WPC, followed by declines to the lowest recorded levels during Response at BBS (0.65 ± 0.16 to 0.37 ±0.11) and RPC (0.56 ± 0.11 to 0.43 ± 0.15). This response was associated with decreased turnover through time at all sites (Table 4.4, Figure 4.4). The exception to the dominant role of turnover occurred at BBS, where nestedness acted significantly in the opposite direction to turnover increasing from 0.05± 0.04 to 0.47 ± 0.34, leading to no significant change in dissimilarity overall from Pre to Post-flood.

Ellipsoid position, size and orientation varied significantly from Pre-flood to Immediate Post-flood at all sites (Figure 4.2; Table 4.1), supporting trends observed in the overall analyses. Pre-flood years demonstrated higher degrees of nesting in individual stream plots than Immediate Post-flood and Response years. Samples from 2015 plotted lower on the NMDS plot (Figure 4.1), associated with *Cinygmula* sp., *Nemoura* sp. and the Pedicidae (Figure 4.1). In 2016, communities demonstrated some convergence, moving towards the position of the youngest site (WPC). However, by 2017 older streams' (RPC, BBS and IVS) samples occupied positions between 2016 and Pre-flood samples. PERMANOVA analyses identified a significant change in community composition between 2012/2013 to 2015, at all streams (Table 4.1). Additionally, at the youngest stream (WPC) community composition changed significantly from 2015 to 2016. In individual streams, persistence generally decreased following the floods, associated with significant differences between time periods in GLM analyses. This response appears to be driven by taxa turnover in lower complexity streams (WPC and IVS) and nestedness at higher complexity streams (RPC and BBS). From 2015 to 2016 persistence remained lower than 2012 to 2013 across sites except IVS. By 2016 to 2017, persistence was higher whilst nestedness and turnover were lower than during other time periods at all sites, except for turnover at RPC and nestedness at IVS.

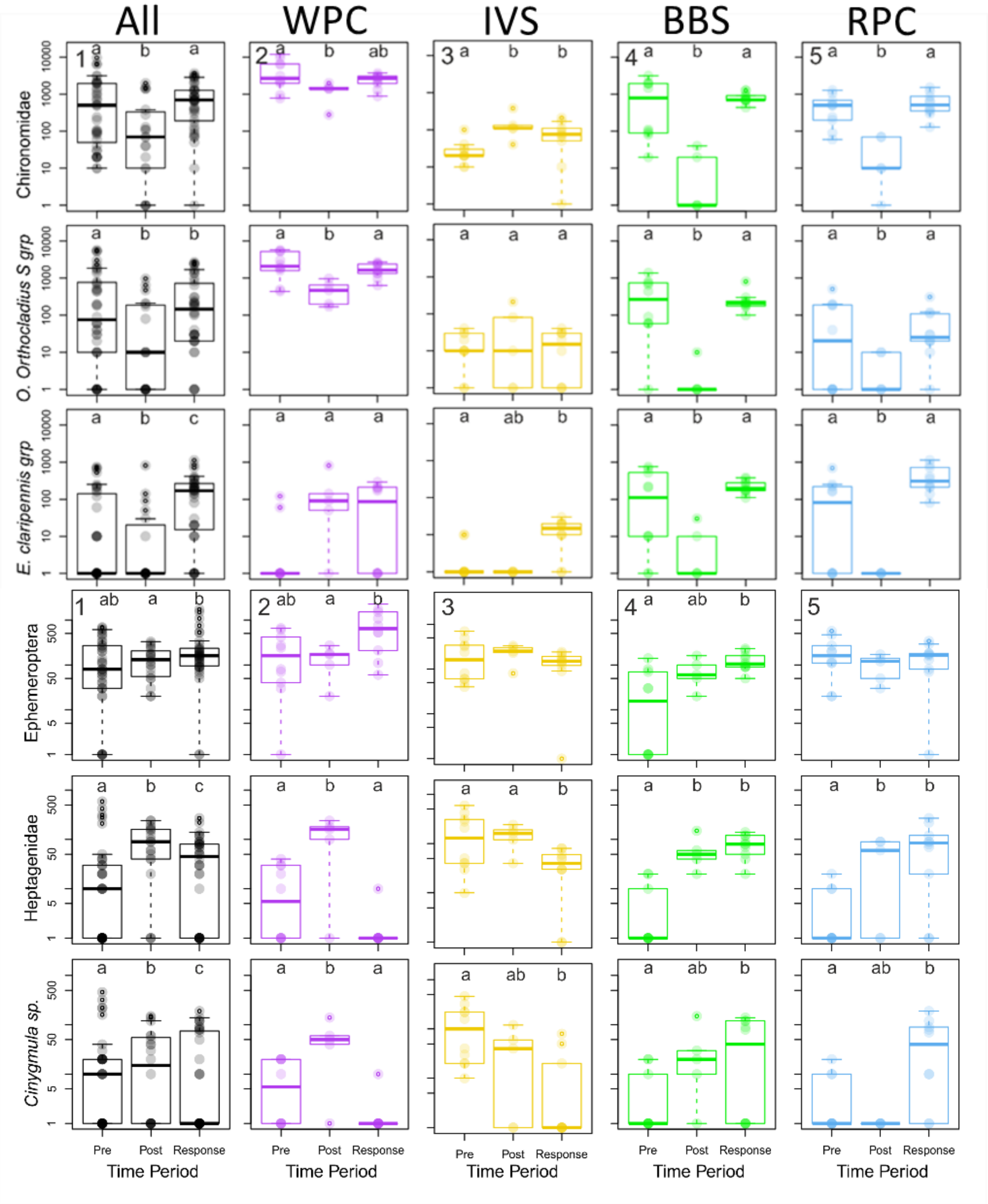

Figure 4.3 Box-dot density plots of taxa density for Pre-flood, Immediate Post-flood and Response time periods. Time periods which share the same letters above a boxplot are not significantly different. Where letters are absent no significant difference was identified in the all group ANOVA. 1 = all streams, 2 = WPC, 3= IVS, 4 = BBS, 5 = RPC.

*Table 4.2. Regression test statistics and post-hoc tests statistics for taxa groups density. Gaps in post hoc tests occur where the original overall model was not significant. P<0.05 - *, P<0.01 - **, P<0.001 - ***.*

Stream	**Test Comparison**	**Ephemoptera (ind/m^2)**	**Heptageniidae (ind/m^2)**	***Cinygmula* sp. (ind/m^2)**	**Chironimidae (ind/m^2)**	***Orthocladius* Type *S* grp (ind/m^2)**	***Eukifferella Claripennis* grp (ind/m^2)**
All	Overall	7.3 *		11.9 **		30.5 ***	
	Pre – Post	0.6	3.4 ***	-3.5 **	-4.0 ***	4.6 ***	-2.1 *
	Pre – Response	2.2	2.5 *	-3.4 **	-0.5	2.8 *	2.4 *
	Post - Response	-2.4 *		-2.4 *		-0.7	
WPC	Overall	14.0 ***	27.1 ***	33.1 ***	6.6 **	11.0 ***	3.8 *
	Pre – Post	0.8	-3.8 ***	-1.9 **	-3.6 ***	-5.1 ***	2.0
	Pre – Response	-2.0	2.3	2.0	-2.2	-1.7	1.8
	Post - Response	-3.7 ***	4.3 ***	3.7 ***	1.8	3.8 ***	-0.6
IVS	Overall	1.4	8.6 **	12.1 **	7.6 **	4.1 *	13.6 ***
	Pre – Post		-0.6	1.6	3.9 ***	2.1	0.0
	Pre – Response		-3.8 ***	3.5 ***	2.9 **	0.0	2.6 *
	Post - Response		-2.6 *	1.4	-1.5	-2.1	0.0
BBS	Overall	4.8 *	22.5 ***	8.3 *	21.2 ***	33.0 ***	14.9 ***
	Pre – Post	1.8	4.8 ***	-2.1	-6.6 ***	4.8 ***	-4.2 ***
	Pre – Response	3.5 **	5.6 ***	-2.9 **	-0.6	1.1	-0.1
	Post - Response	1.1	0.9	-0.3	6.2 ***	-4.3 ***	4.2 ***
RPC	Overall	1.5	15.2 ***	19.1 ***	304 ***	5.1 *	304 ***
	Pre – Post		3.1 **	0.0	7.6 ***	-3.0 **	35.1 ***
	Pre – Response		4.5 ***	-3.4 **	-0.5	-0.7	-1.4
	Post - Response		1.1	-0.0	-15.7 ***	2.6 *	-34.4 ***

4.3.2 Overall analysis (four streams)

Fifty four taxa were collected across the four streams. Pre-flood communities were dominated by *Cinygmula* sp. and *Epeorus* sp. (Heptageniidae)*, Pagastia partica, E. claripennis, Orthocladius S* type grp (Chironomidae), and *Prosimulium* sp*.* (Simuliidae) (Figure 4.1). At the Immediate Post-flood stage, some taxa remained important including *Cinygmula* sp. (Figure 4.1), *E. claripennis and Orthocladius S* type grp, whilst *Seratella ignita* (Ephemerellidae), the small baetid *Acentrella* sp. and the small nemourids (*Zapada* sp. and *Nemoura* sp.) also became more abundant through Immediate Post-flood (2015) and Response communities (2016-2017).

The most abundant taxa in Response samples were *E. claripennis and Orthocladius S* type grp, with densities of approximately 1950 ± 2405 and 5276 ± 8101 inds m^{-2} which represents a four-fold increase for *E. claripennis* (Figure 4.3)*.* Taxonomic richness varied significantly (Table 4.3) with a decrease in a mean of 9.7 ± 4.2 taxa (Pre-flood) to 5.9 ± 2.5 (Immediate Post-flood), but by the Response period had increased to 12.1 ± 4.3 taxa. Shannon diversity varied significantly between time periods in overall glmm analyses. A decrease from 1.6 ± 0.38 Pre-flood to 1.3 ± 0.50 Immediate Post-flood but increased during the Response time period to 1.8 ± 0.44. Total density of benthic macroinvertebrates decreased by 75% in the Immediate Post-flood (2247 ± 3632 to 623 ± 753 inds m^{-2}), although it appeared to subsequently recover to 1463 ± 1400 inds m^{-2} during the Response period.

A significant response was observed in the Ephemeroptera (Table 4.2), as density increased from a mean of 181 ± 203 inds m^{-2} (Pre-flood) to 328 ± 486 inds m^{-2} (Response) with less zero counts observed in Immediate Post-flood and Response time periods than Pre-flood (Figure 4.3). The initial increase in density of Ephemeroptera was driven by increased prevalence of the Heptageniidae (56 ± 127 to 100 ± 77 inds m^{-2}). The Chironomidae and *O. Orthocladius S* type demonstrated significant changes in glmms with 10-fold decreases in density by 2015 (Immediate Post-flood), from 15480 ± 26470 and 8379 ± 15164 inds m^{-2} to 3772 ± 6285 and 1399 ± 2628 inds m^{-2}. *E. claripennis* displayed a significant response with 14 of 20 Post-flood samples no longer containing the taxa. Chironomidae recovered to Pre-flood levels during the Response period, whereas species groups demonstrated divergence with no observed recovery of *O. Orthocladius S* type, in spite of an increasing median, whereas *E. claripennis* density increased to 1957 ± 2405 ind m^{-2} by three years post flood.

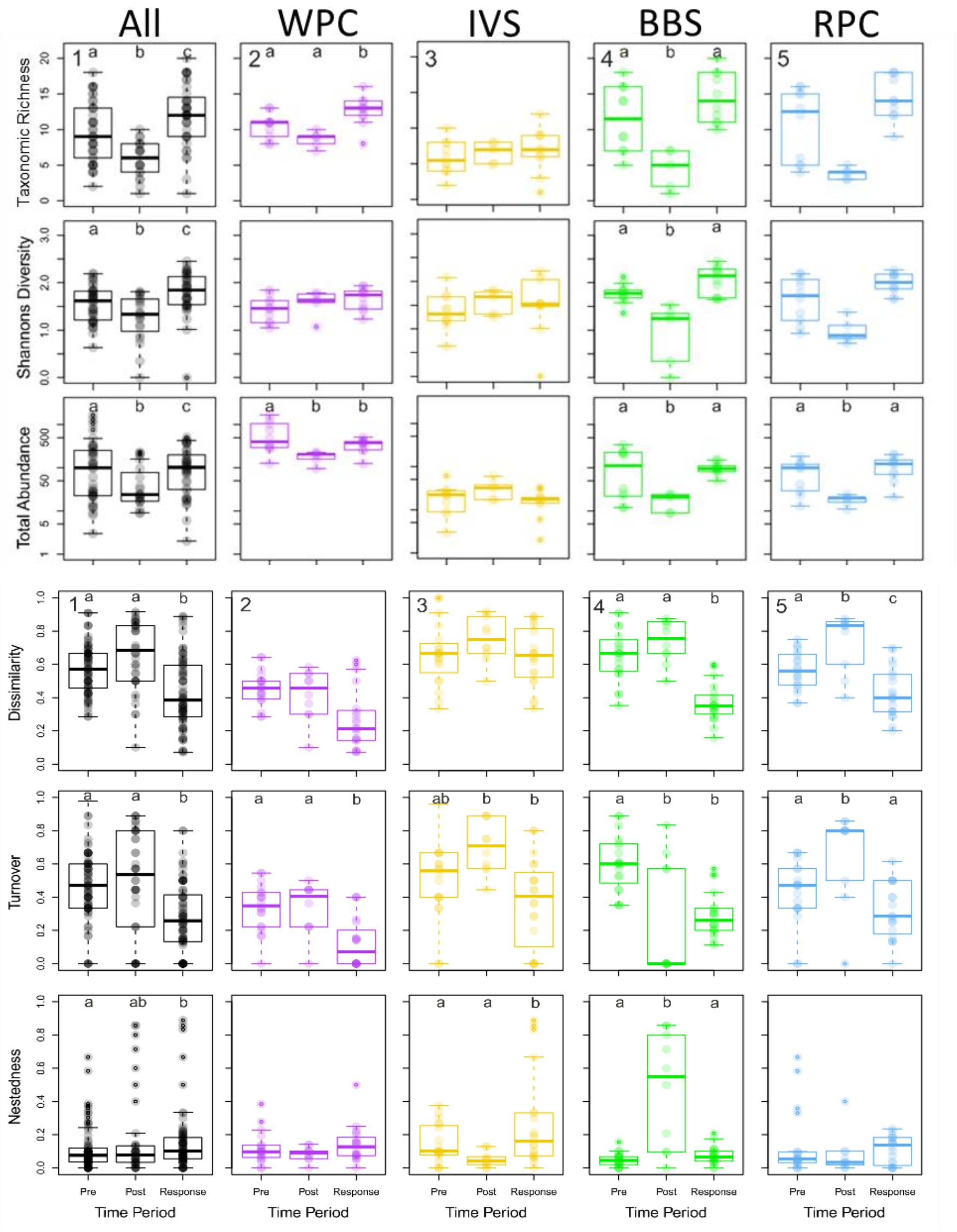

Figure 4.4. Box-dot density plots of summary stats for Pre-flood, Immediate Post-flood and Response time periods. Time periods which share the same letters above a boxplot are not significantly different. Where letters are absent no significant difference was identified in the all group ANOVA. 1 = all streams, 2 = WPC, 3= IVS, 4 = BBS, 5 = RPC.

*Table 4.3. Regression test statistics and post-hoc tests statistics for summary metrics and intra-year beta-diversity metrics. Gaps in post hoc tests occur where the original overall model was not significant. P<0.05 - *, P<0.01 - **, P<0.001 - ***.*

Stream	**Test Comparison**	**Taxa Richness**	**Shannon's diversity**	**Total density (ind/m^2)**	**Jaccard Dissimilarity**	**Jaccard Turnover**	**Jaccard Nestedness**
All	Overall	21.8***	11.8 ***		13.7 ***	10.8 ***	3.0 *
	Pre – Post	-4.0 ***	-2.6 *	-4.6 ***	2.2	0.8	0.3
	Pre – Response	3.2 **	2.6 *	-1.1	-3.5 **	-3.9 ***	2.4*
	Post - Response	6.6 ***	4.8 ***		-5.0 ***	-4.0 ***	1.7
WPC	Overall	16.9 ***	1.6	8.7 **	1.9	4.5 *	1.3
	Pre – Post	-1.9		-4.4 ***		-0.2	
	Pre – Response	2.6 *		-2.6 **		2.7 *	
	Post - Response	4.0 ***		2.3		2.4 *	
IVS	Overall	0.4	0.4	1.8	1.3	6.4 **	9.4
	Pre – Post					1.9	1.3
	Pre – Response					-1.8	-4.1 ***
	Post - Response					-3.5 **	-3.9 ***
BBS	Overall	22.3 ***	16.3 ***	11.5 ***	34.3 ***	14.9 ***	7.3 **
	Pre – Post	-3.3 **	-4.3 ***	-4.8 ***	1.6	-4.3 ***	-3.6 **
	Pre – Response	1.7	1.7	-0.8	-6.8 ***	-4.8 ***	-0.2
	Post - Response	4.7 ***	5.7 ***	4.2 ***	-7.1 ***	-0.3	3.3 **
RPC	Overall	1.2	1.3	1837 ***	16.5 ***	9.6 ***	0.7
	Pre – Post			4.7 ***	3.2 **	3.0 **	
	Pre – Response			-0.8	-3.0 **	-1.7	
	Post - Response			-42.6 ***	-5.7 ***	-4.4 ***	

Intra-year beta-diversity metrics (dissimilarity, turnover and nestedness) demonstrated no significant change Pre-flood to Immediate Post-flood (Figure 4.4). However significant differences were observed in the response time period. During the Response dissimilarity and turnover declined from an average of 0.58 ± 0.16 and 0.47 ± 0.21 to 0.42 ± 0.21 and 0.27 ± 0.21 respectively. Nestedness demonstrated a significant difference between Pre-flood and Response time periods of an increase in mean from 0.11 ± 0.12 to 0.15 ± 0.18.

Major shifts in community composition were evident through time in NMDS plots with a large change to ellipsoid orientation in 2015, followed by a nesting of subsequent years (2016 and 2017) within earlier years' ellipsoids and reduction in area occupied through time (Figure 4.1). These changes were supported by significant differences between year groups in PERMANOVA analyses (Table 4.1). Between 2013 to 2015 significant differences were observed in persistence with a decrease in mean. Whilst a two-fold increase in average nestedness (0.13 ± 0.10 to 0.23 ± 0.27) compared to pre-flood (2012 to 2013) was observed. From 2015 to 2016 the turnover component of persistence was higher than from 2012 to 2013 (0.73 ± 0.22 from 0.58 ± 0.22). Finally, from 2016 to 2017 persistence increased to 0.49 ± 0.15 and turnover decreased from to 0.47 ± 0.20.

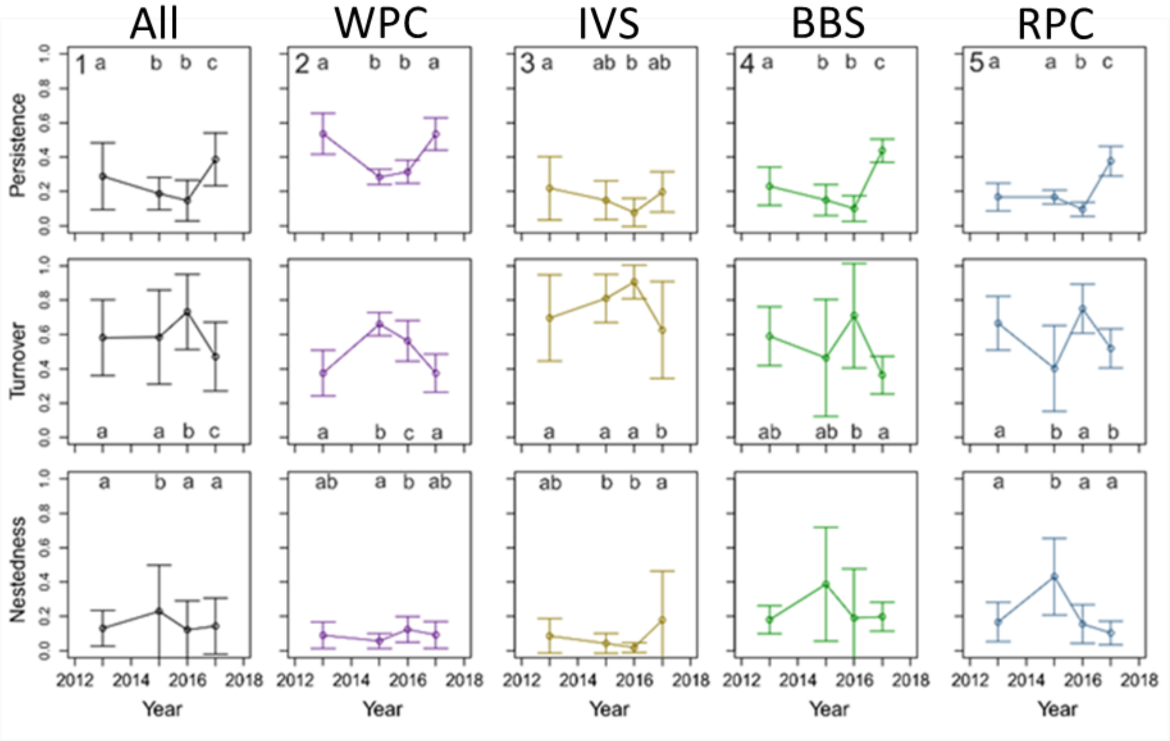

Figure 4.5. Plots of sequential pairs of years persistence, turnover and nestedness metrics through time. Points are plotted on the second year of a pair (e.g. 2012 to 2013 comparison is plotted over 2013). Time periods which share the same letters in a plot are not significantly different from one another. Where letters are absent no significant difference between pairs was identified in the all group ANOVA. Error bars = ± 1 SD. 1= all streams combined, 2 = WPC, 3= IVS, 4 = BBS, 5 = RPC

*Table 4.4. Tests for differences of persistence between all and pairs of years. Gaps in post hoc tests occur where the original overall model was not significant. P<0.05 - *, P<0.01 - **, P<0.001 - ***.*

Stream	**Test Comparison**	**Persistence Jaccard Similarity**	**Jaccard Turnover**	**Jaccard Nestedness**
All	Overall	51.7 ***	13.2 ***	4.5 **
	12 to 13 – 13 to 15	4.9 ***	0.0	3.0 *
	12 to 13 – 15 to 16	6.7 ***	3.5 **	-0.1
	12 to 13 – 16 to 17	-4.5 ***	-2.6 *	0.4
	13 to 15 – 15 to 16	2.0	3.6 **	-3.2 **
	13 to 15 – 16 to 17	-9.3 ***	-2.6 *	-2.6 *
	15 to 16 – 16 to 17	-11.4 ***	-6.2 ***	0.6
WPC	Overall	63.2 ***	41.5 ***	3.9 **
	12 to 13 – 13 to 15	10.4 ***	9.1 ***	-1.7
	12 to 13 – 15 to 16	9.1 ***	6.0 ***	1.7
	12 to 13 – 16 to 17	0.1	-0.1	0.1
	13 to 15 – 15 to 16	-1.5	-3.1 **	3.4 **
	13 to 15 – 16 to 17	-10.3 ***	-9.1 ***	1.8
	15 to 16 – 16 to 17	-9.0 ***	-6.0 ***	-1.6
IVS	Overall	3.0 *	4.3 **	5.2 **
	12 to 13 – 13 to 15	-1.4	-1.5	1.0
	12 to 13 – 15 to 16	-2.8 *	-2.5	1.5
	12 to 13 – 16 to 17	-0.5	0.7	-2.1
	13 to 15 – 15 to 16	-1.4	-1.1	0.6
	13 to 15 – 16 to 17	0.9	2.1	-3.1 *
	15 to 16 – 16 to 17	2.3	3.3 **	-3.6 **
BBS	Overall	52.5 ***	4.8 **	2.4
	12 to 13 – 13 to 15	-2.8 **	1.4	
	12 to 13 – 15 to 16	-4.5 ***	-1.0	
	12 to 13 – 16 to 17	7.1 ***	2.4	
	13 to 15 – 15 to 16	-1.8	-2.5	
	13 to 15 – 16 to 17	9.8 ***	1.0	
	15 to 16 – 16 to 17	11.7 ***	3.5**	
RPC	Overall	63.5 ***	19.8 ***	14.5 ***
	12 to 13 – 13 to 15	-0.1	-5.4 ***	-4.8 ***
	12 to 13 – 15 to 16	-3.4 **	1.7	0.6
	12 to 13 – 16 to 17	9.6 ***	-3.0 *	1.2
	13 to 15 – 15 to 16	-3.3 **	7.1 ***	5.3 ***
	13 to 15 – 16 to 17	9.7 ***	2.4	5.8 ***
	15 to 16 – 16 to 17	13.1 ***	-4.6 ***	0.6

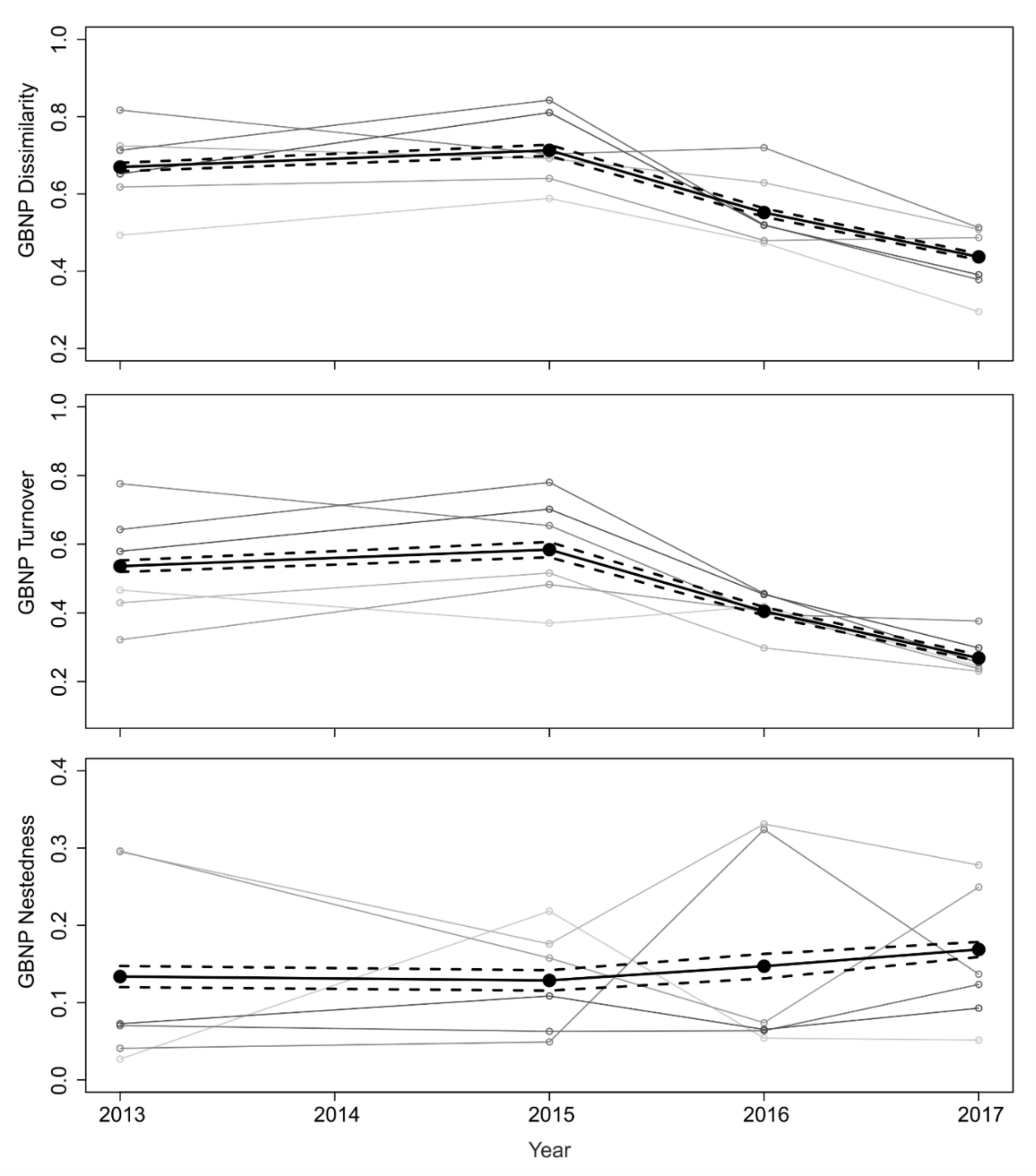

Figure 4.6. Annual pairwise between-stream beta-diversity across all streams. Black = Mean value across all pairwise comparisons, dashed line is 95% confidence interval. Grey lines represent individual pairs of streams, darker lines indicate greater differences in age between streams.

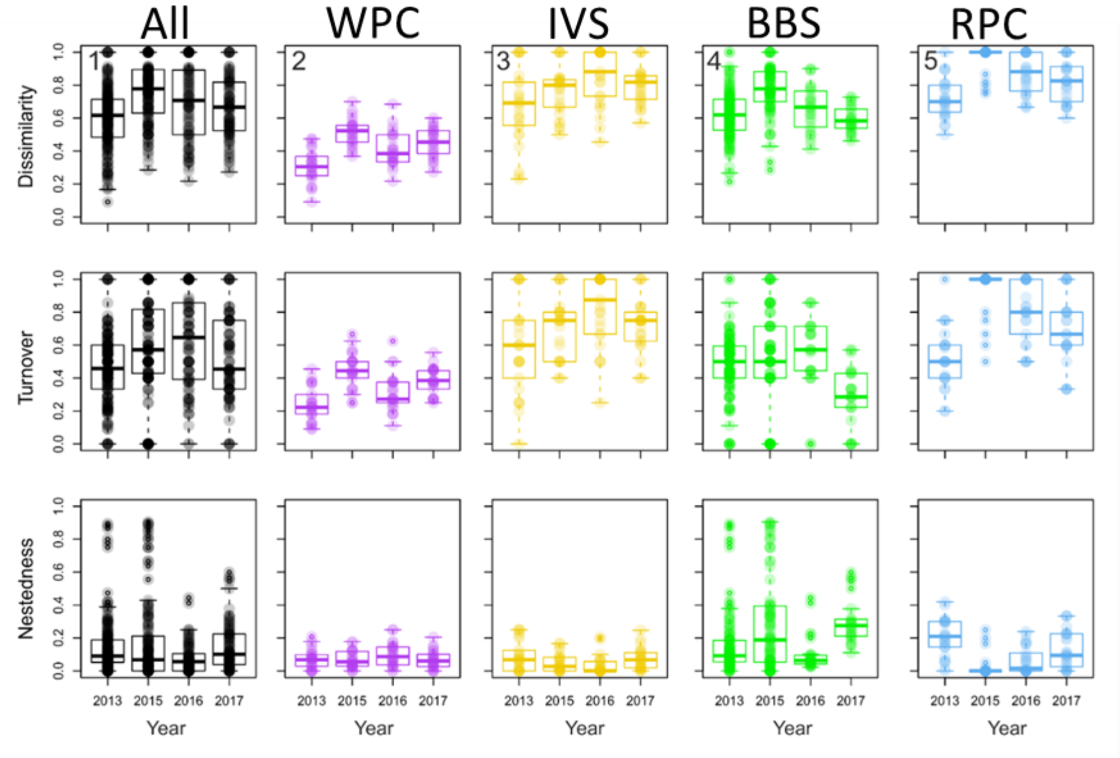

Figure 4.7. Beta-diversity between 2012 and all subsequent years in the study. All streams = 1, WPC = 2, IVS = 3, BBS = 4, RPC = 5.

4.3.3 Community dominance analyses

Community dominance analyses (Table 4.5, Figure 4.8) identified three (*Dentiforcep* grp, *Prosimulium* sp. and *Eperous* sp.) of the nine locally dominant taxa in pre-flood communities that were not recorded at any stream in Flood+1 (2015) communities. Although some Flood-1 (2013) dominant taxa were not recorded at all Flood+1, the mean number of taxa remained at 4. This stable mean was the result of the identification of three taxa not recorded in the Flood-1 community (*Paracladius* sp., *Diamesa* sp. and *Acentrella* sp.) which established in the core of WPC community on year post flood. Another baetid (*Paracloeodes* sp.) moved from a rare to dominant member of the Flood+1 community at IVS and RPC. By 2017, five taxa which were rare in 2015 (Flood+1) had become dominant. Three of these taxa (all Chironomidae - *Orthcladius TypeS* grp., *E. claripennis* grp. and *Limnophyes* grp.) were dominant in at least three streams by 2017.

Alongside changes to the dominant taxa in communities, the floods drove changes to the richness and diversity of rare taxa. The number of rare taxa fell from a mean of 17 (Flood-1) to 8 (Flood+1). This was driven predominantly by the loss of taxa at higher complexity streams where the average declined from 22 to 8. These losses were spread across Diptera, Ephemeroptera, Plecoptera, Trichoptera and the non-insects. Some recovery was observed by the Flood+3 period (mean = 14). A significant increase in the ubiquity of taxa observed at all streams was recorded, increasing from three (Flood-1) to 10 (Flood+3). This increase was driven predominantly by members of the Chironomidae which saw an increase from one to five taxa observed at all streams.

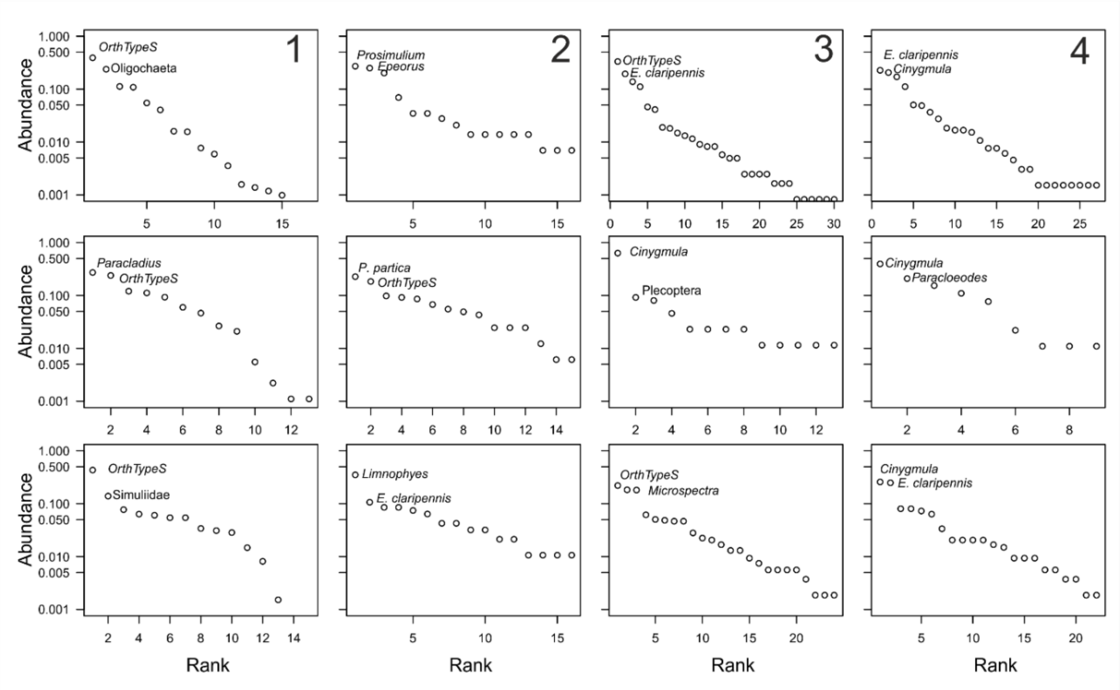

Figure 4.8. Whittaker plots of proportional density of taxa during top- flood-1 (2013), middle – flood+1 (2015) and bottom – flood+3 (2017). Two most abundant taxa are labelled at each stream in each time period. 1 = WPC, 2 = IVS, 3 = BBS and 4 = RPC.

Table 4.5. Dominant and rare taxa across pre-flood (2013), Post-flood (2015) and response (2017) time periods. Streams are numbered 1 = WPC, 2 = IVS, 3 = BBS and 4 = RPC.

Taxa	**Pre-flood**		**Post-flood**		**Response**	
	Dominant	**Rare**	**Dominant**	**Rare**	**Dominant**	**Rare**
Orthcladius TypeS grp.	1,2,3,4		1,2	3,4	1,2,3,4	
Paracladius grp.			1	2		
Paratrichocladius grp.	3	4			2,3	1,4
Cheatocladius grp.				2		2
C. dentiforcep grp.	1			2		
C. bicinctus grp.		3,4				2,3
C. fuscus grp.						3
Crictopus TypeP grp.		1,4				
E. claripennis grp.	3,4	2	1	3	2,3,4	1
E. fittaui grp.		1				
Limnophyes grp.		2,3,4			2,3,4	1
Corynoneura grp.		2,3,4				1,3,4
Onconeura grp.						4
Pagastia partica grp.	3,4	1	2,4	3	3,4	1,2
Diamesa grp.			1			2
PolypSordens grp.		1				
Microspectra grp.		1,3,4			1,3	4
Tanypodinae		1				1
Probezzia sp.		1,3		1	1	3,4
Chelifera sp		4				2,3,4
Limoniinae		3				3,4
Pedicidae				2,3		
Simulium sp		1,2,3,4		1,2,3,4	1,	2,3,4
Prosimulium sp.	2	3,4				
Psychodidae		2,3				
Ephemeroptera		2,3,4	2,3	4		
Ephemerellidae		3,4		3		
Serratella ignita		1,4		1,2,3,4	1,2	3,4
Drunella sp		3,4		3		3
Heptageniidae		3				
Rhithorgena sp.		3,4				
Cinygmula sp.	2,4	3	2,3,4	1	2,4	1,3
Epeorus sp.	2,4				4	2,3
Baetidae		1,2,3				
Paracloeodes sp.		1,3,4	2,4	3		
Acentrella sp.			1			1,2,3,4
Plecoptera		3	3	2,4		
Perlomyia sp.						2,3,4
Chloroperlidae		2,3			3,4	
Suwallia forcipata		1,2,3,4	2	1		1,3,4
Zapada sp.						3,4
Nemoura sp.						2
Rhyacophila sp.		4				4
Glossosoma sp.						4
Mollusca		3				
Parasitiforms		3				
Hydrachnida		1,4		1		
Oligochaeta	1	2,4		1,2,3,4		1,2,3,4

4.4 Discussion

Unique insights from the combined biodiversity and ecological resilience approaches indicate that high-frequency summer floods can significantly alter the macroinvertebrate communities of streams, regardless of a stream’s geomorphological complexity. Low ecological resilience to flood disturbance was observed at all streams, linked to significant declines in both total density and taxonomic richness Immediately Post-flood (2015) and significant shifts in macroinvertebrate community structure during the subsequent Response (2016 and 2017). This study identified novel divergent drivers of community change across streams dependent on their successional context: the loss of taxa dominated change in older, higher complexity streams, whereas turnover of taxa dominated change within the less diverse communities of young, lower complexity streams. Initial divergence was followed by a convergence of community composition between streams during the Response time period linked to Post-flood colonisation by small Ephemeroptera and Chironomidae. Colonisation by these groups at all streams led to a homogenisation of benthic macroinvertebrate communities between streams by 2017.

4.4.1 Initial impact of high-frequency summer floods on benthic macroinvertebrate biodiversity

Distinct differences in taxonomic richness, Shannon diversity and total density were evident across the geomorphological complexity gradient pre-flood. High diversity, low density communities were observed at the highest complexity streams and low diversity, high density communities at lower complexity streams consistent with earlier GBNP studies (Milner et al., 2000, Milner et al., 2008, Milner et al., 2011). In GBNP Pre-flood community composition was controlled by abiotic and biotic processes under the tolerance model of community assembly (Brown and Milner, 2012, Milner et al., 2011). An important finding of this study was the dominance of a small number of shared taxa in communities across all streams pre-flood. These taxa were members of the Chironomidae and Heptageniidae, which possess traits of small and in some cases streamlined bodies and high fecundity (Poff et al., 2006), generally considered to confer resilience to floods (Townsend et al., 1997a).

In spite of theoretically resilient cores, high-frequency summer floods drove significant short term (< two years) losses of macroinvertebrate diversity and density across GBNP streams, in support of $H_{1:}$ that the floods will result in short term declines to total macroinvertebrate diversity and density. These losses to diversity and density occurred from both the resilient, dominant taxa as well as more taxonomically diverse rare taxa. This study demonstrates that the lack of research addressing the ecological implications of high-frequency flooding represents a significant knowledge gap, given the increased likelihood of future persistent precipitation events associated with rising temperatures (Berg et al., 2013) which drive high-frequency flooding. However, diversity and density losses reported here in the short term are consistent with the majority of extreme high-magnitude flood research (Mundahl and Hunt, 2011, Ming-Chih and Mei-Hwa, 2012, Woodward et al., 2015).

The trend of decreased Post-flood overall density was driven strongly by the Chironomidae and is supported by recent work on summer floods in a regulated river in Switzerland (Robinson et al., 2018). However, increased densities of and colonisation by some Chironomidae sp. not observed in 2012 or 2013 occurred following the 2014 floods. Similar increased density following summer floods has been observed elsewhere and is thought to be linked to resistance of particular life stages in the family (Anderson and Ferrington, 2013). Additionally, some Chironomidae, e.g. *Diamesa* sp., may represent fugitive taxa which can exploit reduced competition in Immediate Post-flood communities, as argued in Milner et al. (2013) and Milner et al. (2018).

Similarly, selected predatory benthic macroinvertebrate taxa (e.g. *Suwallia forcipata*, Tanypodinae) demonstrated major reductions in density Post-flood (2015) due to two potential processes; (1) abiotic processes of physical disturbance (Poff et al., 2018) and/or (2) decreased availability of prey resources (Larson et al., 2018), primarily the Chironomidae (Clitherow, 2016). Low mobility of some predatory taxa (Poff et al., 2018) and large body size have also been linked to low resistance to hydrological disturbances (Ming-Chih and Mei-Hwa, 2012, Ledger et al., 2013).

4.4.2 Community compositional change and ecological resilience

Significant changes to the composition of post-flood communities (2015 to 2017) occurred at all streams in support of hypothesis $H_{2:}$ that community composition will change following high-frequency summer floods. Compositional changes were associated with the loss of dominant as well as rare taxa. The loss of dominant taxa from communities could drastically alter ongoing biotic interactions such as basal resource utilisation. However, previously reported pre-flood redundancy of traits in communities (Brown and Milner, 2012) may provide a compensatory mechanism through which ecological function may persist following disturbance. Observed increases in the presence of Baetidae may be linked to this family's high resistance and overall resilience to floods (Nislow et al., 2002, Poff et al., 2018). Their resilience is associated with high mobility, which may increase their access to refugia and thus increase survival through a flood, as well as their high fecundity. This evidence could explain the shift of *Paracloedes* from a rare (Flood-1) to dominant member of the community (Flood+1) observed here at both intermediate and higher complexity streams.

Such a rapid movement of a rare taxa from the periphery of a community to dominance may suggest a special case of extreme resilience to flood disturbances which may represent the need for an extension to Hollings model of resilience. Indeed, understanding the intermediary processes which allow such extremely resilient taxa to dominate post-disturbance communities may provide a framework in which to enhance our understandings of community response to disturbance in line with Poff et al. (2018). Further it may offer a route through which to identify taxa which can act as indicators of the severity of past and resilience to future disturbances.

This study demonstrates the low resilience reported by Milner et al. (2018) at WPC (up to 2015) persists through time, a pattern consistent with higher complexity streams (BBS and RPC). Although, some evidence is available to indicate that dominant taxa in communities at higher complexity streams may have higher resilience than at lower complexity streams, with the return of a number of taxa (Chironomidae and Heptageniidae) to numerical dominance by 2017 and a movement of post-flood years ellipsoids towards pre-flood position in NMDS analyses. Importantly however, by 2017 communities demonstrated a major increase in evenness, with double the number of dominant taxa observed in 2017 than observed in pre-flood (2013) communities. Consequently, community composition three years post-flood remained markedly different to pre-flood composition. These findings indicate there is little support for hypothesis H_3: that high taxonomic diversity of communities in higher complexity streams will confer greater resilience to communities than observed in lower complexity streams. Such results are consistent with current research which has identified changing community composition under new flood regimes, in both natural and managed rivers (Robinson and Uehlinger, 2008, Milner et al., 2018, Robinson et al., 2018).

4.4.3 Divergent pathways of initial ecological resilience

The initial drivers of low benthic macroinvertebrate resilience were divergent across the complexity gradient. This divergence was thought to be linked to differences in pre-flood community composition. At higher complexity streams (BBS and RPC) community change was driven by the loss of taxonomic diversity, seen in the nestedness metric of persistence. In these streams, high-frequency summer floods acted as an environmental filter, eliminating flood intolerant taxa from the community. Some of the taxa not recorded at all post-flood, (e.g. Mollusca and Tricladida), have traits typical of K-selected species (Poff et al., 2006) such as large size, immobility and low fecundity (Ming-Chih and Mei-Hwa, 2012), which may make them susceptible to flooding. Given the near absence of K-selected taxa at lower complexity streams the environmental filtering (species sorting) effect of the floods was not observed to the same extent. This finding is significant for river restoration policy in heavily modified streams and rivers globally, which often targets the recovery of more diverse biotic communities at sites which generally support r-selected taxa (Boon, 1988), high-frequency floods may filter out recolonising K-selected taxa which lack the resilience to tolerate more frequent flood disturbances (Ming-Chih and Mei-Hwa, 2012).

Although streams with lower geomorphological complexity (WPC and IVS) demonstrated less evidence of flood driven environmental filtering, observed changes to persistence were linked to rapid turnover of taxa. This turnover saw the replacement of both dominant and rare taxa with others from the local species pool. Such a response indicates the local species pools dominated by Chironomidae (Milner et al., 2008, Milner et al., 2013) contained numerous taxa capable of rapidly (<1 year) exploiting the disturbed ecosystem, include *Diamesa* sp., *E. Claripennis* grp, *Paracladius* sp..

4.4.4 Community reassembly

Decreased within stream riffle beta-diversity and increased richness of dominant taxa in communities indicated increased community evenness at the riffle scale after three years post-flood (2017). Change to the dominance/evenness dynamic of communities have previously been linked to altered biotic and/or abiotic controls on community assembly (Hillebrand et al., 2008). Indeed, increasing rates and severity of disturbance has been shown to increase evenness in other ecological fields (Kimbro and Grosholz, 2006, Yeboah et al., 2016). Such a trend for increased evenness following extreme high-frequency floods appears to have significant implications for post-flood community reassembly in this study - leading to the homogenisation of communities. It is of further significance given the increasing regularity of extreme floods now reported in North America (Wouter et al., 2017). The trend for homogenisation could be driven by a number of potential controls on community reassembly explored below.

A depleted or significantly altered primary resource base could have acted as a significant selection pressure on taxa post-flood (Singer and Battin, 2007). Reduced autochthonous resource availability is expected in the short term (weeks/months) (Grimm and Fisher, 1989, Tornés et al., 2015). However diatom biomass, the dominant basal resource in study streams (Clitherow, 2016), has been shown to be relatively resilient to extreme floods (Grimm and Fisher, 1989, Tornés et al., 2015). Altered top down pressure could also act as a control on reassembly processes (Therriault and Kolasa, 1999, Shurin J. B. and E.G., 2001). Whilst a short-term release from top down pressure was indeed expected in 2015, as a result of decreased abundance of *S.*

forcipata, predator density recovered during the Response time period, suggesting that there was no persistent shift in top down pressure. Consequently, altered top down effects are not anticipated to constitute a new and ongoing control of reassembly in this case. However, a depleted or significantly altered primary resource base could have acted as a significant selection pressure on taxa post-flood (Singer and Battin, 2007).

Dominance of a small core of taxa in a community can act as a strong biotic control on composition of other community members, through priority effects and competitive exclusion (Hillebrand et al., 2008). Consistent with this theory, in the current study, small groups of taxa dominated pre-flood, whilst spatially heterogeneous composition of rare community members were observed across the streams. Disruption to communities as a result of the high-frequency summer floods is expected to have significantly reduced the effect of such biotic controls, as observed elsewhere in experimental grazer communities (Dudley and D'Antonio, 1991). Release from such priority effects/competition could explain post-flood shifts in community composition and colonisation by previously unrecorded taxa. Low intra-year beta-diversity and increased taxonomic richness across streams during the Response period, supports this line of argument. Elsewhere such increased evenness and richness have been positively linked in species area models (He and Legendre, 2002, Green and Ostling, 2003). Given the observed recovery of total density at all but WPC by 2017, it is anticipated that release from priority effects/competition will not persist long term, although the exact nature of future biotic controls remains hard to predict. Changes in future priority effects could be one mechanism through which ecosystems are prevented from recovering to preflood composition. Indeed, it seems unrealistic to expect communities and ecosystems which are influenced heavily by inter and intra-specific interactions between taxa to recover to a pre-disturbance condition once such interactions are altered.

4.4.5 Convergence of communities across the geomorphological complexity gradient

A major finding of this study was the homogenisation of stream benthic macroinvertebrate communities following the floods. Convergence was driven by the processes of community reassembly following the floods, although the loss of K-selected taxa at higher complexity streams directly following the floods (2015) also played a role. Disruption to biotic interactions as a result of the floods could have facilitated increased invasion rates in post-flood communities, consistent with the observed colonisation of taxa not recorded pre-flood, as reported elsewhere following disturbance (Hobbs and Huenneke, 1992, Lyons and Schwartz, 2001). Given the study streams share a regional taxon pool it could be expected that the most capable colonisers can effectively colonise all streams following disturbance, irrespective of age or geomorphological complexity. This theory is supported by community dominance analyses which showed an increased number of taxa shared by all streams from three (Pre-flood) to ten (Response). Seven of these ubiquitous taxa belonged to just three families: Chironomidae, Heptagenidae and Baetidae. These families are associated with traits typical of r-selected taxa (Poff et al., 2006), and have been reported as important members of post-flood communities elsewhere (Ming-Chih and Mei-Hwa, 2012, Poff et al., 2018).

Reduced between-stream beta-diversity may be linked to the limited and stochastic nature of dispersal in some eliminated groups, e.g. Mollusca, resulting in limited recolonization (Bohonak and Jenkins, 2003). Recolonization of Mollusca has been shown to take up to a decade at within a stream segment, <3 km upstream of a potential source population (Kappes and Haase, 2012). Even lower rates of dispersal can be expected in GBNP due to the presence of intertidal and marine zones, which represents a significant dispersal barrier between all streams. The slow dispersal mechanisms of such taxa are thought to be insufficient to respond to climate change (Kappes and Haase, 2012), which, given increased likelihood of future extreme floods, may indicate that observed losses of these taxa in GBNP will persist.

The convergence of communities between streams during community reassembly observed in this study is a significant novel finding. Whilst similar results have not been reported previously, a trend consistent with this work can be observed across the literature in taxonomic (Herbst and Cooper, 2010, Mundahl and Hunt, 2011, Anderson and Ferrington, 2013) and functional trait analyses (Ming-Chih and Mei-Hwa, 2012, Poff et al., 2018) following extreme floods. Future traits-based analyses of ecological resilience and post-flood community reassembly following the high-frequency summer floods could enhance our understanding greatly. Further, identifying the implications of such convergence of communities across physically distinct streams is necessary to inform future management strategies. Identifying if similar trends are observed for floods with different forms, occurring in different locations, represents an important future challenge in developing a robust understanding of the ecological implications of major floods.

4.5 Conclusion

This study contributes valuable new information highlighting the impacts of high-frequency summer floods, a previously under-represented form of extreme flood in the literature. This chapter demonstrates the value of ecological resilience and community composition focussed research to further our understanding of ecological responses. Crucially the pathways of ecological response appear to initially be divergent with the loss of K-selected taxa at higher complexity streams with diverse pre-flood communities and the turnover of r-selected Chironomidae and small Ephemeroptera at the lowest complexity stream dominated pre-flood by Chironomidae. Following this initial step, stream benthic macroinvertebrate community composition demonstrated convergence between streams. This convergence has major implications for lotic macroinvertebrate communities globally with future increases in the occurrence of extreme disturbance events. Where disturbances occur in sequence, with each event occurring before the response to the last has been completed, could result in significant directional change in communities in the future.

4.6 References

ABBE, T. B. & MONTGOMERY, D. R. 1996. Large woody debris dams, channel hydraulics and habitat formation in large rivers. *Regulated Rivers: Research & Management,* 12**,** 201-221.

AICKIN, M. & GENSLER, H. 1996. Adjusting for multiple testing when reporting research results: the Bonferroni vs Holm methods. *American Journal of Public Health,* 86**,** 726-728.

ANDERSEN, T., CRANSTON, P. S. & EPLER, J. H. 2017. *Chironomidae of the Holarctic Region: Keys and Diagnoses, Part 1: Larvae*, Entomological Society of Lund, Sweden.

ANDERSON, A. M. & FERRINGTON, L. C. 2013. Resistance and resilience of winter-emerging Chironomidae (Diptera) to a flood event: implications for Minnesota trout streams. *Hydrobiologia,* 707**,** 59-71.

ANDERSON, M. J. 2014. Permutational Multivariate Analysis of Variance (PERMANOVA). *Wiley StatsRef: Statistics Reference Online.*

BASELGA, A. 2010. Partitioning the turnover and nestedness components of beta-diversity. *Global Ecology and Biogeography,* 19**,** 134-143.

BASELGA, A., ORME, D., VILLEGER, S., DE BORTOLI, J., LEPRIEUR, F. & 2018. betapart: Partitioning Beta-diversity into Turnover and Nestedness Components.

BATES, D., MAECHLER;, M., BOLKER;, B. & WALKER, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software,* 67**,** 1-48.

BERG, P., MOSELEY, C. & HAERTER, J. O. 2013. Strong increase in convective precipitation in response to higher temperatures. *Nature Geoscience,* 6**,** 181.

BERGEY, E. A. & RESH, V. H. 2006. Differential Response of Algae on Small Streambed Substrates to Floods. *The American Midland Naturalist,* 155**,** 270-277.

BOHONAK, A. J. & JENKINS, D. G. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters,* 6**,** 783-796.

BOND, N. A., CRONIN, M. F., FREELAND, H. & MANTUA, N. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters,* 42**,** 3414-3420.

BOON, P. J. 1988. The impact of river regulation on invertebrate communities in the U.K. *Regulated Rivers: Research & Management,* 2**,** 389-409.

BROOKS, S., LANGDON, P. & HEIRI, O. 2008. *The Identification and Use of Palaearctic Chironomidae Larvae in Palaeoecology*.

BROWN, L. E., KHAMIS, K., WILKES, M., BLAEN, P., BRITTAIN, J. E., CARRIVICK, J. L., FELL, S., FRIBERG, N., FÜREDER, L., GISLASON, G. M., HAINIE, S., HANNAH, D. M., JAMES, W. H. M., LENCIONI, V., OLAFSSON, J. S., ROBINSON, C. T., SALTVEIT, S. J., THOMPSON, C. & MILNER, A. M. 2018. Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nature Ecology & Evolution,* 2**,** 325-333.

BROWN, L. E. & MILNER, A. M. 2012. Rapid loss of glacial ice reveals stream community assembly processes. *Global Change Biology,* 18**,** 2195-2204.

CHAPIN, F. S., WALKER, L. R., FASTIE, C. L. & SHARMAN, L. C. 1994. Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska. *Ecological Monographs,* 64**,** 149-175.

CHAPPELL, A., HERITAGE, G. L., FULLER, I. C., LARGE, A. R. G. & MILAN, D. J. 2003. Geostatistical analysis of ground-survey elevation data to elucidate spatial and temporal river channel change. *Earth Surface Processes and Landforms,* 28**,** 349-370.

CLITHEROW, L. R. 2016. *Terrestrial-Aquatic Food Web Linkages across Floodplains of Different Ages, Glacier Bay, Alaska.* PhD, University of Birmingham.

COSTA, J. E. & O'CONNOR, J. E. 1995. Geomorphically Effective Floods. *Natural and Anthropogenic Influences in Fluvial Geomorphology.* American Geophysical Union.

CROCKER, R. L. & MAJOR, J. 1955. Soil Development in Relation to Vegetation and Surface Age at Glacier Bay, Alaska. *Journal of Ecology,* 43**,** 427-448.

DIEZ, J. M., D'ANTONIO, C. M., DUKES, J. S., GROSHOLZ, E. D., OLDEN, J. D., SORTE, C. J., BLUMENTHAL, D. M., BRADLEY, B. A., EARLY, R., IBÁÑEZ, I., JONES, S. J., LAWLER, J. J. & MILLER, L. P. 2012. Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment,* 10**,** 249-257.

DUDLEY, T. L. & D'ANTONIO, C. M. 1991. The Effects of Substrate Texture, Grazing, and Disturbance on Macroalgal Establishment in Streams. *Ecology,* 72**,** 297-309.

ENGSTROM, D. R. & FRITZ, S. C. 2006. Coupling between primary terrestrial succession and the trophic development of lakes at Glacier Bay, Alaska. *Journal of Paleolimnology,* 35**,** 873-880.

FASTIE, C. L. 1995. Causes and Ecosystem Consequences of Multiple Pathways of Primary Succession at Glacier Bay, Alaska. *Ecology,* 76**,** 1899-1916.

FIELD, W. O., JR. 1947. Glacier recession in the Muir Inlet, Glacier BAy, Alaska. *Geographical Review,* 37**,** 369-399.

FLATHER, C. H. & SIEG, C. H. 2007. Species Rarity: Definition, Causes, and Classification. *In:* M.G;, R. & R, M. (eds.) *Conservation of Rare or Little-Known Species.* Washington, Covelo, London: Island Press.

FLORY, E. A. & MILNER, A. M. 1999. Influence of riparian vegetation on invertebrate assemblages in a recently formed stream in Glacier Bay National Park, Alaska. *Journal of the North American Benthological Society,* 18**,** 261-273.

FRASER, C. I., BANKS, S. C. & WATERS, J. M. 2015. Priority effects can lead to underestimation of dispersal and invasion potential. *Biological Invasions,* 17**,** 1-8.

FRITZ, S. C., ENGSTROM, D. R. & JUGGINS, S. 2004. Patterns of early lake evolution in boreal landscapes: a comparison of stratigraphic inferences with a modern chronosequence in Glacier Bay, Alaska. *Holocene,* 14**,** 828-840.

GASTON, K. J. 1994. *Rarity,* London, Chapman and Hall.

GEORGE, S. D., BALDIGO, B. P., SMITH, A. J. & ROBINSON, G. R. 2015. Effects of extreme floods on trout populations and fish communities in a Catskill Mountain river. *Freshwater Biology,* 60**,** 2511-2522.

GREEN, J. L. & OSTLING, A. 2003. Endemics–Area Relationships: The Influence of Species Dominance and Spatial Aggreggation *Ecology,* 84**,** 3090-3097.

GRIMM, N. B. & FISHER, S. G. 1989. Stability of Periphyton and Macroinvertebrates to Disturbance by Flash Floods in a Desert Stream. *Journal of the North American Benthological Society,* 8**,** 293-307.

HAJSGAARD, S., HALEKOH, U. & YAN, J. 2006. The R Package geepack for Generalized Estimating Equations *Journal of Statistical Software,* 15**,** 1--11.

HALL, D. K., BENSON, C. S. & FIELD, W. O. 1995. Changes of Glaciers in Glacier Bay, Alaska, Using Ground and Satellite Measurements. *Physical Geography,* 16**,** 27-41.

HANSKI, I. 2001. Spatially realistic theory of metapopulation ecology. *Naturwissenschaften,* 88**,** 372-381.

HE, F. & LEGENDRE, P. 2002. Species Diversity Patterns Derived from Species-Area Models. *Ecology,* 83**,** 1185-1198.

HEINO, J., LOUHI, P. & MUOTKA, T. 2004. Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure. *Freshwater Biology,* 49**,** 1230-1239.

HERBST, D. B. & COOPER, S. D. 2010. Before and after the deluge: rain-on-snow flooding effects on aquatic invertebrate communities of small streams in the Sierra Nevada, California. *Journal of the North American Benthological Society,* 29**,** 1354-1366.

HERING, D., GERHARD, M., MANDERBACH, R. & REICH, M. 2004. Impact of a 100-year flood on vegetation, benthic invertebrates, riparian fauna and large woody debris standing stock in an alpine floodplain. *River Research and Applications,* 20**,** 445-457.

HILLEBRAND, H., BENNETT, D. M. & CADOTTE, M. W. 2008. Consequences of Dominance: A Review of Evenness Effects on Local and Regional Ecosystem Proceses *Ecology,* 89**,** 1510-1520.

HOBBS, R. J. & HUENNEKE, L. F. 1992. Disturbance, Diversity, and Invasion: Implications for Conservation. *Conservation Biology,* 6**,** 324-337.

HOLLING, C. S. 1973. Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics,* 4**,** 1-23.

JACCARD, P. 1912. The distribution of the flora in the alpine zone. *New Phytologist,* 11**,** 37-50.

JACKMAN, S. 2017. pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory. 1.5.2. ed. United States Studies Centre, University of Sydney. Sydney, New South Wales, Australia.

JOWETT, I. G. & RICHARDSON, J. 1989. Effects of a severe flood on instream habitat and trout populations in seven New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research,* 23**,** 11-17.

JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E. 1989. The Flood Pulse Concept in River-Floodplain Systems. *Canadian Special Publication of Fisheries and Aquatic Science,* 106**,** 110 - 127.

KAPPES, H. & HAASE, P. 2012. Slow, but steady: dispersal of freshwater molluscs. *Aquatic Sciences,* 74**,** 1-14.

KIMBRO, D. L. & GROSHOLZ, E. D. 2006. Disturbance Influences Oyster Community Richness and Evenness, but not Diversity. *Ecology,* 87**,** 2378-2388.

KLAAR, M. J., HILL, D. F., MADDOCK, I. & MILNER, A. M. 2011. Interactions between instream wood and hydrogeomorphic development within recently deglaciated streams in Glacier Bay National Park, Alaska. *Geomorphology,* 130**,** 208-220.

KLAAR, M. J., MADDOCK, I. & MILNER, A. M. 2009. The Development of Hydraulic and Geomorphic Complexity in Recently Formed Streams in Glacier Bay National Park, Alaska. *River Research and Applications,* 25**,** 1331-1338.

LAKE, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society,* 19**,** 573-592.

LAKE, P. S. 2008. Flow-generated Disturbances and Ecoloigical Responses: Floods and Droughts. *In:* WOOD P.J., HANNAH D.M. & J.P., S. (eds.) *Hydroecology and Ecohydrology: Past, Present and Future.* Chichester, England: John Wiley and Sons Limited.

LANGTON, P. H. & CASAS, J. 1998. Changes in chironomid assemblage composition in two Mediterranean mountain streams over a period of extreme hydrological conditions. *Hydrobiologia,* 390**,** 37-49.

LARSON, E. I., POFF, N. L., ATKINSON, C. L. & FLECKER, A. S. 2018. Extreme flooding decreases stream consumer autochthony by increasing detrital resource availability. *Freshwater Biology,* 0.

LAWRENCE, D. B., SCHOENIKE, R. E., QUISPEL, A. & BOND, G. 1967. The Role of Dryas Drummondii in Vegetation Development Following Ice Recession at Glacier Bay, Alaska, with Special Reference to Its Nitrogen Fixation by Root Nodules. *Journal of Ecology,* 55**,** 793-813.

LEDGER, M., M L HARRIS, R., MILNER, A. & ARMITAGE, P. 2006. *Disturbance, biological legacies and community development in stream mesocosms*.

LEDGER, M. E., BROWN, L. E., EDWARDS, F. K., MILNER, A. M. & WOODWARD, G. 2013. Drought alters the structure and functioning of complex food webs. *Nature Climate Change,* 3**,** 223-227.

LEDGER, M. E. & MILNER, A. M. 2015. Extreme events in running waters. *Freshwater Biology,* 60**,** 2455-2460.

LU, X., GRAY, C., BROWN, L. E., LEDGER, M. E., MILNER, A. M., MONDRAGÓN, R. J., WOODWARD, G. & MA, A. 2016. Drought rewires the cores of food webs. *Nature Climate Change,* 6**,** 875.

LYONS, K. G. & SCHWARTZ, M. W. 2001. Rare species loss alters ecosystem function – invasion resistance. *Ecology Letters,* 4**,** 358-365.

LYTLE, D. A. & POFF, N. L. 2004. Adaptation to natural flow regimes. *Trends in Ecology & Evolution,* 19**,** 94-100.

MAGILLIGAN, F. J., BURAAS, E. M. & RENSHAW, C. E. 2015. The efficacy of stream power and flow duration on geomorphic responses to catastrophic flooding. *Geomorphology,* 228**,** 175-188.

MATHERS, K. L., RICE, S. P. & WOOD, P. J. 2017. Temporal effects of enhanced fine sediment loading on macroinvertebrate community structure and functional traits. *Science of The Total Environment,* 599-600**,** 513-522.

MERRITT, R. W. & CUMMINS, K. W. 1996. *An introduction to the aquatic insects of North America*, Kendall Hunt.

MILLY, P. C., DUNNE, K. A. & VECCHIA, A. V. 2005. Global pattern of trends in streamflow and water availability in a changing climate. *Nature,* 438**,** 347-350.

MILLY, P. C. D., WETHERALD, R. T., DUNNE, K. A. & DELWORTH, T. L. 2002. Increasing risk of great floods in a changing climate. *Nature,* 415**,** 514.

MILNER, A. M. 1987. Colonization and ecological development of new streams in Glacier Bay National Park, Alaska. *Freshwater Biology,* 18**,** 53-70.

MILNER, A. M. & BAILEY, R. G. 1989. Salmonid colonization of new streams in Glacier Bay National Park Alaska USA. *Aquaculture and Fisheries Management,* 20**,** 179-192.

MILNER, A. M., FASTIE, C. L., CHAPIN, F. S., ENGSTROM, D. R. & SHARMAN, L. C. 2007. Interactions and linkages among ecosystems during landscape evolution. *Bioscience,* 57**,** 237-247.

MILNER, A. M., KNUDSEN, E. E., SOISETH, C., ROBERTSON, A. L., SCHELL, D., PHILLIPS, I. T. & MAGNUSSON, K. 2000. Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences,* 57**,** 2319-2335.

MILNER, A. M., PICKEN, J. L., KLAAR, M. J., ROBERTSON, A. L., CLITHEROW, L. R., EAGLE, L. & BROWN, L. E. 2018. River ecosystem resilience to extreme flood events. *Ecology and Evolution,* 0.

MILNER, A. M., ROBERTSON, A. L., BROWN, L. E., SØNDERLAND, S. H., MCDERMOTT, M. & VEAL, A. J. 2011. Evolution of a stream ecosystem in recently deglaciated terrain. *Ecology,* 92**,** 1924-1935.

MILNER, A. M., ROBERTSON, A. L., MCDERMOTT, M. J., KLAAR, M. J. & BROWN, L. E. 2013. Major flood disturbance alters river ecosystem evolution. *Nature Climate Change,* 3**,** 137-141.

MILNER, A. M., ROBERTSON, A. L., MONAGHAN, K. A., VEAL, A. J. & FLORY, E. A. 2008. Colonization and development of an Alaskan stream community over 28 years. *Frontiers in Ecology and the Environment,* 6**,** 413-419.

MING-CHIH, C. & MEI-HWA, K. 2012. Application of r/K selection to macroinvertebrate responses to extreme floods. *Ecological Entomology,* 37**,** 145-154.

MUNDAHL, N. D. & HUNT, A. M. 2011. Recovery of stream invertebrates after catastrophic flooding in southeastern Minnesota, USA. *Journal of Freshwater Ecology,* 26**,** 445-457.

NEGISHI, J. N., INOUE, M. & NUNOKAWA, M. 2002. Effects of channelisation on stream habitat in relation to a spate and flow refugia for macroinvertebrates in northern Japan. *Freshwater Biology,* 47**,** 1515-1529.

NISLOW, K. H., MAGILLIGAN, F. J., FOLT, C. L. & KENNEDY, B. P. 2002. Within-Basin Variation in the Short-Term Effects of a Major Flood on Stream Fishes and Invertebrates. *Journal of Freshwater Ecology,* 17**,** 305-318.

OKSANEN, J., BLANCHET, F. G., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGLINN, D., MINCHIN, P. R., O'HARA, R. B., SIMPSON, G. L., SOLYMOS, P., STEVENS, M. H. H., SZOECS, E. & WAGNER, H. 2018. vegan: Community Ecology Package. 2.5-2 ed.

PASTERNACK, G. B. & WYRICK, J. R. 2017. Flood-driven topographic changes in a gravel-cobble river over segment, reach, and morphological unit scales. *Earth Surface Processes and Landforms,* 42**,** 487-502.

PINHEIRO, J., BATES, D., DEBROY, S., SARKAR, D. & TEAM, R. C. 2018. nlme: Linear and Nonlinear Mixed Effects Models. 3.1-137 ed.

POFF, N. L. 1997. Landscape Filters and Species Traits: Towards Mechanistic Understanding and Prediction in Stream Ecology. *Journal of the North American Benthological Society,* 16**,** 391-409.

POFF, N. L. 2002. Ecological response to and management of increased flooding caused by climate change. *Philosophical Transactions of the Royal Society of London. Series A: Mathematical, Physical and Engineering Sciences,* 360**,** 1497-1510.

POFF, N. L., ALLAN, J. D., BAIN, M. B., KARR, J. R., PRESTEGAARD, K. L., RICHTER, B. D., SPARKS, R. E. & STROMBERG, J. C. 1997. The Natural Flow Regime. *BioScience,* 47**,** 769-784.

POFF, N. L., LARSON, E. I., SALERNO, P. E., MORTON, S. G., KONDRATIEFF, B. C., FLECKER, A. S., ZAMUDIO, K. R. & FUNK, W. C. 2018. Extreme streams: species persistence and genomic change in montane insect populations across a flooding gradient. *Ecology Letters,* 21**,** 525-535.

POFF, N. L., OLDEN, J. D., VIEIRA, N. K. M., FINN, D. S., SIMMONS, M. P. & KONDRATIEFF, B. C. 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society,* 25**,** 730-755.

POWER, M. E. & STEWART, A. J. 1987. Disturbance and Recovery of an Algal Assemblage Following Flooding in an Oklahoma Stream. *The American Midland Naturalist,* 117**,** 333-345.

R-CORE-TEAM 2017. R: A language and environment for statistical computing. . Vienna, Austria.: R Foundation for Statistical Computing.

RADER, R. B., VOELZ, N. J. & WARD, J. V. 2008. Post-Flood Recovery of a Macroinvertebrate Community in a Regulated River: Resilience of an Anthropogenically Altered Ecosystem. *Restoration Ecology,* 16**,** 24-33.

RICKENMANN, D. & KOSCHNI, A. 2010. Sediment loads due to fluvial transport and debris flows during the 2005 flood events in Switzerland. *Hydrological Processes,* 24**,** 993-1007.

ROBERTSON, A. L., BROWN, L. E., KLAAR, M. J. & MILNER, A. M. 2015. Stream ecosystem responses to an extreme rainfall event across multiple catchments in southeast Alaska. *Freshwater Biology,* 60**,** 2523-2534.

ROBINSON, C. T. 2012. Long-term changes in community assembly, resistance, and resilience following experimental floods. *Ecological Applications,* 22**,** 1949-1961.

ROBINSON, C. T., SIEBERS, A. R. & ORTLEPP, J. 2018. Long-term ecological responses of the River Spöl to experimental floods. *Freshwater Science,* 37**,** 433-447.

ROBINSON, C. T. & UEHLINGER, U. 2008. Experimental Floods Cause Ecosystem Regime Shift in a Regulated River. *Ecological Applications,* 18**,** 511-526.

ROGHAIR, C. N., DOLLOFF, C. A. & UNDERWOOD, M. K. 2002. Response of a Brook Trout Population and Instream Habitat to a Catastrophic Flood and Debris Flow. *Transactions of the American Fisheries Society,* 131**,** 718-730.

SEDELL, J. R., REEVES, G. H., HAUER, F. R., STANFORD, J. A. & HAWKINS, C. P. 1990. Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. *Environmental Management,* 14**,** 711-724.

SHURIN J. B. & E.G., A. 2001. Effects of Competition, Predation, and Dispersal on Species Richness at Local and Regional Scales. *The American Naturalist,* 158**,** 624-637.

SINGER, G. A. & BATTIN, T. J. 2007. Anthropogenic Subsidies Alter Stream Consumer-Resource Stoichiometry, Biodiversity, and Food Chains. *Ecological Applications,* 17**,** 376-389.

SUNDERMANN, A., STOLL, S. & HAASE, P. 2011. River restoration success depends on the species pool of the immediate surroundings. *Ecological Applications,* 21**,** 1962-1971.

SZCZERKOWSKA-MAJCHRZAK, E., LIK, J. & LESZCZYŃSKA, J. 2014. Resistance of riverine macroinvertebrate assemblages to hydrological extremes. *Oceanological and Hydrobiological Studies.*

THERRIAULT, T. W. & KOLASA, J. 1999. Physical determinants of richness, diversity, evenness and abundance in natural aquatic microcosms. *Hydrobiologia,* 412**,** 123-130.

THORP, J. H. & COVICH, A. P. 2009. *Ecology and classification of North American freshwater invertebrates*, Academic press.

TORNÉS, E., ACUÑA, V., DAHM, C. N. & SABATER, S. 2015. Flood disturbance effects on benthic diatom assemblage structure in a semiarid river network. *Journal of Phycology,* 51**,** 133-143.

TOWNSEND, C. R. & HILDREW, A. G. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology,* 31**,** 265-275.

TOWNSEND, C. R., SCARSBROOK, M. R., DOL, XE & DEC, S. 1997a. Quantifying Disturbance in Streams: Alternative Measures of Disturbance in Relation to Macroinvertebrate Species Traits and Species Richness. *Journal of the North American Benthological Society,* 16**,** 531-544.

TOWNSEND, C. R., SCARSBROOK, M. R. & DOLÉDEC, S. 1997b. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography,* 42**,** 938-949.

UEHLINGER, U., KAWECKA, B. & ROBINSON, C. T. 2003. Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (River Spöl). *Aquatic Sciences,* 65**,** 199-209.

VENABLES, W. N. & RIPLEY, B. D. 2002. *Modern Applied Statistics with S,* New York, Springer.

VILLNÄS, A., NORKKO, J., HIETANEN, S., JOSEFSON, A. B., LUKKARI, K. & NORKKO, A. 2013. The role of recurrent disturbances for ecosystem multifunctionality. *Ecology,* 94**,** 2275-2287.

WENZEL, R., REINHARDT-IMJELA, C., SCHULTE, A. & BÖLSCHER, J. 2014. The potential of in-channel large woody debris in transforming discharge hydrographs in headwater areas (Ore Mountains, Southeastern Germany). *Ecological Engineering,* 71**,** 1-9.

WOHL, E. 2011. Threshold-induced complex behavior of wood in mountain streams. *Geology,* 39**,** 587-590.

WOLMAN, M. G. & MILLER, J. P. 1960. Magnitude and Frequency of Forces in Geomorphic Processes. *The Journal of Geology,* 68**,** 54-74.

WOODWARD, G., BONADA, N., FEELEY, H. B. & GILLER, P. S. 2015. Resilience of a stream community to extreme climatic events and long-term recovery from a catastrophic flood. *Freshwater Biology,* 60**,** 2497-2510.

WOUTER, R. B., EMMA, E. A., JOSHUA, R. L., RALPH, T. & ROSS, A. W. 2017. Recent changes in extreme floods across multiple continents. *Environmental Research Letters,* 12**,** 114035.

YEBOAH, D., CHEN, H. & KINGSTON, S. 2016. *Tree species richness decreases while species evenness increases with disturbance frequency in a natural boreal forest landscape*.

ZEILEIS, A., CHRISTIAN, K. & SIMON, J. 2008. Regression Models for Count Data in R. *Journal of Statistical Software,* 27.

5. Extreme high-frequency summer floods disrupt juvenile salmon community size structure and food web linkages

5.1 Introduction

Migratory Pacific salmon have an annual estimated value exceeding $4.8 billion to the economies of Canada and USA (Gislason et al., 2017) and represent a central component of important commercial, sport and subsistence fisheries. Through multidirectional nutrient subsidies, Pacific salmon represent important links between marine, freshwater and terrestrial biomes (Willson and Halupka, 1995, Bartels et al., 2012, Collins et al., 2016), and perform a crucial role within their native ecosystems, by providing annual nutrient pulses post-spawning (Pinay et al., 2009, Tiegs et al., 2011) and mobilising bed sediments which alter geomorphological dynamics (Hassan et al., 2008). In spite of this importance and an increasing focus on their conservation (Ruckelshaus et al., 2002), populations are in decline across their native range (Nehlsen et al., 1991). One significant threat to salmon is reduced availability and quality of spawning and rearing habitat (Ruckelshaus et al., 2002), which in freshwaters is utilised for up to 4 years (De Groot, 1993), driven by a number of factors including: barriers to fish passage (Sheer and Steel, 2006), sedimentation (Suttle et al., 2004a) and climate change related alteration to habitat (Battin et al., 2007).

To date, research linking climate change and salmon populations has focused principally on increased mean water temperature (Jonsson and Jonsson, 2009), reduced water availability (Mantua et al., 2010) and increased annual peak flows (Sloat et al., 2017). Whilst these gradual changes represent important controls on both the survival of current and development of future salmon stocks, other climate driven disturbances such as unpredictable floods have the capacity to significantly impact individual generations of salmon (Milner et al., 2018). Extreme flow events may act synergistically with other threats to populations, exacerbating negative effects, but few studies have considered such synergistic effects (Harley et al., 2006). This work becomes pressing as extreme floods have increased in frequency and magnitude in recent decades (Wouter et al., 2017). In this study, extreme floods are defined as rare or unusual weather or climatic driven events (sensu Ledger and Milner, 2015). Such floods have already been shown to drive significant negative impacts to benthic macroinvertebrate communities in river ecosystems, including the loss of non-invertebrate taxa and driving sequential shifts in overall composition (Milner et al., 2013, Milner et al., 2018). However, the threat such changes to prey resources poses to salmon communities has not been explored thoroughly (Piniewski et al., 2017).

Predictable and small floods are considered an essential part of natural flow regimes in streams (Poff, 2002, Costa and O'Connor, 1995, Poff et al., 1997), acting as important environmental filters influencing community assembly (Poff, 1997), regulating fine sediment deposition (Malmon et al., 2004) and providing a crucial link between a river and its floodplain for a diverse suite of species, including salmon (Junk et al., 1989, Sommer et al., 2001, Jeffres et al., 2008, Takata et al., 2017). In contrast, extreme floods can reduce both fish biomass and abundance (Roghair et al., 2002, Milner et al., 2013). The extent of a flood's direct ecological impact is related to flood timing, as well as its magnitude and duration (Pearsons et al., 1992, Death et al., 2015, George et al., 2015). For instance, negative impacts to salmon have been associated with the scour of eggs from redds (Milner et al., 2013) and decreased fitness and survival of alevin (Jensen and Johnsen, 1999), whose presence varies by species and geographic location (e.g. Withler, 1966, Holtby et al., 1989, Lisi et al., 2013).

In addition to direct impacts, extreme floods have the potential to indirectly impact fish (Roghair et al., 2002). For example, extreme flood-driven geomorphological change to river channels (Costa and O'Connor, 1995, Pasternack and Wyrick, 2017, Chapter 3) could influence instream salmon habitat availability (Herdrich et al., 2018). This may alter stream carrying capacity, although this has yet to be explored thoroughly in the literature (Scrimgeour and Townsend, 1996). Floods can also reduce the abundance of benthic macroinvertebrates (Milner et al., 2013, Chapter 4), a vital prey resource for juvenile salmons (Nakano and Kaeriyama, 1995). Reduced prey availability may increase both inter- and intra-specific competition post-flood (Fausch and White, 1986, Dill et al., 1981), which has in other circumstances been linked to reduced individual fish condition and survival (Nislow et al., 1998). Further, post-flood dominance of r-selected macroinvertebrates (Ming-Chih and Mei-Hwa, 2012, Chapter 4), could markedly alter feeding energetics of salmon populations. Significantly, juvenile salmon also utilise terrestrial and marine sourced nutrients (Wipfli, 1997, Johnson and Ringler, 1980, Nakano and Murakami, 2001, Wipfli and Baxter, 2010), which represent energetic subsidies (Kawaguchi and Nakano, 2001, Eberle and Stanford, 2010). However, the extent to which such subsidies confer resilience to extreme events in juvenile salmon communities remains unclear and may vary depending upon typical feeding behaviour and feeding plasticity of species within a given community (Nakano and Kaeriyama, 1995).

In spite of short-term impacts, salmon populations typically demonstrate high resilience to floods in their spawning and rearing habitat (Roghair et al., 2002, Milner et al., 2013, Milner et al., 2018). This resilience has been linked to their anadromous life cycles, alternative life histories (Koski, 2009) and capacity to migrate rapidly through river systems (Roghair and Dolloff, 2005). Additionally, multiple years spent at sea before spawning prevent the entire population from being exposed to floods in natal streams. Salmon are adept at colonising unpopulated streams and consequently can rapidly re-establish communities following localised extinction (Keefer and Caudill, 2014). In contrast to floods, resilience to persistent disturbances such as sedimentation (Heywood and Walling, 2007), lost connectivity (Steel, 2006), stream temperature rises (Isaak et al., 2010) or water shortages (Elliott et al., 1997), which limit access to historic spawning and rearing habitat (Garbe et al., 2016) and decrease juvenile survival (Suttle et al., 2004b), appears to be lower. The increasing frequency of extreme floods now observed in North America (Wouter et al., 2017) could alter resilience to floods as these disturbances occur in sequences more regularly. Importantly, juvenile salmon escapement is necessary for recruitment to adult salmon populations (Nickelson et al., 1992). For successful escapement in many salmon species, instream recruitment of individuals through age classes (often two or more) is necessary (Bell and Duffy, 2007), and thus recruitment to the adult population could be tightly coupled to juvenile salmon size structure observed in natal streams.

The study of extreme hydrological events, including floods, is difficult because of their unpredictable nature, such that generally data are not available from before a disturbance with which for comparison following the disturbance. This has limited our capacity to identify how extreme floods drive ecological change and generally the focus of flood studies is on reporting change. To further our ecological understanding complex pre-flood datasets may be necessary. One source of such data may be available where in-depth long-term research and monitoring is established at a site. Stream research established in Glacier Bay National Park and Preserve (GBNP) in the 1970s (Milner, 1987) which has explored the processes of community assembly, habitat development and trophic interactions represents one such long term dataset in which to explore the processes and drivers of community reassembly (Clitherow, 2016, Sønderland, 2017, Milner and Bailey, 1989, Milner et al., 2008, Klaar et al., 2009).

In this chapter four hypotheses were tested to identify the implications of extreme high-frequency summer floods for juvenile salmon community size structure and resource utilisation in GBNP:

H_1 The floods altered resource utilisation across salmon species following changes to benthic macroinvertebrate community structure post-flood, reflecting a strong indirect effect of floods (Goertler et al., 2018, Chapter 4);

H_2 Condition of all juvenile salmon will decrease directly post-flood, as a result of altered resource availability and utilisation (Adams et al., 1982);

H_3 Juvenile salmon community size structure will be controlled through the flood time periods by a combination of both direct and indirect effects, through alterations to habitat and freshwater prey availability (Nickelson et al., 1992, Herdrich et al., 2018);

H_4 Re-establishment of pre-flood population size structure will occur as a result of readily available source populations (Lamberti et al., 1991) and recovery of total benthic prey density (Chapter 4) and habitat availability (Chapter 3)

5.2 Methods

5.2.1 Study site

Glacier Bay National Park (GBNP) covers over 11, 030 km^2 of marine and terrestrial terrain in southeast Alaska which in the 1860s, at the Neoglacial maximum, was dominated by a single large glacier (Field, 1937, Hall et al., 1995). With the retreat of this glacier, a large tidal fjord with two major arms was exposed. Terrestrial landscapes exposed following this retreat have undergone primary vegetative succession (Fastie, 1995, Chapin et al., 1994). Succession has been documented in lentic (Engstrom et al., 2000, Fritz et al., 2004) and extensively in lotic environments (Milner and Bailey, 1989, Sidle and Milner, 1989, Brown and Milner, 2012, Milner et al., 2000, Milner et al., 2007, Milner et al., 2008, Milner et al., 2011). Colonisation in lotic environments is relatively rapid and within less than a decade, some newly exposed GBNP streams have been colonised by salmon (Milner et al., 2011). Given the temporal aspect to release of ground from glaciation, development of lotic environments across GBNP drives a spatial gradient in the geomorphological complexity (Klaar et al., 2009). In this study four streams were selected which represented a range of pre-flood geomorphological complexities (Milner et al., 2000, Klaar et al., 2009, Klaar et al., 2011).

Juvenile salmon communities in Glacier Bay National Park (GBNP) streams are dominated by two salmon species: coho salmon *Oncorhynchus kisutch* and Dolly Varden charr *Salvelinus malma*. Studies in southeast Alaska suggest terrestrial subsidies can be important for juvenile salmon in the region, however, their contribution is most important at younger streams with dense willow and alder dominated riparian vegetation (Wipfli, 1997), once streams establish a wide gravel floodplain terrestrial subsidies decline. Studies of summer prey utilisation in GBNP support this theory and suggest terrestrial prey resources may be less important than freshwater prey resources as a result of their low abundance in diets (Clitherow, 2016, Sønderland, 2017). Further, the dominant salmon species' observed in GBNP demonstrate a high capacity for plasticity in feeding behaviour, depending upon resource availability (Nakano et al., 1999), intra-specific and inter-specific competition (Nielsen, 1992, Nakano, 1995).

5.2.2 Sampling and identification

In each of the four study streams, fish sampling was undertaken at a fixed study reach, which incorporated the dominant geomorphological unit types present within a given stream. A minimum of nine baited minnow traps (400 mm x 220 mm, with a 6 mm mesh) were fished for approximately 1.5 hours each (July-August) in 2009, 2010, 2013, 2014, 2015, 2016 and 2017. Traps were baited with red salmon eggs (sterilised in Betadyne iodine solution) sealed in punctured "Kinder egg" containers to prevent fish consuming the bait but allowing the odour to enter the stream.

Captured juvenile salmon were identified to species and fork length recorded to the nearest mm. For each stream, a subset of individuals were weighed to the nearest 0.1 g in 2009, 2015, 2016 and 2017 and the nearest whole gram in 2010, 2013 and 2014. Catch per unit effort (CPUE) was calculated for all streams in all years by dividing the total abundance of each species by the number of traps. Stomach contents were collected by gut flushing (all years except 2015), whereby a blunt ended syringe containing stream water was used to flush stomach contents directly into sample bags (Meehan and Miller, 1978) and preserved in 70% ethanol.

Gut contents were identified to the lowest possible taxonomic level under a dissecting microscope. The remains of freshwater benthic macroinvertebrates were identified to Genus where possible (although more typically Family), using the keys of Merritt and Cummins (1996), Thorp and Covich (2009), Brooks et al. (2008), and Andersen et al. (2017) and using non-digested specimens as a reference. Non-digested macroinvertebrate specimens were collected using a Surber sampler (0.092 m^2 area; 330 µm mesh) from a study riffle within the fish sampling reach and identified using the same keys (see Chapter 4). Terrestrial food items were identified to Order where possible using Eaton and Kaufman (2007). Due to heavy digestion in some samples, consumed items were often broken apart, and therefore subsequent enumeration counted only the number of heads in a sample. This approach prevented double counting of some individuals. However, as a result of this approach, abundance estimates should be considered conservative as some groups which lack obvious and sclerotised head structures could be under estimated (e.g. members of some dipteran families). Marine food items were enumerated using a total count of pieces, based on the presence of fish scales, eggs or flesh. Sea lice (*Lepeophtheirus salmonis)* were also found in the diet, consistent with previous research in GBNP (Sønderland, 2017). Length and width measurements were collected for all prey items in samples from Berg Bay South (BBS) in 2016. However, due to changes in the composition of taxa found in some families between years and the lack of measurements from 2009, 2010 and 2014, biomass was not calculated for all prey items in all guts in all years.

5.2.3 Data analysis:

Analyses in this chapter were completed in R studio version 1. 1. 456, R version 3. 5. 1 (R-Core-Team, 2017). Analyses in this chapter are split into four main sections: (1) Exploration of juvenile salmon diet via resource utilisation through time using tests for differences between prey abundance from different sources, the influence of invertebrate biomass on dietary composition, Odds ratios (Szumilas, 2010) and regression to link odds ratios to total freshwater prey density and time since the last extreme flood; (2) calculation of length mass relationships and analysis of salmon condition pre- to post-flood; (3) the development and comparison of mass abundance models for all streams in all years, and; (4) modelling of community size structure with direct and indirect effects of floods as predictor variables.

5.2.3.1 Juvenile salmon diet

Biomass of freshwater prey items were calculated for each gut at BBS in 2016 using published length to ash free dry mass regressions (Benke et al., 1999). Due to the lack of available prey item length data for the pre-flood time period it was not possible to statistically compare biomass pre- and post-flood. As a result, regression models were used to test for differences in the abundance of prey items from freshwater, terrestrial and marine sources between pre-flood (2009 and 2010) and post-flood time periods (2016 and 2017). Generalised linear models (GLM) were constructed with negative binomial error distributions, using the glm.nb function in the MASS package (Venables and Ripley, 2002) to account for overdispersion in the count data. F tests were used to test for differences between pre-flood and post-flood groups, using the Anova function in the car package (Fox and Weisberg, 2011).

Odds ratios were calculated to compare the positive or negative selection of freshwater macroinvertebrate prey by juvenile salmons in relation to macroinvertebrate densities in the stream benthic community (Gabriel 1978). Regression was used to test for relationships between specific taxonomic group Odds ratios and $\log_{10}$ total freshwater prey density (m^{-2}) and time since floods (years), through the entire study period (2009, 2014, 2016 and 2017) with GLM (Gaussian error distribution) used in all cases. Models take the form:

$$\text{Odds ratios} = \alpha + \beta * \text{predictor variable} \qquad \text{Equation 1}$$

Where α is the constant and β is the coefficient of the model. For post-flood years (2016 and 2017), where data were available at finer taxonomic resolution, Odds ratios were also calculated in the Plecoptera and Ephemeroptera at the family level and the Chironomidae at subfamily, to explore if patterns in Order scale odds ratios were consistent at finer taxonomic resolutions.

5.2.3.2 Length mass relationships and salmon condition

Length mass plots and regressions were created for all streams in 2009, 2010, 2014, 2015, 2016, and 2017. Mass was predicted separately for both juvenile coho salmon and Dolly Varden in each year using length ~ mass models. Initially, separate models were constructed for each year given potential changes to the intercept and slope of models following the floods in 2014. However, comparisons of slopes and intercepts (95% confidence intervals) demonstrated significant overlap between slopes and intercepts for both species across years. As such, a single model was constructed for juvenile coho salmon and Dolly Varden which incorporated data from all available years. These models assumed isometric growth and take the form:

$$log10(W) = \alpha + \beta * log10(L) \qquad \text{Equation 2}$$

where W is mass (g), and L is length (mm), α is the constant and β the coefficient of the model. Juvenile salmon condition was compared between pre-flood (2009), initial post-flood (2015) and response post-flood (2017) where mass data were available to the nearest 0.1 g. Fulton's condition factor (K) was calculated using the method of Ricker (1975) for all juvenile salmons whose mass and length were measured. This metric links an individual's mass to its length and suggests how good a condition a fish is in. Individuals who have access to poor quality food, have low fat reserves or poor muscular development will be of lower condition than fish with access to high quality food, with high fat reserves and high muscular development. This metric allows for comparisons of individuals or populations of fish to be made. Generalised linear models of $\log_{10}(K)$ were constructed with Gaussian error distribution prior to F tests and subsequent post hoc Tukey’s HSD tests between pairs of years. Given consistent patterns observed in 0+ and 1+ cohorts (Figure 9.1) all individuals’ condition was compared simultaneously.

5.2.3.3 Mass abundance models

Coefficients from length~mass (M) models were used to predict $\log_{10}$(mass) for all salmon with length measurements. Subsequently, predicted masses were used to produce annual mass (M)-abundance ($N_{\%}$) models. $N_{\%}$ was calculated by controlling the count of individuals per class by sampling effort (Minnow traps). These models were built by grouping organisms into classes or bins based on their mass. When organisms are included across multiple trophic levels such models are effective at describing energy flow through food webs (Kerr and Dickie, 2001). However here, where a community of secondary consumers are the topic of models, they provide an effective descriptor of size distribution. To construct $MN_{\%}$ models, the range of $\log_{10}(M)$ was split into n equal classes and individual juvenile salmons were allocated to a class based on M. The $\log_{10}$ mean of each class was then plotted against $N_{\%}$. Plots were created using four, five, six and ten classes and compared to assess suitability; the number of M classes used in the final analyses (n = 5) was selected to maximise linearity and the number of zero $N_{\%}$ classes after Dossena et al. (2012). Minnow traps can allow small fish to escape through trap mesh aperture and incomplete seals between the two halves of a trap can also prevent the capture of small fish. As such, the smallest and generally rare individuals (<40 mm) were dropped from analyses in all cases to reduce the sampling bias of this size class in minnow traps. Generalised linear regression was used to identify the slope of the $MN_{\%}$ relationship at each stream.

5.2.3.4 Size structure response to floods

An information-theoretic approach was applied to consider the validity of a range of exploratory models, describing the effects of extreme high-frequency floods on the size structure of juvenile salmon communities (Burnham and Anderson, 2002). Prior to model construction the collection of predictor variables was examined for collinearity, which was not observed. The predictor variables selected for this study were: time since last extreme flood (years) – selected because disturbances are considered a fundamental control on biotic communities in stream ecology (Poff, 2002), and expected to be closely tied to resilience an important measure of ecological stability (Donohue et al., 2013); the availability of slower flowing habitat - beneficial to juvenile salmon abundance (Elliot and Armstrong, 1972, Beecher et al., 2002), and total freshwater prey availability - positively associated with increased stream salmon density and biomass (Herdrich et al., 2018).

Models selected are not a comprehensive list of potential controls on juvenile salmon community size structure. Rather, the model set represents the hypotheses deemed most likely to represent controls on juvenile salmon community size structure in the current study. In future studies, where an alternate or more extensive study region is selected, or where a different range of streams are studied, a new set of hypotheses might be considered.

Slow flow habitat availability was calculated as a percentage of the total available instream habitat, recorded in stream habitat surveys during pre-flood and post-flood years. This is based on a visual classification of habitat unit types (Chapter 3) a habitat unit type (e.g. backwater, pool, riffle, run) was considered to be suitable habitat if its type's mean flow and/or depth fell within reported boundaries for juvenile coho salmon and Dolly Varden (Elliot and Armstrong, 1972, Stewart et al., 2007). The methodology for surveys and calculation of percentage availability are described in Chapter 3. Total freshwater prey density (m^{-2}) was estimated from a minimum of three Surber samples collected from a single study reach in each river in 2009, 2014, 2015, 2016 and 2017.

Seven models were constructed each containing a subset of the three predictor variables, the five top ranked models are reported in Table 8. A null model was also developed which allowed an assessment of the value of all other models in the set (Burnham and Anderson, 2002). Comparisons of model fit were made using a small sample adjusted version of AIC (Akaike, 1992) called AIC_C (Hurvich and Tsai, 1989). Akaike weights (weights) for all candidate models were used to compare the likelihood of each model in the set (Burnham and Anderson, 2002). Comparisons of 95% confidence intervals of predictor variable slope coefficients were used to identify good predictors in a given model. Model averaging was considered as an approach to handle uncertainty in the developed models; however, given the exploratory nature of the analyses and relatively small sample size, the full set of developed models and their associated mass are presented. This recognises that new or larger datasets could provide evidence for the importance of different predictor variables. All models were fitted using GLM with Gaussian error distributions, utilising the glm function in R. GLMM were considered unsuitable due to insufficient numbers of streams and years per stream in this study.

5.3 Results

Across the four study streams >2700 juvenile salmon were captured, dominated by juvenile coho salmon (>1650 inds) and Dolly Varden (>1050 inds). A small number of other salmon were sampled: one juvenile sockeye salmon *Oncorhynchus nerka* was captured at BBS in 2016; whilst three rainbow trout *Oncorhynchus mykiss* and five coastal cutthroat trout *Oncorhynchus clarkia* were captured across 2016 and 2017, between BBS and Ice Valley Stream (IVS). Three-spined stickleback *Gasterosteus aculeatus* and sculpin *Cottus* sp. were also caught in minnow traps. CPUE for the dominant two salmon species are reported in Table 5.1

Table 5.1. Juvenile salmon catch per unit effort (CPUE) for each stream in each year.

	Coho				**Dolly Varden**			
	WPC	**IVS**	**BBS**	**RPC**	**WPC**	**IVS**	**BBS**	**RPC**
2009	13.1	1.5	1.2	7.7	3.4	1.0	5.0	5.9
2010	2.3	2.4	1.6	5.0	0.2	0.2	0.8	3.3
2013	0.9	0.8	1.0	1.5	0.8	1.4	2.8	0.0
2014	1.6	2.8	2.8	4.5	3.4	1.4	11.9	6.6
2015	0.0	2.6	9.7	8.8	0.1	0.2	0.7	1.0
2016	0.3	3.7	6.3	6.0	0.1	0.8	1.2	3.0
2017	3.7	3.1	4.9	5.8	0.4	0.7	1.4	5.5

5.3.1 Juvenile salmon diet

In total, 714 salmon guts were flushed, and their contents identified, across 2009, 2010, 2014, 2016 and 2017. Juvenile salmon diet varied across streams and salmon species pre-flood (Appendix Figure 9.2). Post-flood differences in juvenile coho salmon consumption of freshwater and marine sourced prey were not significantly different from pre-flood (Table 5.2; Figure 5.1a and Figure 5.1c), but a significant difference was observed in terrestrial prey consumption which decreased from a mean of 4.6 to 1.2 items per gut (Table 5.2, Figure 5.1b). This pattern was visually consistent across size classes (Figure 5.2). The mean abundance of items in Dolly Varden guts saw no significant change pre- to post-flood (Table 2, Figure 5.1d-f). During all time periods, >90 % of both juvenile coho salmon and Dolly Varden guts contained freshwater prey items, with the exception of Dolly Varden at BBS (2009 to 2014) and Rush Point Creek (2017) which had <80 % of guts containing freshwater prey items predominantly from the Chironomidae and Ephemeroptera (Appendix Figure 9.2). A greater proportional contribution of terrestrial and marine derived resources was observed at intermediate and higher geomorphologically complex streams (IVS, BBS and RPC; Appendix Figure 9.4). The proportional contribution of freshwater prey items increased in stomach contents during the summer of 2014 (summer of the floods), with the exception of BBS and Dolly Varden at WPC.

Chironomidae were by abundance dominant prey resource for both salmon species (Appendix Figure 9.3). The exceptions to this were found pre-flood: for coho salmon at BBS where guts contents were dominated by Hydrachnidia, and for Dolly Varden at WPC (2010) where gut contents were dominated by Simuliidae. However, the biomass of ingested invertebrates per gut at BBS in 2016 indicated the bioenergetic importance of invertebrates other than individuals from the family Chironomidae (Figure 5.3).

Table 5.2. Pre- to post-flood comparisons between dietary item abundance from three main sources using Fisher's F test.

Species	Freshwater		Terrestrial		Marine	
	F	p	F	p	F	p
coho salmon	1.427	0.254	12.707	0.003	3.839	0.072
Dolly Varden	1.087	0.318	4.497	0.055	2.329	0.153

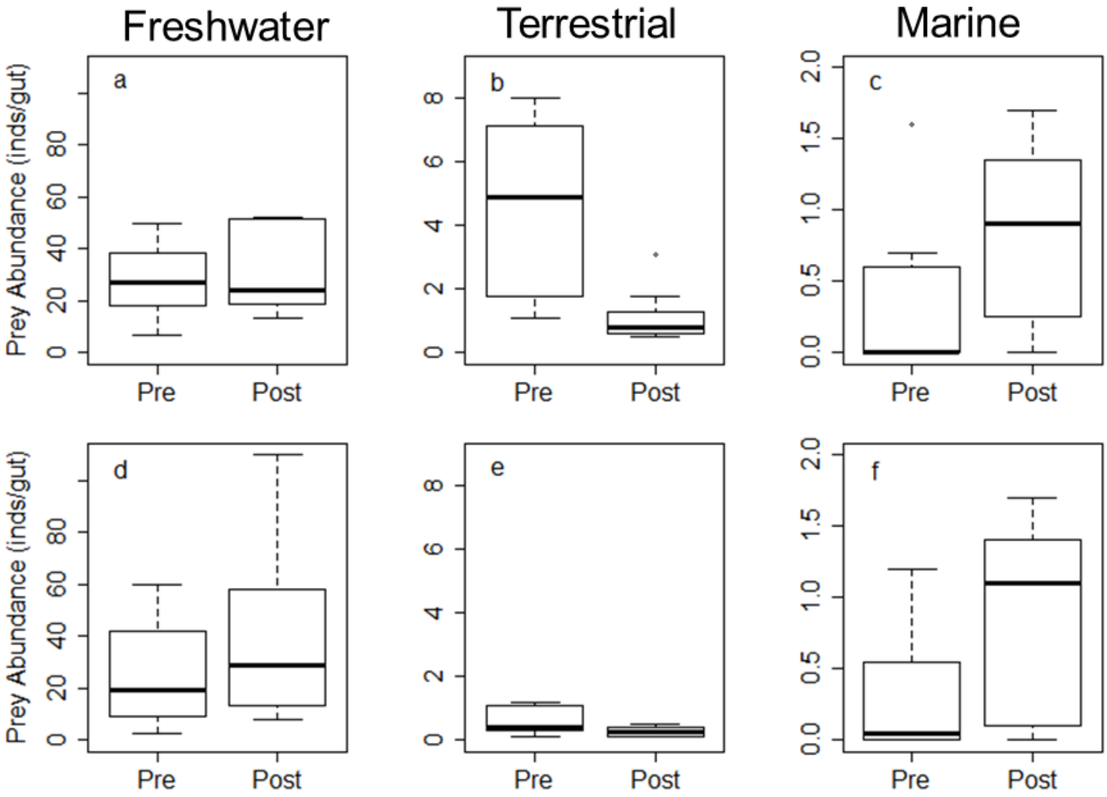

Figure 5.1. Boxplots of mean prey abundance in juvenile salmon guts. Coho salmon a) freshwater b) terrestrial and c) marine sourced items and Dolly Varden d) freshwater e) terrestrial and f) marine sourced items.

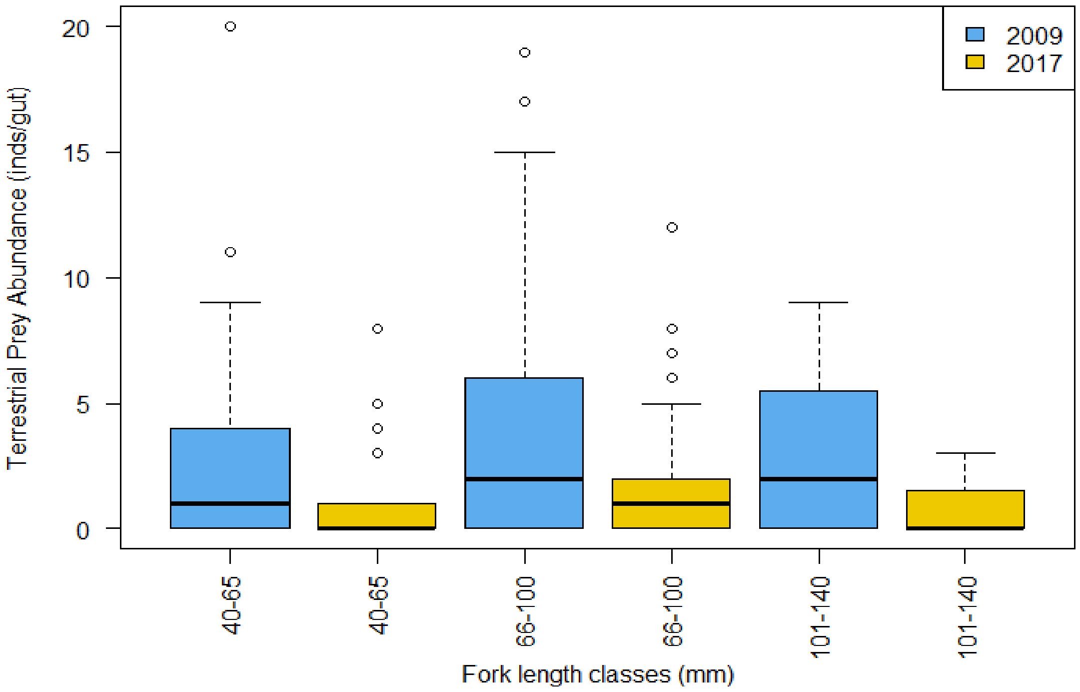

Figure 5.2. Boxplots of juvenile coho salmon mean terrestrial prey consumption by size classes which relate to 0+, 1+ (split into two groups) age classes

In juvenile coho salmon, Chironomidae contributed 66% of the total abundance of prey items but 27% of the total freshwater prey biomass. However, Chironomidae still contributed more than double the consumed invertebrate biomass when compared to the next most abundant family (Baetidae – 14 %). Proportionally, Tipulidae and Ephemerellidae showed the greatest disparity in contribution from abundance to biomass, increasing from 0.5 % and 1.7 % to 9.2 % and 12.4 % respectively. Similar patterns were observed in juvenile Dolly Varden, where Chironomidae contributed 84 % of the total abundance of prey items but only 47 % of the biomass. The second most important contributor to prey biomass of juvenile Dolly Varden were the Baetidae (22 %), which contributed only 6 % of the total abundance. Notably, the Tipulidae (0.5 to 3.6 %), Ephemerellidae (1.6 to 8.2 %) and Heptageniidae (1.4 to 9.9 %) all contributed > eight times more to total consumed biomass than total consumed abundance in juvenile Dolly Varden diet (Figure 5.3).

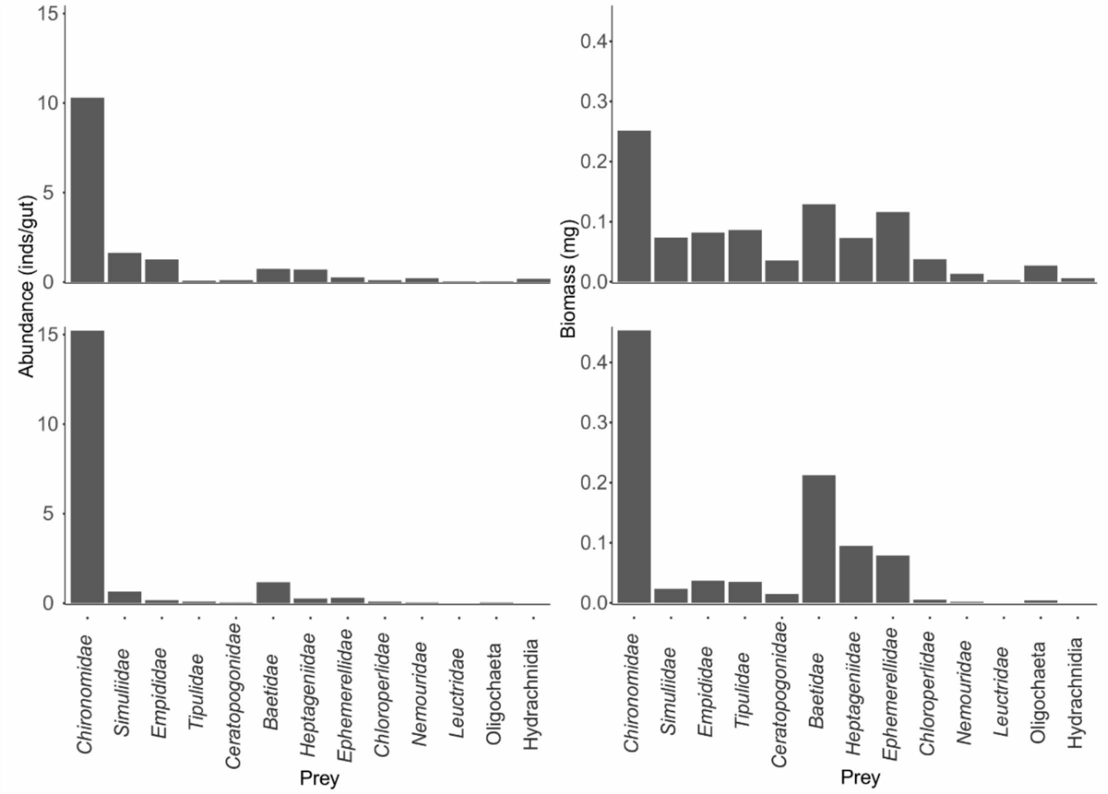

Figure 5.3. Average abundance (left) and biomass (right) of freshwater prey items in juvenile salmon guts at BBS in 2016. Top – coho salmon, Bottom – Dolly Varden.

Significant differences in prey resource selection were observed over time for both juvenile coho salmon and Dolly Varden (Table 5.3) at all streams. Pre-flood, Chironomidae were negatively selected as prey resources by both species at all streams, except IVS. In contrast, Ephemeroptera, Plecoptera and Trichoptera were positively selected for by juvenile salmon in all cases. During the flood year (2014), Chironomidae became positively selected for in all streams, whist the Ephemeroptera and Plecoptera were negatively selected, a trend consistent across both salmon species. Positive selection of Chironomidae persisted to 2017 in both species at all streams, except the lowest complexity stream (WPC). Both Chironomidae (Figure 5.4a) and Trichoptera (Figure 5.4e) selection decreased significantly with increasing total density of freshwater prey. Contrastingly, Ephemeroptera (Figure 5.4c) and Plecoptera (Figure 5.4d) selection significantly increased with density of freshwater prey. No relationship was observed between Simuliidae selection and density of freshwater prey (Figure 5.4b).

Table 5.3. Freshwater prey items odds ratios vs log $_{10}$*(Total Freshwater Prey Density (*m^{-2}*) and time since flood (years) 95% confidence intervals in parentheses). Bold =* $p < 0.05$

	Chironomidae	**Simuliidae**	**Ephemeroptera**	**Plecoptera**	**Trichoptera**
			Freshwater Prey Density		
α	6.2 (4.0, 8.5)	-3.4 (-5.7, -1.2)	-6.3 (-9.0, -3.6)	-5.2 (-8.2, -2.1)	6.1 (3.0, 9.1)
β	-1.9 (-2.7, -1.2)	1.2 (0.5, 1.9)	2.0 (1.1, 2.8)	1.6 (0.6, 2.5)	-1.5 (-2.5, -0.5)
F	27.01	11.23	19.84	9.88	9.04
p	**< 0.001**	**0.004**	**< 0.001**	**0.006**	**0.013**
			Time Since Flood		
α	2.5 (0.1, 4.9)	1.0 (-0.9, 3.0)	-3.4 (-5.9, -1.0)	-2.9 (-5.4, -0.4)	6.8 (3.9, 9.7)
β	-0.7 (-1.5, 0.1)	-0.2 (-0.8, 0.4)	1.0 (0.2, 1.8)	0.8, (0.1, 1.6)	-1.5 (-2.3, -0.7)
F	3.40	0.44	6.57	4.40	13.60
p	0.080	0.515	0.019	0.052	**0.004**

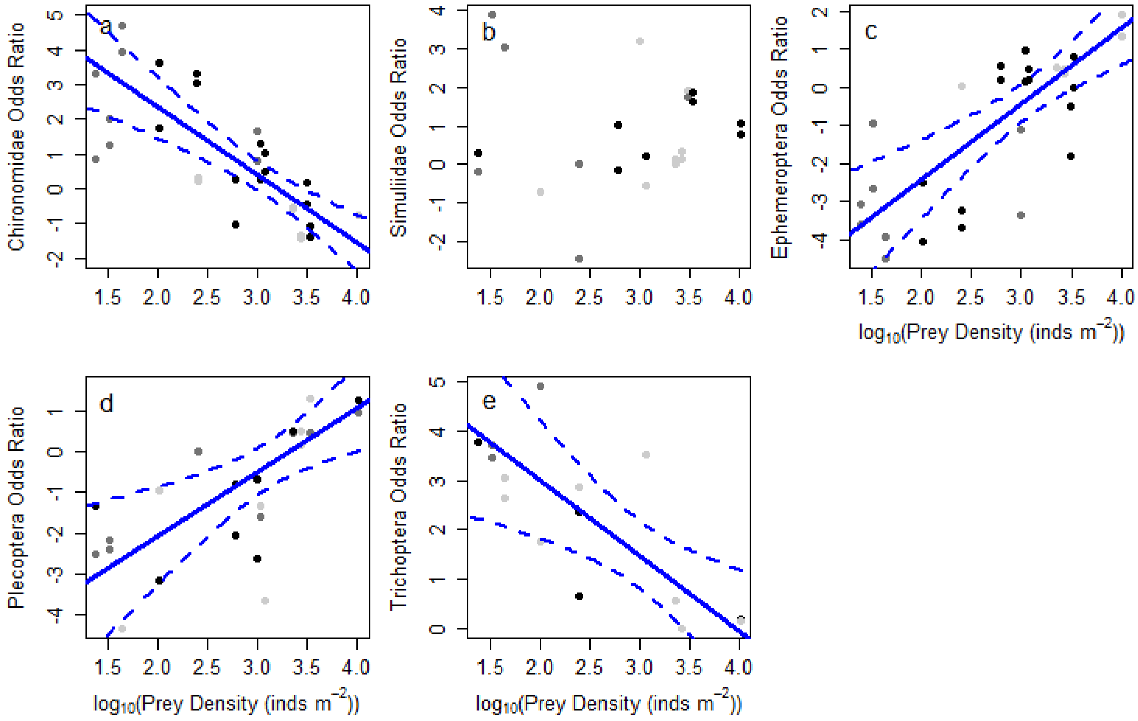

Figure 5.4. Scatterplots of freshwater prey resource Odds ratio's and freshwater prey density. Blue lines represent significant relationships at $p < 0.05$*. a) Chironomidae, b) Simuliidae, c) Ephemeroptera, d) Plecoptera, e) Trichoptera.*

Higher taxonomic resolution odds ratios for juvenile coho salmon in 2016 and 2017 indicated that the persistence of positive selection in the Chironomidae at higher complexity streams was driven by selection of *Tanypodinae* at BBS and *Tanypodinae* and *Diamesinae* at RPC (Table 5.4). At IVS *Orthocladiinae/Chironominae* were positively selected for post-flood. Ephemerellidae and Heptageniidae were generally negatively selected by juvenile coho salmon, except at BBS and WPC (2017). Similarly, the Baetidae were negatively selected for at all streams and in all years, other than RPC in 2017. Chloroperlidae were positively selected for at WPC and RPC, whilst the Leuctridae and Nemouridae were negatively selected for in all cases. These patterns were generally consistent with those observed for Dolly Varden (Table 5.3), with the additional positive selection of *Orthocladiinae/Chironominae* observed in Dolly Varden at BBS.

Table 5.4. Odds ratios for post-flood juvenile coho salmon and Dolly Varden diets

Species	**Site**	**Year**	***Orthocladiinae/ Chironominae***	***Diamesiae***	***Tanypodinae***	**Ephemerellidae**	**Hetageniidae**	**Baetidae**	**Chloroperlidae**	**Leuctridae**	**Nemouridae**
Coho salmon	**WPC**	2016	-1.25	0.28	-21.28	0.04	-18.87	-0.59	5.21	-19.97	-15.87
		2017	-2.29	-0.36	-1.64	-0.01	1.41	-0.51	6.36	-20.97	-15.19
	IVS	2016	3.10	-22.55	-19.55	-2.01	-1.74	-4.62	-2.72	-22.55	-2.97
		2017	3.36	-1.67	-20.09	-5.30	-2.61	-2.57	-24.21	-20.09	-3.48
	BBS	2016	-1.11	-0.01	-0.71	1.61	1.24	-0.35	-0.01	-1.97	-0.98
		2017	0.31	-2.07	2.28	-1.01	1.03	-0.73	-1.98	-23.99	-23.83
	RPC	2016									
		2017	-0.50	1.83	4.47	-1.73	-1.50	0.18	1.56	-3.09	-1.86
Dolly Varden	**WPC**	2016	-0.17	-23.46	-21.80	-22.97	-19.39	-1.27	-16.40	-20.49	-16.40
		2017	-1.74	-0.33	-1.79	-0.51	0.97	-1.07	5.76	-22.07	-16.29
	IVS	2016	2.13	-21.21	-18.20	0.93	-0.90	-3.05	0.65	-21.21	-22.86
		2017	3.40	-2.72	-19.91	-3.17	-3.35	-3.44	-3.15	-19.91	-24.03
	BBS	2016	0.34	0.41	-20.36	0.84	0.14	-0.09	-0.55	-21.62	-2.09
		2017	0.65	-2.23	3.37	-1.02	0.68	-0.61	-2.28	-24.12	-4.27
	RPC	2016									
		2017	-0.65	0.26	-15.79	-0.70	-0.82	0.90	0.88	-3.17	-1.54

5.3.2 Length Mass relationships and salmon condition

Juvenile coho salmon mass was strongly related to length (Appendix Figure 9.6a). Individual year models were also typically good at predicting mass with R^2 ranging from 0.63 (2014) to 0.97 (2017) (Table 5.5). Intercepts of lines varied from -5.26 two years post-flood to -4.66 one-year post-flood, whilst model slopes ranged from 2.78 (2015) to greater than 3.1 (2016 and 2017). Similarly, Dolly Varden length mass relationships were successfully modelled by linear regression (Figure 9.6b). The fit of individual year models was also generally good, with R^2 values ranging from 0.65 (2015) to 0.97 (2009; Table 5.5). Model intercepts ranged from -5.05 (2010 and 2017) to -3.88 (2015). Dolly Varden slopes were in all cases shallower than for juvenile coho salmon ranging from 2.40 (2015) to 3.02 (2017). For both species, the slope of models in 2015 (Table 5.5) were shallowest, indicating smaller individuals were in relatively better condition than larger individuals in 2015 compared to other study years. In contrast, during subsequent post-flood years coho salmon (2016 and 2017) and Dolly Varden (2017) demonstrated the steepest regression slopes, indicating greater condition in larger individuals than smaller individuals.

Table 5.5. Mass length regressions for each species in each year, used to predict mass for all individuals with recorded length data. (95% confidence intervals)

		All years	2009	2010	2014	2015	2016	2017
Coho salmon	α	-5.24 (-5.37, -5.11)	-4.99 (-5.15, -4.82)	-5.00 (-5.26, -4.74)	-4.91 (-5.49, -4.33)	-4.66 (-5.36 -3.97)	-5.26 (-7.11, -3.41)	-5.14 (-5.23, -5.04)
	β	3.15 (3.08, 3.22)	3.07 (2.98, 3.16)	3.00 (2.86, 3.14)	2.94 (2.62, 3.26)	2.78 (2.38, 3.17)	3.17 (2.16, 4.18)	3.10 (3.04, 3.14)
	R^2	0.86	0.96	0.89	0.63	0.71	0.91	0.97
	F	7849	4668	1686	329	195	65	14460
	p	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Dolly Varden	α	-5.09 (-5.22, -4.96)	-4.63 (-4.78, -4.48)	-5.05 (-5.34, -4.77)	-4.30 (-4.59, -4.02)	-3.88 (-6.13, -1.62)		-5.05 (-5.23, -4.87)
	β	3.04 (2.98, 3.11)	2.86 (2.79, 2.94)	3.00 (2.84, 3.15)	2.62 (2.48, 2.77)	2.40 (1.25, 3.54)		3.02 (2.93, 3.11)
	R^2	0.90	0.97	0.92	0.80	0.65		0.95
	F	8148	5681	1504	1207	22		4224
	p	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		< 0.001

Significant differences were observed in both juvenile salmon (Table 5.6, Figure 5.5b) condition from 2013 (pre-flood) to 2017 (final post-flood survey). Coho salmon condition decreased from a pre-flood mean of 1.39 (2009) to 0.93 directly post-flood (2015). By 2017, condition had increased to 1.10, but did not recover to pre-flood levels. Dolly Varden condition demonstrated a consistent significant pattern to juvenile coho salmon through time. The highest overall fish condition for the four streams was observed pre-flood (K = 1.25, 2009) but decreased to 0.88 in 2015), but despite significantly increasing to 0.98 by 2017 (Table 5.6), K remained lower than pre-flood.

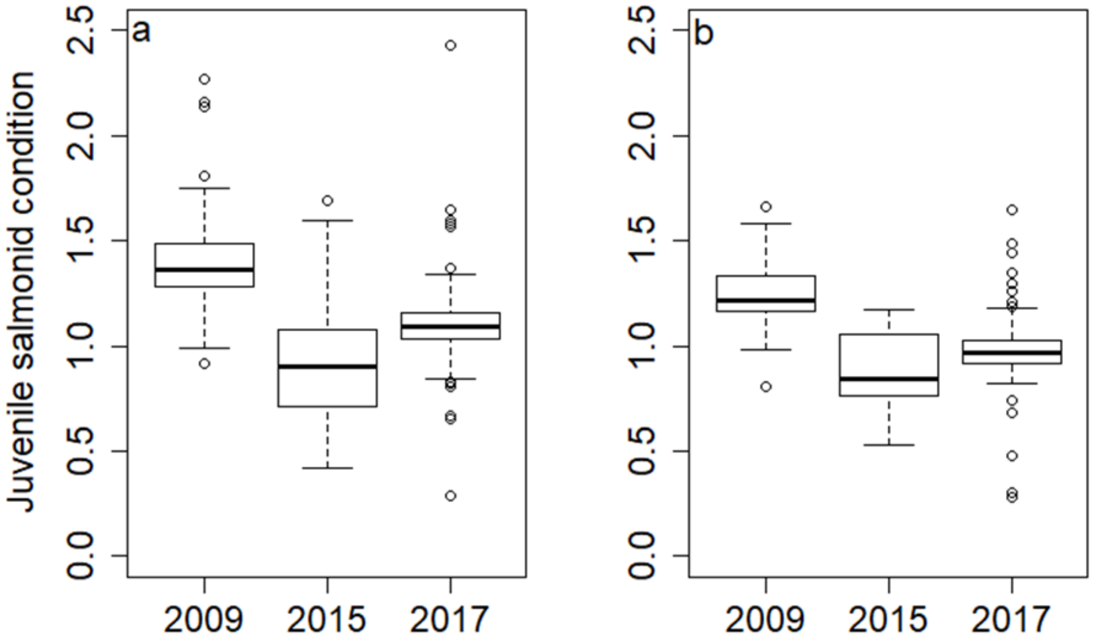

Figure 5.5. Juvenile salmon condition (K) in 2009 (pre-flood), 2015 (Initial post-flood) and 2017 (Final post-flood). a) coho salmon and b) Dolly Varden. Significant differences are observed in all within species pairwise comparisons.

Table 5.6. Results of tests for differences in juvenile salmon condition through time. F tests statistics and pairwise Tukeys post-hoc Z scores

Species	Overall	2009-2015	2009-2017	2015-2017
Coho salmon	F = 186.37, p < 0.001	Z = 18.84, p < 0.001	Z = 14.18, p < 0.001	Z = -10.51, p < 0.001
Dolly Varden	F = 118.26, p < 0.001	Z = 8.50, p <0.001	Z = 14.79, p < 0.001	Z = -2.41, p = 0.042

5.3.3 Mass abundance

Positive $MN_{\%}$ relationships were observed at all streams pre-flood (Figure 5.6), a pattern that persisted through the first half of 2014 (the summer of the floods), with the exception of IVS. Positive slopes indicated numerical dominance of larger individuals over smaller individuals. One-year post-flood, a switch in the sign of regression slopes was observed across streams with slope coefficients becoming negative. In 2015 insufficient fish were caught at Wolf Point Creek (WPC) to allow a $MN_{\%}$ model to be created but negative slopes persisted in 2016, although in some cases (IVS and RPC) they become shallower. By 2017 slopes were typically close to zero and slightly positive at RPC.

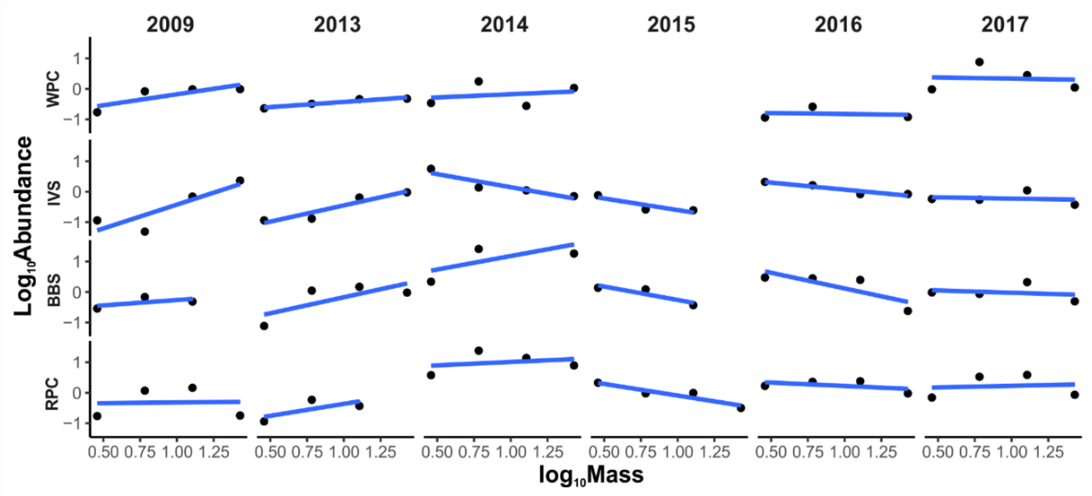

Figure 5.6. Mass relative abundance plots for entire juvenile salmon community. Blue lines = generalised linear model lines.

The most effective predictor of $MN_{\%}$ slope was time since flood, which was included in all four of the best fitting models (Table 5.7; Figure 5.7). Increasing time since flood had a positive effect on $MN_{\%}$ slope and was a good predictor variable. Models containing time since flood made up >99 % of total model weight. The most likely candidate model accounted for 54 % of total model weight and contained time since flood as well as total freshwater prey density, almost twice the weight of the next best model, which only contained time since flood and explained 31 % of total model weight.

Only one model in this study, containing only slow flow habitat availability, was identified as a poor predictor model. This model carried less weight than a null model and was predicted to be 10,400 times less likely than the best candidate model to fit the data (Appendices Table 9.10). Further, slow flow habitat availability was an ineffective predictor in all models, with 95 % confidence intervals for the coefficient of slope overlapping zero.

*Table 5.7. Model selection results for MN slopes, placed in rank order. + and – indicate the sign of a coefficient and * indicates coefficients with 95% confidence intervals not including zero. K = the number of parameters in model*

Time Since Flood	Slow flow habitat availability	Total freshwater prey density	k	AICc	weight	Evidence ratio
+X*		+X*	5	7.76	0.5406	1.0
+X*			3	8.85	0.3136	1.7
+X*	-X		5	11.2	0.0946	5.7
+X*	-X	+X	7	12.8	0.0445	12.1
		+X*	3	16.8	0.0057	94.2

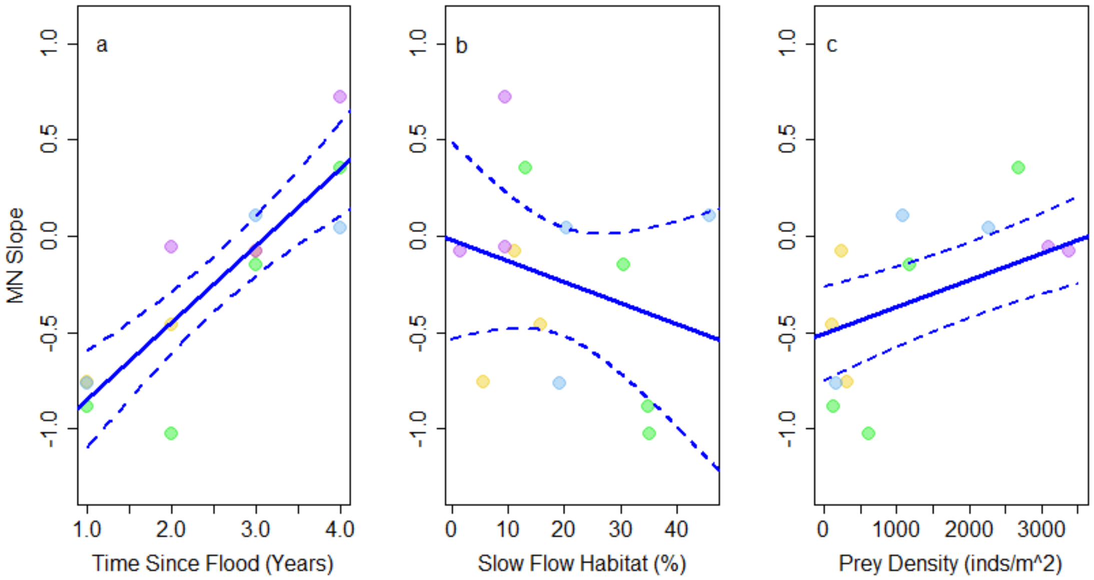

Figure 5.7. Scatterplots of individual predictor variables plotted against mass abundance regression slopes (MN Slope). Black lines = generalised linear models of the form MN slope~predictor variable. WPC = Purple, IVS = Gold, BBS = Green and RPC = Blue

5.4 Discussion

This study has identified some key impacts of extreme high-frequency floods on instream juvenile salmon communities. Whilst CPUE initially declined post-flood for Dolly Varden, an increase in juvenile coho salmon CPUE was observed, at all except the youngest stream (WPC). However, in both species novel analyses identified reduced salmon condition in post-flood years. Further, the mass abundance modelling approach demonstrated significant changes in juvenile salmon community size structure through the study period, linked to changing time since the last extreme flood and total freshwater prey density. These findings add considerable insights that time since disturbance can be crucial in understanding ecological resilience to disturbance events. The exploration of dietary response in juvenile coho salmon pre- to post-flood demonstrated significant reductions in the contribution of terrestrial prey post-flood, a further important novel contribution to the understanding of temporal dynamics (linked to flow regimes) across habitat boundary resource subsidies (Nakano and Murakami, 2001). This reduction of terrestrial prey occurred during a period of reduced freshwater prey availability. Additionally it occurred alongside positive selection of Chironomidae and Trichoptera larvae, both of which are known to rarely enter the drift (Rader, 1997). Together these results could provide evidence for potential changes in feeding behaviour post-flood. These findings challenge the assumption that juvenile salmon communities are resilient to floods when density/abundance of individuals recovers rapidly post-flood. Rather, it suggests that a juvenile fish community might demonstrate resilience only when size structure and condition recover to pre-flood levels. Further, it demonstrates the complexities of developing our understanding of ecological stability and disturbance events highlighted previously by Donohue et al. (2013).

5.4.1 Juvenile salmon diet

Pre-flood utilisation of terrestrial prey resources by juvenile coho salmon was generally low compared to other studies (Nielsen, 1992, Eberle and Stanford, 2010). This low terrestrial prey utilisation may be as a result of differences in riparian invertebrate communities in higher versus lower latitude systems or the reduced growing season associated with lower air and ground temperatures observed at higher latitudes. The low (<10 %) utilisation of terrestrial prey resources throughout this study by Dolly Varden is consistent with other studies of successional habitats (Eberle and Stanford, 2010) and is consistent with the life history traits. This evidence offers support to studies highlighting the importance of both drift and benthos feeding behaviours in this species (Nakano et al., 1999).

Following extreme high-frequency summer floods in GBNP, a significant immediate decrease in total macroinvertebrate abundance occurred, with significant changes to community composition (Chapter 4). These community changes appear to be responsible for changing prey selection in both juvenile coho salmon and Dolly Varden. Decreased resource availability, which can be expected to lead to increased inter- and intra-specific competition, is likely to drive changes in feeding behaviour in both salmon species as reported for experimental studies elsewhere (e.g. Nielsen, 1992, Svanbäck and Bolnick, 2007, Nakano et al., 1999). Increased positive selection of Ephemeroptera and Plecoptera which in southeast Alaska streams are generally mobile (Chapter 4) during periods of high freshwater prey availability provides evidence to suggest that selective drift feeding is the favoured feeding behaviour for both juvenile coho salmon and Dolly Varden in GBNP consistent with past research (Nielsen, 1992, Nakano et al., 1999). These taxa's mobility increases the likelihood they will enter the drift when compared to Chironomidae, Simuliidae and Trichoptera which are typically infrequent components of the drift (Rader, 1997). Further, their large size compared to other available prey such as many Chironomidae and Simuliidae may increase their likelihood of selection when a surplus of prey is available.

In contrast, the increased positive selection of the comparatively less mobile Chironomidae and Trichoptera when freshwater prey availability is low, may indicate a consistent shift from drift feeding to active searching of the benthos observed in Dolly Varden before when drift prey availability is low (Nakano et al., 1999). When feeding from the benthos, differential mobility of prey items could alter the likelihood of success in each predation effort, indeed the importance of Chironomidae (which are relatively immobile (Poff et al., 2006)) to benthos foraging has previously been reported in Dolly Varden (Nakano et al., 1999). This theory is further supported by the significant decrease in terrestrial prey consumption post-flood in juvenile coho salmon. When foraging from the benthos the likelihood of encounters with terrestrial prey items is likely to decline as they land on the water's surface and drift downstream. Alternatively, reduced freshwater to riparian zone energetic subsides, as a result of reduced benthic macroinvertebrate density and thus density of aerial adults, could reduce survival and consequently abundance of predatory spiders and beetles in the riparian zone (Kawaguchi and Nakano, 2001, Nakano et al., 1999, Henschel et al., 2001), which typically represent a large component of total terrestrial prey items recorded in this study.

High resolution Odds ratios highlight the value of high taxonomic resolution in studies of feeding behaviour. Both species in this study demonstrated differential selection of prey resources from within Orders (Family in the Chironomidae) which had previously been "lumped together" (Clitherow, 2016, Sønderland, 2017). This is particularly significant given the diverse size ranges observed within taxa at the Order resolution in benthic macroinvertebrate communities (for instance the difference between the 'large' (1.2 mm long) *Pagastia partica* (Diamesinae) and (0.6 mm long) *Eukiefferiella* spp. (Orthocladiinae). Differences in prey item size in this study were highlighted by biomass analyses at BBS in 2016, where increased biomass and therefore bioenergetic contribution of individuals from different families, particularly within the Ephemeroptera and Plecoptera, were observed. This analysis also highlighted the relatively small bioenergetic contribution gained from an individual *Chironomidae*, the numerically dominant freshwater prey resource in salmon guts across space and time in this study.

Overall, changing resource consumption from pre-flood to post-flood and changing prey item selection with total availability of freshwater prey support H_1: that high-frequency summer floods will alter resource utilisation across juvenile salmon species following changes to benthic macroinvertebrate communities observed at all streams post-flood. However, the consistent patterns of terrestrial prey consumption across size classes in coho salmon reported may indicate that top down effects are less likely to represent the dominant driver in this study. Importantly, changing prey resource utilisation could have major implications for salmon condition, survival and population size structure at the population and community levels.

5.4.2 Juvenile salmon condition

The significant decrease in juvenile salmon condition from pre-flood to post-flood (both 2015 and 2017) was potentially due to two main drivers; (1) an overall increase in the abundance of juvenile salmon (across both species) in the first-year post-flood, and (2) a significant decrease in total prey availability (benthic macroinvertebrates) in the first year post-flood (Chapter 4). Both processes can be expected to increase inter- and intra-specific competition between individuals (Myrvold and Kennedy, 2015a). With increased fish abundance there are more individuals who may attempt to establish a territory, which are generally thought to have a minimum size (m^{-10}) (Wood et al., 2012) and with decreased prey availability each individual will have access to less resources and therefore less energy (Imre et al., 2004). The subsequent failure of juvenile salmon condition to recover to pre-flood levels may be linked to changes in benthic macroinvertebrate community composition and therefore differences in bioenergetic availability. The less energetically valuable r-selected macroinvertebrate taxa which became more dominant in the post-flood invertebrate community (2017, Chapter 4) may have resulted in a lower net gain of energy per item consumed (net gain = energy expended vs energy consumed) than observed pre- flood, a pattern consistent with predatory fish experiments on prey profitability (e.g. Scharf et al., 1998). These findings provide evidence in support of H_2: condition of juvenile salmon will decrease post-flood and as a result of altered resource availability and utilisation.

5.4.3 Potential shifts in habitat availability across streams

Alongside changes to prey resource availability, geomorphological complexity varied at all streams post-flood (Chapter 3), with an increase in slow flow habitat availability and increased abundance of instream wood from pre-flood to post-flood, with the exception of WPC. A relationship between fish abundance and slow flow habitat availability and wood abundance has been reported for salmon populations elsewhere in North America (Herdrich et al., 2018), and has previously been reported in GBNP streams (Klaar, 2011), although it represented the weakest model in the current study. The apparent lack of importance of slow flow habitat availability in mass abundance regression models within this study may be due to the positive post-flood response observed in this aspect of niche space (habitat availability). In contrast, during the post-flood time period other aspects of niche space (prey availability) and the legacy effects of the floods were acting negatively on salmon populations. This finding further highlights the importance of monitoring all aspects of niche space when attempting to understand responses of ecological communities to disturbance events.

5.4.4 Salmon community size structure

Pre-flood juvenile salmon community size structure was consistently (temporally and spatially) dominated by larger individuals from 1+ age classes. This may be the result of competitive exclusion of smaller size classes from primary juvenile salmon habitat in the main channel, studied here, or the result of differential habitat utilisation with changing body size in both juvenile coho salmon and Dolly Varden. Elsewhere, smaller juvenile coho salmon have been shown to utilise smaller and shallower low flow habitat than larger fish (Kahler et al., 2001). Such fish migrate as their size increases, which has been linked to changing niche space, because individuals which undertake this migratory behaviour have higher growth rates than fish which remain in a single habitat unit as they grow (Kahler et al., 2001). However, it is important to note that the Kahler et al. (2001) study does not directly rule out competitive exclusion as a driver of habitat utilisation. Indeed, in numerous feeding studies changing behaviour and habitat use has been linked to exclusion from primary feeding sites (White, 1986, Nielsen, 1992, Nakano et al., 1999). Crucially, source populations of 0+ individuals must be present within the catchment to support strong recruitment into the larger size classes observed in main channel habitats post-flood. Higher abundance of 1+ individuals in pre-flood communities suggest streams contribute effectively to smolt production, whereas if communities had 0+ dominated size structures it could suggest low levels of instream survival from the 0+ to 1+ age classes and should be expected to result in reduced contribution to regional smolt production.

Major changes in size structure of juvenile salmon communities were observed post-flood. Slopes of $MN_{\%}$ relationships became negative in 2015 at all streams, and a major shift in the dominance hierarchy of salmon occurred, with 0+ individuals becoming numerically dominant over 1+ individuals at all streams until 2017. This shift in dominance from larger to smaller fish is consistent with timing-based flood effects. Summer floods are likely to impact at least two generations of juvenile coho salmon and Dolly Varden, based upon their life cycles. However, because both coho salmon (Kovach et al., 2015) and Dolly Varden (Armstrong, 1974) spawn in the autumn, it can be expected that a complete new 0+ generation will hatch in the streams less than one year post-flood. This new source population can then colonise suitable habitats throughout the stream network. The increased abundance of 0+ fish in main channel habitats post-flood, where larger more dominant individuals from previous year classes have been lost, supports the importance of competitive exclusion in controlling juvenile salmon habitat utilisation in GBNP streams. This theory is further supported by the gradual recovery of pre-flood community size structure, with increasing abundance of larger compared to smaller individuals. In contrast, if individuals were all following an evolving niche with increasing size (e.g. Kahler et al., 2001), it might be expected that lower abundance of juvenile salmon would be observed post-flood in habitats preferred by larger juvenile salmon pre-flood; however, this was not the case.

The information-theoretic approach used here identified time since floods and total freshwater prey availability as the most effective predictor variables of juvenile salmon size structure. This study would suggest that as individuals increase in size and establish subsequent generations, the size structure of the population becomes increasingly dominated by larger individuals. The relationship between high total freshwater prey availability and dominance of larger individuals in salmon communities may be linked to increased survival of individuals from smaller size classes to larger size classes. Hence positive mass abundance relationship slopes are observed where stream secondary productivity is high. In contrast, during periods of low prey availability and thus high inter- and intra-specific competition, survival is low. Consequently 0+ fish, which have lower metabolic demands and therefore require less prey to survive, can become dominant over more energetically demanding larger fish (Myrvold and Kennedy, 2015b). These findings offered some support for H_4: juvenile salmon community size structure will be controlled by a combination both direct and indirect effects of the floods, through floods alterations to habitat and freshwater prey availability. However, they also suggest limited importance of slow flow habitat availability to size structure, which elsewhere has been identified as important for salmon populations in general (Herdrich et al., 2018) and juvenile coho salmon (Nickelson et al., 1992) and young of the year and 1+ Dolly Varden (Stewart et al., 2010) in particular. Crucially, following the extreme high-frequency floods habitat availability generally increased (at 3 of the 4 streams; Chapter 3), and as a result may play less of a role as a limiting factor to recovery of juvenile salmon, in comparison to total prey density which declined significantly following the floods.

5.4.5 Salmon resilience

Whilst Dolly Varden abundance increased one year after the floods, salmon communities demonstrated low resistance to the extreme high-frequency summer floods. The communities surveyed in 2015 contained almost no 1+ individuals, which demonstrates limited survival of individuals from 2014’s 0+ and larger cohorts. This low resistance of juvenile salmon communities is consistent with other studies of extreme floods (McCullough, 2003), in which authors have argued that juvenile salmon, alevin and eggs are displaced by flood waters (Milner et al., 2013, Robertson et al., 2015, Milner et al., 2018). Crucially, the present study provides new understanding of post-flood population demographics by highlighting significant impacts to community size structure and significant decreases in condition of surviving individuals. The implications of these findings for ongoing community resilience are major, with decreased juvenile salmon condition individuals have lower survival probabilities (Hostetter et al., 2014) and therefore lower likelihood of recruitment into the breeding population. Without successful recruitment to the adult population, total instream population densities can be expected to decline after which populations may become even less resilient to subsequent disturbance events.

Major declines in the abundance of juvenile coho salmon and Dolly Varden one year post-flood in the low geomorphological complexity system (WPC), where habitat availability was already low, suggests that floods are likely to impact juvenile salmon communities more severely where there is limited availability of slow flow habitat to act as refugia. Indeed, post-flood declines in geomorphological complexity, availability of slow flow habitats, and instream wood abundance (Chapter 3) could further reduce the resilience of stream dwelling juvenile salmon. Whilst speculation about the effects of low geomorphological complexity and habitat availability have been raised in previous studies (Roghair et al., 2002), they have yet to be demonstrated in a study comparing across a habitat complexity gradient as seen here. In the current study the direct ecological impacts of floods appear to have been exacerbated by low habitat complexity at WPC. Furthermore, through physical changes to instream geomorphological complexity caused by flood events, the potential ecological and geomorphological impact of future flood events may be increased. It is likely, therefore, that where ecosystems experience activities (anthropogenic) that reduce habitat complexity, such as the removal of instream wood or channelization (Jones et al., 2014), there will be a greater risk of fish populations demonstrating low ecological resilience, and thus a much greater risk of localised extinctions.

The observed low resilience of juvenile salmon communities, supported through the persistent reported decreases in juvenile salmon condition post-flood and the slow recovery of community size structure, extends our understanding of extreme floods impacts to salmon communities from the past focus on recovery of total abundance often reported. These persistent impacts contrast with reports of recovery, and thus high resilience, as a result of increased density (predominantly from the 0+ cohort) one-year post-flood in studies of extreme floods in North American streams (Roghair et al., 2002, George et al., 2015). However, such evidence for a temporal delay in recovery is consistent with the life histories of both coho salmon and Dolly Varden (De Groot, 1993, Stewart et al., 2010). At high latitudes both species spend typically spend two years rearing instream, and thus impacts to a generation due to the floods must persist for multiple years until recovery occurs. This study provides further support for arguments made for the need to consider a number of metrics of ecological stability to understand ecological response to disturbance events proposed by Donohue et al. (2013) and Donohue et al. (2016). Additionally, it suggests that even the multidimensional approach to ecological stability proposed by Donohue and applied in a range of experimental analyses subsequently (Donohue et al., 2013, Hillebrand et al., 2018, Radchuk et al., 2019) is insufficient and multidimensional approaches to stability must not only consider community composition but also population and community size structure.

In addition, increased post-flood 0+ cohort density may be the result of increased relative survival, due to reduced competition (Pess et al., 2011) and hence access to better feeding positions in systems which no longer support larger (dominant) cohorts, as observed in the current study. Only where sufficient survival from this abundant 0+ generation occurs, to replace the lost older cohorts, should a community be considered to have recovered. Indeed, in this study two new generations, spawned in autumn 2014 and 2015, were necessary before a significant response in population size structure was observed.

The low survival from 0+ to older cohorts was likely to be the result of direct and ongoing indirect geomorphological and ecological effects of the floods on habitat and prey availability. Crucially Dolly Varden CPUE decreased markedly at all streams one year post-flood which would be consistent with a significant direct effect of floods on fish. At all streams in this study channel positional persistence decreased during and remained lower post-flood (Chapter 3) than observed pre-flood, and freshwater prey density had only recovered by two years post-flood (Chapter 4). Whilst low habitat stability is thought to particularly impact juvenile coho salmon (Nickelson et al., 1992), reduced prey availability (Herdrich et al., 2018) is expected to be partially responsible for not only reduced survival from one age class to the next, but also the reported decline in fish condition.

Crucially, the current study was focussed on natural streams, which, whilst varying in their geomorphological complexities and catchment age, do not experience significant direct anthropogenic pressure. Even within these streams there appears to be variation in response to extreme floods, between higher and lower complexity streams. Higher geomorphological complexity streams demonstrated higher resilience of fish abundance than lower complexity streams. However, a necessary next step in developing our understanding is to extend approaches applied here to study juvenile salmon communities in anthropogenically impacted systems. In such systems it is possible that floods could act synergistically or antagonistically with other anthropogenic pressures (Buma, 2015, Folt et al., 1999, Ormerod et al., 2010). This study suggests the increasing frequency of extreme floods (Wouter et al., 2017) has the capacity to threaten economically and ecologically important fish species globally by altering trophic interactions and community size structure as well as decreasing fish condition.

5.5 Conclusion

This chapter demonstrates the capacity of high-frequency floods to substantially alter trophic interactions, fish condition and size structure in juvenile salmonid communities. As such it demonstrates the potential limitations of past approaches to assessing salmonid resilience to extreme floods. By utilising comprehensive data sets this study demonstrates persistent negative impact to the salmonid community. Changing prey selection is directly linked to changing total prey availability. Whilst community size structure can be effectively explained by variables times since flood and total prey density. Given the regularly reported shifts in benthic macroinvertebrate community composition following extreme hydrological disturbance events, this study suggests that shifts in prey selection and potentially feeding behaviour associated with disturbances may be relatively common features of salmonid response to floods. As such it identifies an important field of research which must be further explored to fully elucidate juvenile salmonid response to extreme floods.

5.6 References

ADAMS, S. M., MCLEAN, R. B. & HUFFMAN, M. M. 1982. Structuring of a Predator Population Through Temperature-Mediated Effects on Prey Availability. *Canadian Journal of Fisheries and Aquatic Sciences,* 39**,** 1175-1184.

AKAIKE, H. 1992. Information Theory and an Extension of the Maximum Likelihood Principle. *In:* KOTZ, S. & JOHNSON, N. L. (eds.) *Breakthroughs in Statistics: Foundations and Basic Theory.* New York, NY: Springer New York.

ANDERSEN, T., CRANSTON, P. S. & EPLER, J. H. 2017. *Chironomidae of the Holarctic Region: Keys and Diagnoses, Part 1: Larvae*, Entomological Society of Lund, Sweden.

ARMSTRONG, R. H. 1974. Migration of Anadromous Dolly Varden (Salvelinus malma) in Southeastern Alaska. *Journal of the Fisheries Research Board of Canada,* 31**,** 435-444.

BARTELS, P., CUCHEROUSSET, J., STEGER, K., EKLÖV, P., TRANVIK, L. J. & HILLEBRAND, H. 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology,* 93**,** 1173-1182.

BATTIN, J., WILEY, M. W., RUCKELSHAUS, M. H., PALMER, R. N., KORB, E., BARTZ, K. K. & IMAKI, H. 2007. Projected impacts of climate change on salmon habitat restoration. *Proceedings of the National Academy of Sciences,* 104**,** 6720-6725.

BELL, E. & DUFFY, W. G. 2007. Previously Undocumented Two-Year Freshwater Residency of Juvenile Coho Salmon in Prairie Creek, California. *Transactions of the American Fisheries Society,* 136**,** 966-970.

BENKE, A. C., HURYN, A. D., SMOCK, L. A. & WALLACE, J. B. 1999. Length-Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States. *Journal of the North American Benthological Society,* 18**,** 308-343.

BROOKS, S., LANGDON, P. & HEIRI, O. 2008. *The Identification and Use of Palaearctic Chironomidae Larvae in Palaeoecology*.

BROWN, L. E. & MILNER, A. M. 2012. Rapid loss of glacial ice reveals stream community assembly processes. *Global Change Biology,* 18**,** 2195-2204.

BUMA, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere,* 6**,** art70.

BURNHAM, K. P. & ANDERSON, D. R. 2002. *Model selection and multimodel inference: A practical information-theoretic approach,* New York, NY, Springer.

CHAPIN, F. S., WALKER, L. R., FASTIE, C. L. & SHARMAN, L. C. 1994. Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska. *Ecological Monographs,* 64**,** 149-175.

CLITHEROW, L. R. 2016. *Terrestrial-Aquatic Food Web Linkages across Floodplains of Different Ages, Glacier Bay, Alaska.* PhD, University of Birmingham.

COLLINS, S. F., BAXTER, C. V., MARCARELLI, A. M. & WIPFLI, M. S. 2016. Effects of experimentally added salmon subsidies on resident fishes via direct and indirect pathways. *Ecosphere,* 7**,** e01248.

COSTA, J. E. & O'CONNOR, J. E. 1995. Geomorphically Effective Floods. *Natural and Anthropogenic Influences in Fluvial Geomorphology.* American Geophysical Union.

DE GROOT, S. J. 1993. *Pacific salmon life histories*.

DEATH, R. G., FULLER, I. C. & MACKLIN, M. G. 2015. Resetting the river template: the potential for climate-related extreme floods to transform river geomorphology and ecology. *Freshwater Biology,* 60**,** 2477-2496.

DILL, L. M., YDENBERG, R. C. & FRASER, A. H. G. 1981. Food abundance and territory size in juvenile coho salmon (Oncorhynchus kisutch). *Canadian Journal of Zoology,* 59**,** 1801-1809.

DONOHUE, I., HILLEBRAND, H., MONTOYA, J. M., PETCHEY, O. L., PIMM, S. L., FOWLER, M. S., HEALY, K., JACKSON, A. L., LURGI, M., MCCLEAN, D., O'CONNOR, N. E., O'GORMAN, E. J. & YANG, Q. 2016. Navigating the complexity of ecological stability. *Ecology Letters,* 19**,** 1172-1185.

DONOHUE, I., PETCHEY, O. L., MONTOYA, J. M., JACKSON, A. L., MCNALLY, L., VIANA, M., HEALY, K., LURGI, M., O'CONNOR, N. E. & EMMERSON, M. C. 2013. On the dimensionality of ecological stability. *Ecology Letters,* 16**,** 421-429.

DOSSENA, M., YVON-DUROCHER, G., GREY, J., MONTOYA, J. M., PERKINS, D. M., TRIMMER, M. & WOODWARD, G. 2012. Warming alters community size structure and ecosystem functioning. *Proceedings of the Royal Society B: Biological Sciences,* 279**,** 3011-3019.

EATON, E. R. & KAUFMAN, K. 2007. *Field Guide to Insects of North America*, Houghton Mifflin Harcourt.

EBERLE, L. C. & STANFORD, J. A. 2010. Importance and seasonal availability of terrestrial invertebrates as prey for juvenile salmonids in floodplain spring brooks of the Kol River (Kamchatka, Russian Federation). *River Research and Applications,* 26**,** 682-694.

ELLIOT, S. T. & ARMSTRONG, R. H. 1972. A Study of Dolly Varden in Alaska. . *In:* GAME, A. D. O. F. A. (ed.).

ELLIOTT, J. M., HURLEY, M. A. & ELLIOTT, J. A. 1997. Variable Effects of Droughts on the Density of a Sea-Trout Salmo trutta Population Over 30 Years. *Journal of Applied Ecology,* 34**,** 1229-1238.

ENGSTROM, D. R., FRITZ, S. C., ALMENDINGER, J. E. & JUGGINS, S. 2000. Chemical and biological trends during lake evolution in recently deglaciated terrain. *Nature,* 408**,** 161-166.

FASTIE, C. L. 1995. Causes and Ecosystem Consequences of Multiple Pathways of Primary Succession at Glacier Bay, Alaska. *Ecology,* 76**,** 1899-1916.

FAUSCH, K. D. & WHITE, R. J. 1986. Competition among Juveniles of Coho Salmon, Brook Trout, and Brown Trout in a Laboratory Stream, and Implications for Great Lakes Tributaries. *Transactions of the American Fisheries Society,* 115**,** 363-381.

FIELD, W. O. 1937. Observations on Alaskan Coastal Glaciers in 1935. *Geographical Review,* 27**,** 63-81.

FOLT, C. L., CHEN, C. Y., MOORE, M. V. & BURNAFORD, J. 1999. Synergism and antagonism among multiple stressors. *Limnology and Oceanography,* 44**,** 864-877.

FOX, J. & WEISBERG, S. 2011. *An {R} Companion to Applied Regression,* Thousand Oaks CA, Sage.

FRITZ, S. C., ENGSTROM, D. R. & JUGGINS, S. 2004. Patterns of early lake evolution in boreal landscapes: a comparison of stratigraphic inferences with a modern chronosequence in Glacier Bay, Alaska. *Holocene,* 14**,** 828-840.

GARBE, J., BEEVERS, L. & PENDER, G. 2016. The interaction of low flow conditions and spawning brown trout (Salmo trutta) habitat availability. *Ecological Engineering,* 88**,** 53-63.

GEORGE, S. D., BALDIGO, B. P., SMITH, A. J. & ROBINSON, G. R. 2015. Effects of extreme floods on trout populations and fish communities in a Catskill Mountain river. *Freshwater Biology,* 60**,** 2511-2522.

GISLASON, G., LAM, E., KNAPP, G. & GUETTABI, M. 2017. Economic Impacts of Pacific Salmon Fisheries. Voncouver, Canda: Pacific Salmon Commision.

GOERTLER, P., JONES, K., CORDELL, J., SCHREIER, B. & SOMMER, T. 2018. Effects of Extreme Hydrologic Regimes on Juvenile Chinook Salmon Prey Resources and Diet Composition in a Large River Floodplain. *Transactions of the American Fisheries Society,* 147**,** 287-299.

HALL, D. K., BENSON, C. S. & FIELD, W. O. 1995. Changes of Glaciers in Glacier Bay, Alaska, Using Ground and Satellite Measurements. *Physical Geography,* 16**,** 27-41.

HARLEY, C. D. G., RANDALL HUGHES, A., HULTGREN, K. M., MINER, B. G., SORTE, C. J. B., THORNBER, C. S., RODRIGUEZ, L. F., TOMANEK, L. & WILLIAMS, S. L. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters,* 9**,** 228-241.

HASSAN, M. A., GOTTESFELD, A. S., MONTGOMERY, D. R., TUNNICLIFFE, J. F., CLARKE, G. K. C., WYNN, G., JONES-COX, H., POIRIER, R., MACISAAC, E., HERUNTER, H. & MACDONALD, S. J. 2008. Salmon-driven bed load transport and bed morphology in mountain streams. *Geophysical Research Letters,* 35.

HENSCHEL, J. R., MAHSBERG, D. & STUMPF, H. 2001. Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. *Oikos,* 93**,** 429-438.

HERDRICH, A. T., WINKELMAN, D. L., VENARSKY, M. P., WALTERS, D. M. & WOHL, E. 2018. The loss of large wood affects rocky mountain trout populations. *Ecology of Freshwater Fish,* 27**,** 1023-1036.

HEYWOOD, M. J. T. & WALLING, D. E. 2007. The sedimentation of salmonid spawning gravels in the Hampshire Avon catchment, UK: implications for the dissolved oxygen content of intragravel water and embryo survival. *Hydrological Processes,* 21**,** 770-788.

HILLEBRAND, H., LANGENHEDER, S., LEBRET, K., LINDSTRÖM, E., ÖSTMAN, Ö. & STRIEBEL, M. 2018. Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters,* 21**,** 21-30.

HOLTBY, L. B., MCMAHON, T. E. & SCRIVENER, J. C. 1989. Stream Temperatures and Inter-Annual Variability in the Emigration Timing of Coho Salmon (Oncorhynchus kisutch) Smolts and fry and Chum Salmon (O. Keta) Fry from Carnation Creek, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences,* 46**,** 1396-1405.

HOSTETTER, N. J., COLLIS, K., ROBY, D. D. & LOGE, F. J. 2014. Relationship between Juvenile Fish Condition and Survival to Adulthood in Steelhead *Transactions of the American Fisheries Society,* 143**,** 899-909.

HURVICH, C. M. & TSAI, C.-L. 1989. Regression and time series model selection in small samples. *Biometrika,* 76**,** 297-307.

IMRE, I., GRANT, J. W. A. & KEELEY, E. R. 2004. The Effect of Food Abundance on Territory Size and Population Density of Juvenile Steelhead Trout (Oncorhynchus mykiss). *Oecologia,* 138**,** 371-378.

ISAAK, D. J., LUCE, C. H., RIEMAN, B. E., NAGEL, D. E., PETERSON, E. E., HORAN, D. L., PARKES, S. & CHANDLER, G. L. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications,* 20**,** 1350-1371.

JEFFRES, C. A., OPPERMAN, J. J. & MOYLE, P. B. 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. *Environmental Biology of Fishes,* 83**,** 449-458.

JENSEN, A. J. & JOHNSEN, B. O. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic Salmon (Salmo salar) and Brown Trout (Salmo trutta). *Functional Ecology,* 13**,** 778-785.

JOHNSON, J. H. & RINGLER, N. H. 1980. Diets of juvenile coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri) relative to prey availability. *Canadian Journal of Zoology,* 58**,** 553-558.

JONES, K. K., ANLAUF-DUNN, K., S. JACOBSEN, P., STRICKLAND, M., TENNANT, L. & E. TIPPERY, S. 2014. *Effectiveness of Instream Wood Treatments to Restore Stream Complexity and Winter Rearing Habitat for Juvenile Coho Salmon*.

JONSSON, B. & JONSSON, N. 2009. A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. *Journal of Fish Biology,* 75**,** 2381-2447.

JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E. 1989. The Flood Pulse Concept in River-Floodplain Systems. *Canadian Special Publication of Fisheries and Aquatic Science,* 106**,** 110 - 127.

KAHLER, T. H., RONI, P. & QUINN, T. P. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences,* 58**,** 1947-1956.

KAWAGUCHI, Y. & NAKANO, S. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. *Freshwater Biology,* 46**,** 303-316.

KEEFER, M. L. & CAUDILL, C. C. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. *Reviews in Fish Biology and Fisheries,* 24**,** 333-368.

KERR, S. R. & DICKIE, L. M. 2001. *The biomass spectrum : a predator-prey theory of aqautic production,* New York ; Chichester, Columbia University Press.

KLAAR, M. J. 2010. *The development of geomorphic and hydraulic complexity within streams and its influence on fish communtiites following glacial recession in Glacier Bay, Alaska.* DOCTOR OF PHILOSOPHY, The University of Birmingham.

KLAAR, M. J., HILL, D. F., MADDOCK, I. & MILNER, A. M. 2011. Interactions between instream wood and hydrogeomorphic development within recently deglaciated streams in Glacier Bay National Park, Alaska. *Geomorphology,* 130**,** 208-220.

KLAAR, M. J., MADDOCK, I. & MILNER, A. M. 2009. The Development of Hydraulic and Geomorphic Complexity in Recently Formed Streams in Glacier Bay National Park, Alaska. *River Research and Applications,* 25**,** 1331-1338.

KOSKI, K. V. 2009. The fate of coho salmon nomads: the story of an estuarine-rearing strategy promoting resilience. *Ecology and Society,* 14(1).

KOVACH, R. P., ELLISON, S. C., PYARE, S. & TALLMON, D. A. 2015. Temporal patterns in adult salmon migration timing across southeast Alaska. *Global Change Biology,* 21**,** 1821-1833.

LAMBERTI, G. A., GREGORY, S. V., ASHKENAS, L. R., WILDMAN, R. C. & MOORE, K. M. S. 1991. Stream Ecosystem Recovery Following a Catastrophic Debris Flow. *Canadian Journal of Fisheries and Aquatic Sciences,* 48**,** 196-208.

LEDGER, M. E. & MILNER, A. M. 2015. Extreme events in running waters. *Freshwater Biology,* 60**,** 2455-2460.

LISI, P. J., SCHINDLER, D. E., BENTLEY, K. T. & PESS, G. R. 2013. Association between geomorphic attributes of watersheds, water temperature, and salmon spawn timing in Alaskan streams. *Geomorphology,* 185**,** 78-86.

MALMON, D. V., RENEAU, S. L. & DUNNE, T. 2004. Sediment sorting and transport by flash floods. *Journal of Geophysical Research: Earth Surface,* 109.

MANTUA, N., TOHVER, I. & HAMLET, A. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. *Climatic Change,* 102**,** 187-223.

MCCULLOUGH, B. J. 2003. Effects of Floods on Brook Trout Populations in the Monongahela National Forest, West Virginia AU - Carline, Robert F. *Transactions of the American Fisheries Society,* 132**,** 1014-1020.

MEEHAN, W. R. & MILLER, R. A. 1978. Stomach Flushing: Effectiveness and Influence on Survival and Condition of Juvenile Salmonids. *Journal of the Fisheries Research Board of Canada,* 35**,** 1359-1363.

MERRITT, R. W. & CUMMINS, K. W. 1996. *An introduction to the aquatic insects of North America*, Kendall Hunt.

MILNER, A. M. 1987. Colonization and ecological development of new streams in Glacier Bay National Park, Alaska. *Freshwater Biology,* 18**,** 53-70.

MILNER, A. M. & BAILEY, R. G. 1989. Salmonid colonization of new streams in Glacier Bay National Park Alaska USA. *Aquaculture and Fisheries Management,* 20**,** 179-192.

MILNER, A. M., FASTIE, C. L., CHAPIN, F. S., ENGSTROM, D. R. & SHARMAN, L. C. 2007. Interactions and linkages among ecosystems during landscape evolution. *Bioscience,* 57**,** 237-247.

MILNER, A. M., KNUDSEN, E. E., SOISETH, C., ROBERTSON, A. L., SCHELL, D., PHILLIPS, I. T. & MAGNUSSON, K. 2000. Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences,* 57**,** 2319-2335.

MILNER, A. M., PICKEN, J. L., KLAAR, M. J., ROBERTSON, A. L., CLITHEROW, L. R., EAGLE, L. & BROWN, L. E. 2018. River ecosystem resilience to extreme flood events. *Ecology and Evolution,* 0.

MILNER, A. M., ROBERTSON, A. L., BROWN, L. E., SØNDERLAND, S. H., MCDERMOTT, M. & VEAL, A. J. 2011. Evolution of a stream ecosystem in recently deglaciated terrain. *Ecology,* 92**,** 1924-1935.

MILNER, A. M., ROBERTSON, A. L., MCDERMOTT, M. J., KLAAR, M. J. & BROWN, L. E. 2013. Major flood disturbance alters river ecosystem evolution. *Nature Climate Change,* 3**,** 137-141.

MILNER, A. M., ROBERTSON, A. L., MONAGHAN, K. A., VEAL, A. J. & FLORY, E. A. 2008. Colonization and development of an Alaskan stream community over 28 years. *Frontiers in Ecology and the Environment,* 6**,** 413-419.

MING-CHIH, C. & MEI-HWA, K. 2012. Application of r/K selection to macroinvertebrate responses to extreme floods. *Ecological Entomology,* 37**,** 145-154.

MYRVOLD, K. M. & KENNEDY, B. P. 2015a. Density dependence and its impact on individual growth rates in an age-structured stream salmonid population. *Ecosphere,* 6**,** 1-16.

MYRVOLD, K. M. & KENNEDY, B. P. 2015b. Interactions between body mass and water temperature cause energetic bottlenecks in juvenile steelhead. *Ecology of Freshwater Fish,* 24**,** 373-383.

NAKANO, S. 1995. Competitive interactions for foraging microhabitats in a size-structured interspecific dominance hierarchy of two sympatric stream salmonids in a natural habitat. *Canadian Journal of Zoology,* 73**,** 1845-1854.

NAKANO, S., FAUSCH, K. D. & KITANO, S. 1999. Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *Journal of Animal Ecology,* 68**,** 1079-1092.

NAKANO, S. & KAERIYAMA, M. 1995. Summer Microhabitat Use and Four Sympatric Stream-dwelling Salmonids in a Kamchatkan Stream. *Fisheries science,* 61**,** 926-930.

NAKANO, S. & MURAKAMI, M. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences,* 98**,** 166-170.

NEHLSEN, W., WILLIAMS, J. E. & LICHATOWICH, J. A. 1991. Pacific Salmon at the Crossroads: Stocks at Risk from California, Oregon, Idaho, and Washington. *Fisheries,* 16**,** 4-21.

NICKELSON, T. E., RODGERS, J. D., JOHNSON, S. L. & SOLAZZI, M. F. 1992. Seasonal Changes in Habitat Use by Juvenile Coho Salmon (Oncorhynchus kisutch) in Oregon Coastal Streams. *Canadian Journal of Fisheries and Aquatic Sciences,* 49**,** 783-789.

NIELSEN, J. L. 1992. Microhabitat-Specific Foraging Behavior, Diet, and Growth of Juvenile Coho Salmon AU - Nielsen, Jennifer L. *Transactions of the American Fisheries Society,* 121**,** 617-634.

NISLOW, K. H., FOLT, C. & SEANDEL, M. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences,* 55**,** 116-127.

ORMEROD, S. J., DOBSON, M., HILDREW, A. G. & TOWNSEND, C. R. 2010. Multiple stressors in freshwater ecosystems. *Freshwater Biology,* 55**,** 1-4.

PASTERNACK, G. B. & WYRICK, J. R. 2017. Flood-driven topographic changes in a gravel-cobble river over segment, reach, and morphological unit scales. *Earth Surface Processes and Landforms,* 42**,** 487-502.

PEARSONS, T. N., LI, H. W. & LAMBERTI, G. A. 1992. Influence of Habitat Complexity on Resistance to Flooding and Resilience of Stream Fish Assemblages. *Transactions of the American Fisheries Society,* 121**,** 427-436.

PESS, G. R., KIFFNEY, P. M., LIERMANN, M. C., BENNETT, T. R., ANDERSON, J. H. & QUINN, T. P. 2011. The Influences of Body Size, Habitat Quality, and Competition on the Movement and Survival of Juvenile Coho Salmon during the Early Stages of Stream Recolonization. *Transactions of the American Fisheries Society,* 140**,** 883-897.

PINAY, G., C. O'KEEFE, T., T. EDWARDS, R. & J. NAIMAN, R. 2009. *Nitrate removal in the hyporheic zone of a salmon river in Alaska*.

PINIEWSKI, M., PRUDHOMME, C., ACREMAN, M. C., TYLEC, L., OGLĘCKI, P. & OKRUSZKO, T. 2017. Responses of fish and invertebrates to floods and droughts in Europe. *Ecohydrology,* 10**,** e1793.

POFF, N. L. 1997. Landscape Filters and Species Traits: Towards Mechanistic Understanding and Prediction in Stream Ecology. *Journal of the North American Benthological Society,* 16**,** 391-409.

POFF, N. L. 2002. Ecological response to and management of increased flooding caused by climate change. *Philosophical Transactions of the Royal Society of London. Series A: Mathematical, Physical and Engineering Sciences,* 360**,** 1497-1510.

POFF, N. L., ALLAN, J. D., BAIN, M. B., KARR, J. R., PRESTEGAARD, K. L., RICHTER, B. D., SPARKS, R. E. & STROMBERG, J. C. 1997. The Natural Flow Regime. *BioScience,* 47**,** 769-784.

POFF, N. L., OLDEN, J. D., VIEIRA, N. K. M., FINN, D. S., SIMMONS, M. P. & KONDRATIEFF, B. C. 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society,* 25**,** 730-755.

R-CORE-TEAM 2017. R: A language and environment for statistical computing. . Vienna, Austria.: R Foundation for Statistical Computing.

RADCHUK, V., LAENDER, F. D., CABRAL, J. S., BOULANGEAT, I., CRAWFORD, M., BOHN, F., RAEDT, J. D., SCHERER, C., SVENNING, J.-C., THONICKE, K., SCHURR, F. M., GRIMM, V. & KRAMER-SCHADT, S. 2019. The dimensionality of stability depends on disturbance type. *Ecology Letters,* 0.

RADER, R. B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences,* 54**,** 1211-1234.

RICKER, W. E. 1975. *Computation and Interpretation of Biological Statistics of Fish Populations*.

ROBERTSON, A. L., BROWN, L. E., KLAAR, M. J. & MILNER, A. M. 2015. Stream ecosystem responses to an extreme rainfall event across multiple catchments in southeast Alaska. *Freshwater Biology,* 60**,** 2523-2534.

ROGHAIR, C. N. & DOLLOFF, C. A. 2005. Brook Trout Movement during and after Recolonization of a Naturally Defaunated Stream Reach. *North American Journal of Fisheries Management,* 25**,** 777-784.

ROGHAIR, C. N., DOLLOFF, C. A. & UNDERWOOD, M. K. 2002. Response of a Brook Trout Population and Instream Habitat to a Catastrophic Flood and Debris Flow. *Transactions of the American Fisheries Society,* 131**,** 718-730.

RUCKELSHAUS, M. H., LEVIN, P., JOHNSON, J. B. & KAREIVA, P. M. 2002. The Pacific Salmon Wars: What Science Brings to the Challenge of Recovering Species. *Annual Review of Ecology and Systematics,* 33**,** 665-706.

SCHARF, F. S., BUCKEL, J. A., JUANES, F. & CONOVER, D. O. 1998. Predation by juvenile piscivorous bluefish (Pomatomus saltatrix): the influence of prey to predator size ratio and prey type on predator capture success and prey profitability. *Canadian Journal of Fisheries and Aquatic Sciences,* 55**,** 1695-1703.

SCRIMGEOUR, G. J. & TOWNSEND, G. D. 1996. Simulated Fine Woody Debris Accumulations in a Stream Increase Rainbow Trout Fry Abundance AU - Culp, Joseph M. *Transactions of the American Fisheries Society,* 125**,** 472-479.

SHEER, M. B. & STEEL, E. A. 2006. Lost Watersheds: Barriers, Aquatic Habitat Connectivity, and Salmon Persistence in the Willamette and Lower Columbia River Basins. *Transactions of the American Fisheries Society,* 135**,** 1654-1669.

SIDLE, R. C. & MILNER, A. M. 1989. Stream Development in Glacier Bay National Park, Alaska, U.S.A. *Arctic and Alpine Research,* 21**,** 350-363.

SLOAT, M. R., REEVES, G. H. & CHRISTIANSEN, K. R. 2017. Stream network geomorphology mediates predicted vulnerability of anadromous fish habitat to hydrologic change in southeast Alaska. *Global Change Biology,* 23**,** 604-620.

SOMMER, T. R., NOBRIGA, M. L., HARRELL, W. C., BATHAM, W. & KIMMERER, W. J. 2001. Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences,* 58**,** 325-333.

SØNDERLAND, S. H. 2017. *Salmon population in watersheds of different complexities following ice recession in Glacier Bay as determined by the physical habitat template.* Ph.D., University of Birmingham.

STEEL, E. A. 2006. Lost Watersheds: Barriers, Aquatic Habitat Connectivity, and Salmon Persistence in the Willamette and Lower Columbia River Basins AU - Sheer, M. B. *Transactions of the American Fisheries Society,* 135**,** 1654-1669.

STEWART, D. B., MOCHNACZ, N., D. SAWATZKY, C., CARMICHAEL, T. & REIST, J. 2007. *Fish life history and habitat use in the Northwest Territories: bull trout (Salvelinus confluentus)*.

STEWART, D. B., MOCHNACZ, N. J., REIST, J. D., CARMICHEAL, T. J. & SAWATZKY, D. D. 2010. Fish life history and habitat use in the Northwest Territories: Dolly Varden (*Salvelinus malma*). *Canadian Manuscript Report of Fisheries and Aquatic Sciences 2915.* Canada Winnipeg: Central and Arctic Region Fisheries and Oceans

SUTTLE, K. B., POWER, M. E., LEVINE, J. M. & MCNEELY, C. 2004a. HOW FINE SEDIMENT IN RIVERBEDS IMPAIRS GROWTH AND SURVIVAL OF JUVENILE SALMONIDS. *Ecological Applications,* 14**,** 969-974.

SUTTLE, K. B., POWER, M. E., LEVINE, J. M. & MCNEELY, C. 2004b. How fine sediment in riverbeds impairs growth and survivial of juvenile salmonids *Ecological Applications,* 14**,** 969-974.

SVANBÄCK, R. & BOLNICK, D. I. 2007. Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences,* 274**,** 839-844.

SZUMILAS, M. 2010. Explaining odds ratios. *Journal of the Canadian Academy of Child and Adolescent Psychiatry = Journal de l'Academie canadienne de psychiatrie de l'enfant et de l'adolescent,* 19**,** 227-229.

TAKATA, L., SOMMER, T. R., LOUISE CONRAD, J. & SCHREIER, B. M. 2017. Rearing and migration of juvenile Chinook salmon (Oncorhynchus tshawytscha) in a large river floodplain. *Environmental Biology of Fishes,* 100**,** 1105-1120.

THORP, J. H. & COVICH, A. P. 2009. *Ecology and classification of North American freshwater invertebrates*, Academic press.

TIEGS, S. D., LEVI, P. S., RÜEGG, J., CHALONER, D. T., TANK, J. L. & LAMBERTI, G. A. 2011. Ecological Effects of Live Salmon Exceed Those of Carcasses During an Annual Spawning Migration. *Ecosystems,* 14**,** 598-614.

VENABLES, W. N. & RIPLEY, B. D. 2002. *Modern Applied Statistics with S,* New York, Springer.

WHITE, R. J. 1986. Competition among Juveniles of Coho Salmon, Brook Trout, and Brown Trout in a Laboratory Stream, and Implications for Great Lakes Tributaries AU - Fausch, Kurt D. *Transactions of the American Fisheries Society,* 115**,** 363-381.

WILLSON, M. F. & HALUPKA, K. C. 1995. Anadromous Fish as Keystone Species in Vertebrate Communities. *Conservation Biology,* 9**,** 489-497.

WIPFLI, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences,* 54**,** 1259-1269.

WIPFLI, M. S. & BAXTER, C. V. 2010. Linking Ecosystems, Food Webs, and Fish Production: Subsidies in Salmonid Watersheds. *Fisheries,* 35**,** 373-387.

WITHLER, I. L. 1966. Variability in Life History Characteristics of Steelhead Trout (Salmo gairdneri) Along the Pacific Coast of North America. *Journal of the Fisheries Research Board of Canada,* 23**,** 365-393.

WOOD, J. L. A., GRANT, J. W. A. & BELANGER, M. H. 2012. Population density and territory size in juvenile rainbow trout, Oncorhynchus mykiss: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences,* 69**,** 1121-1128.

WOUTER, R. B., EMMA, E. A., JOSHUA, R. L., RALPH, T. & ROSS, A. W. 2017. Recent changes in extreme floods across multiple continents. *Environmental Research Letters,* 12**,** 114035.

6. Extreme floods reduce river invertebrate beta-diversity and resilience to further floods.

6.1 Introduction

Climate and weather driven disturbance events, including floods, are becoming more frequent with the increasing pressure of anthropogenic climate change (Trenberth, 2011, Berg et al., 2013, Diffenbaugh et al., 2015, Wouter et al., 2017). Floods represent one end of the spectrum of water availability and have the capacity to drive major changes in the geomorphology and ecology of stream ecosystems (e.g. Poff et al., 1997). Floods can be defined by five critical components; magnitude, frequency, duration, timing, and rate of change of hydrologic conditions (Poff et al., 1997), which together provide a description of the form of a given flood. Individual extreme floods (defined here as rare or unusual weather or climatic driven flood occurrence (sensu Ledger and Milner, 2015)) have been shown to drive significantly different responses in geomorphology and ecology, such as the loss of non-insects and persistent alterations to community composition (e.g. Herbst and Cooper, 2010, Milner et al., 2013, Szczerkowska-Majchrzak et al., 2014, Woodward et al., 2015). This variation has been linked to differences in the form of each flood event and the catchment in which it occurs (e.g. Roghair et al., 2002, Milner et al., 2013, George et al., 2015).

One critical component, the timing of a flood event, has been identified as particularly important in controlling ecological response to disturbances (Crawley, 2004, Li and Pennings, 2017). Within a single stream, floods of different timings are likely to impact taxa within an ecosystem to differing extents. When a flood coincides with a particularly susceptible period of a taxon’s life cycle it can be expected to have a greater effect. For example, the effects of bed mobilising floods on salmon populations are likely to be more pronounced when eggs or alevins are present in bed sediments (Lapointe et al., 2000). These early life stages lack mobility and cannot resist high flows and thus are more likely than other life stages to be displaced or suffer mortality. Salmon species breed at different times of the year (Burger et al., 1985, Ford et al., 2006), and therefore individual floods can impact populations of one species to a greater extent than another within the same system (George et al., 2015). Similar timing based variations in the effect of floods on benthic macroinvertebrate taxa should also be expected, because their life cycles often include aquatic and aerial stages which influence instream population densities (Reich and Downes, 2004). Where floods disrupt these lifecycles most we should expect the greatest effect on a population.

In addition to differing effects of disturbance across species, similarly timed floods could have different impacts across a species' range, because the timing of life history events often varies geographically (Burger et al., 1985), depending upon antecedent environmental conditions. In addition differences in local habitat and resource conditions could alter a flood's impact (Lake, 2000) within communities at small spatial scales ($<10^0$ m^2). Diversity approaches can elucidate these differences in how disturbances, which can act locally (such as floods) on communities (alpha diversity) and therefore modify biodiversity patterns at broader (between catchment/regional) spatial scales (beta-diversity). Beta-diversity is generally defined as the dissimilarity of species/taxa identities between samples (Anderson et al., 2011). In spite of its capacity to identify change, few studies have addressed beta-diversity response to floods (Bozelli et al., 2015).

The rising frequency of extreme disturbance events (Wouter et al., 2017) increases the likelihood of sequences (Vieira et al., 2004, Calderon et al., 2017) and/or the co-occurrence (Rahel and Olden, 2008) of extreme disturbance events (Wilson et al., 2006), which could drive additive and non-linear impacts in ecosystems (Eklöf et al., 2009). Disturbances can create system wide legacy effects (Seidl et al., 2014) which can alter how ecosystems reassemble (Ledger et al., 2006) and hence respond to subsequent disturbances (Buma and Wessman, 2011, Stanley et al., 2010). One important example of legacy effects following floods is the reduced stability of post-flood geomorphological conditions during which increased sediment availability drives ongoing geomorphological change (Milan, 2012). Importantly, such change can alter available niche space within an ecosystem and may have lasting effects on community composition (Robinson et al., 2018). Further, recolonization by pre-flood taxa may be linked to their dispersal capacity which can act as a crucial limiting factor in ecological responses to disturbance (Brown et al., 2018). These temporal extensions of flood effects have been reported to last for over a decade in some species (e.g. Kappes and Haase, 2012).

A factor limiting the number of multiple disturbance studies in lotic systems is the difficulty of studying unpredictable events in natural systems. Given this difficulty and the subsequent rarity of studies of sequences of floods, it is crucial to exploit all available opportunities to develop our understanding of multiple disturbance effects in lotic systems. In November 2005, Glacier Bay National Park and Preserve (GBNP) experienced an extreme rain on snow hydrological event which caused significant floods (>1 in 100 year; Milner et al., 2013, Robertson et al., 2015). Subsequently in 2014 heavy and sustained precipitation, associated with the Pacific blob (Bond et al., 2015), resulted in one of the wettest summers on record across southeast Alaska - the wettest in a 30-year record for GBNP. This sustained precipitation drove extreme high-frequency floods throughout July and August (Chapter 2) leading to geomorphological (Chapter 3) and biotic community (Chapter 4) change in streams across the park. This sequence of extreme events provided a rare opportunity to study the effect of multiple disturbances on lotic systems. The effects of this sequence of floods on one stream (WPC low geomorphic complexity) was examined by Milner et al. (2018). In this chapter, two additional streams were added to this data set for analysis (IVS and BBS), representing streams of intermediate and higher geomorphological complexity respectively (Table 6.1).

This chapter aims to compare the response of the stream benthic macroinvertebrate community to the high-magnitude winter flood of 2005 with the summer recurrent high-frequency floods of 2014 and examine community resilience following these disturbances. Three hypotheses will be tested:

> H_1 Both flood regimes will have driven significant declines in the density and richness of benthic macroinvertebrate taxa (Szczerkowska-Majchrzak et al., 2014, Woodward et al., 2015);
>
> H_2 The summer 2014 high-frequency floods will have caused greater reductions in macroinvertebrate taxa density and richness than the 2005 winter high-magnitude flood due to differences in flood timing and duration and persistence of niche space change (Power and Stewart, 1987, Scrimgeour and Winterbourn, 1989); and
>
> H_3 A sequence of recurrent floods will drive ongoing declines in intra- and inter-stream beta-diversity, as each event excludes additional taxa from stream communities, through alterations to resource availability (Larson et al., 2018) and differential capacity of taxa to recolonise (Brown et al., 2018).

6.2 Methods

6.2.1 Study site

The three streams have in depth and long-term historic geomorphological and biological datasets available. Data collection was established at WPC in the late 1970's (Milner, 1987) and at IVS and BBS by 1997 (Milner et al., 2000). These 2nd or 3rd order streams varied in age by 115 years with riparian vegetation of alder, cottonwood and Sitka spruce (Table 6.1), representing a gradient of terrestrial and lotic geomorphological complexity (Klaar et al., 2009, Klaar et al., 2015).

Table 6.1. Study stream catchment profiles. Adapted from Klaar et al. (2009) and Chapter 3.

Site	Stream age (years)	Stream length (km)	Catchment size (km^2)	Average Discharge (m^3/s)	Stream order	Dominant substrate type	Dominant riparian vegetation
WPC	70	5.6	29.8	2.29	2	Boulder	Alder
IVS	146	8.3	19.2	3.02	2	Cobble	Alder/ cottonwood
BBS	186	7.2	27.3	4.95	3	Gravel	Sitka spruce

6.2.2 Sampling and identification

Stream benthic macroinvertebrate sampling was undertaken in a study reach of ~25 m previously selected for long-term study (Milner et al., 2000). In each study reach a minimum of five benthic macroinvertebrate samples were collected during each sampling event using a modified Surber sampler (0.092 m^2 area; 330 µm mesh). Sampling took place in July, August or early September in 2005 to 2007 and 2013 to 2017. Once collected, samples were preserved onsite in 70 % ethanol. Subsequently these samples were sorted and benthic macroinvertebrates were identified under a binocular microscope to the lowest possible taxonomic level, using the most up to date keys available for North America (Merritt and Cummins, 1996, Thorp and Covich, 2009). Oligochaeta were identified to class. Chironomidae larvae were identified to species group using Brooks et al. (2008), Andersen et al. (2017) and previous versions, under a light microscope.

6.2.3 Data analysis:

All statistical analyses were undertaken in R studio version 1. 1. 456 (R version 3. 5. 1; R-Core-Team, 2017). Benthic macroinvertebrate community responses to the series of extreme flood events was undertaken using the nested sampling design described in Chapter 4. This method considered the three streams combined in an ‘overall’ analysis and as well as each stream in an ‘individual’ analysis. This nested approach was applied to: regression models of taxa richness, Shannon Diversity, Pielou Evenness, total density and beta-diversity, non-metric multidimensional scaling (NMDS) and PERMANOVA analyses of $\log_{10}(+1)$ macroinvertebrate data. NMDS plots of species, ellipsoids of individual years in overall analyses and in individual stream analyses were plotted using 95% confidence ellipsoids of year group centroids using the vegan package (Oksanen et al., 2018). PERMANOVA was used to test for differences between pairwise year comparisons of specific interest. Specifically, overall analyses 2005 against 2006, 2013 and 2017 as well as 2013 against 2017 . A balanced PERMANOVA design was used in this study, because it is robust to differences in within group dispersion and thus can identify responses in group dispersion (Anderson, 2014). Pairwise PERMANOVA were completed in the vegan package and p values were corrected for the multiple testing procedure using the Holm adjustment (Aickin and Gensler, 1996).

Pielou/Shannon's evenness has a value between 0 and 1 where a completely even community has a value of 1 and increasingly uneven (dominated by a subset of taxa) communities have Pielou evenness values approaching 0 and is derived from Shannon's diversity. Beta-diversity was calculated using metrics based on Jaccard's dissimilarity (Jaccard, 1912). Comparisons of both within and between-stream beta-diversity scores were made within each study year. Beta-diversity analyses were undertaken on binary presence-absence data. Two component parts of beta-diversity have been defined; (1) turnover defined as the component of beta-diversity made up of replacement of some species in a community with others, and (2) nestedness made up of the remaining difference in taxonomic richness between samples (Baselga and Orme, 2012). Dissimilarity, turnover and nestedness metrics of beta-diversity were calculated (Baselga, 2010) using the betapart package in R (Baselga et al., 2018).

Generalized linear mixed effects models (GLMM) were constructed using the MASS package (Fox and Weisberg, 2011) and generalized least squares regression (GLS) in R, to test for the effects of each extreme flood events and subsequent recovery on taxa richness, Shannon diversity, Pielou evenness, total density and intra-stream beta-diversity. Taxa richness, Shannon diversity, Pielou evenness and intra-stream beta-diversity models were constructed with Gaussian error distributions. Total density was constructed with a negative binomial error distribution, and since this value was based on overdispersed count data, overdispersion was tested for using an overdispersion function in r. In the 'individual stream' analyses, year of sample collection was used as the explanatory variable. In the 'overall' analyses year of sample collection was used as the fixed effect and stream was applied as a random effect, to account for differences in developmental age, geomorphological complexity (Klaar et al., 2009) and pre-flood community composition (Milner et al., 2000). The presence of temporal autocorrelation in all regression models was explored using the acf in R. Where autocorrelation was identified, in GLMMs, new models were constructed incorporating a correlation structure. This correlation structure accounted for the within-stream between-year autocorrelation observed.

Taxa were classified as a dominant member or rare member of a community based on the total cumulative density of individuals at a site in a given year. A boundary for delineating the core of communities from the taxa at their periphery was set as the 90th percentile of total density as described in Flather and Sieg (2007) based on the argument of Gaston (1994). This allowed observations to be made about changes to the relative importance of taxa which remained in, returned to or joined communities after the floods.

6.3 Results

6.3.1 Individual stream analyses

Total density, Shannon diversity, taxonomic richness and Pielou's evenness demonstrated no significant change following the high-magnitude winter floods at either IVS or BBS (Figure 6.1.; Table 6.2). In addition, no significant response in any metric of the benthic macroinvertebrate community at IVS was observed in response to the 2014 floods as reported in Chapter 4. In contrast at BBS, total density, Shannon's diversity and taxonomic richness demonstrated significant change following the 2014 high-frequency summer floods. Total density declined from 2432 ± 573 inds m^{-2} in 2013 to 174 ± 78 inds m^{-2} in 2015. Shannon's diversity declined from 1.85 ± 0.16 in 2013 to 0.89 ± 0.68 in 2015. Taxonomic richness declined from 15.4 ± 1.3 in 2013 to 4.4 ± 2.8 in 2015. Taxonomic richness (17.4 ± 1.5) and Shannon's diversity (2.31 ± 0.09) recovered to 2013 levels by 2017. In contrast total density failed to recover to pre-flood levels by 2017. NMDS analyses indicate that at both WPC and IVS a core of taxa persisted through the floods, with a decreasing area of annual ellipsoids from 2005 to 2006 (Figure 6.2.b and c). At BBS no major change in ellipsoid position occurred following the 2005 high-magnitude floods (Figure 6.3.d). By 2013, before the high-frequency summer floods, all streams ellipsoids had moved substantially, consistent with post-flood reassembly of communities. Ellipsoid response to the 2014 floods varied. IVS and BBS underwent more substantial shifts in community composition, with little to no overlap between 2013 and 2015 ellipsoids, whereas at WPC a greater degree of overlap remained.

Intra-stream beta-diversity analyses demonstrated significant differences between years. A decline in Jaccard's dissimilarity following the 2005 floods at WPC was observed with a change in mean from 0.69 ± 0.21 (2005) to 0.46 ± 0.09 (2006), whilst no response was observed at IVS or BBS (Figure 6.4.). In contrast following the summer floods of 2014 an increase in intra-stream beta-diversity was observed at BBS, from 0.52 ± 0.10 (2013) to 0.74 ± 0.13 (2015), whilst no significant response was seen at either WPC or IVS. Through time after the 2014 floods all streams demonstrated lower dissimilarity than observed during earlier time periods reaching means of 0.13 ± 0.05 at WPC, 0.56 ± 0.12 at IVS and 0.28 ± 0.06 at BBS, in 2017. This decline in beta-diversity appears to be driven by a decreased role of turnover between samples through time declining from 0.26 ± 0.28, 0.70 ± 0.48 and 0.49 ± 0.09 in 2005 to 0.03 ± 0.06, 0.42 ± 0.15, and 0.21 ± 0.06 in 2017 at WPC, IVS and BBS respectively.

6.3.2 Overall analyses

Significant change in Shannon diversity and Pielou evenness occurred with an increase in mean from0.96 ± 0.81 to 1.50 ± 0.56 and 0.66 ± 0.30 to 0.82 ± 0.09 respectively recorded from 2005 to 2006 (Figure 6.1, Table 6.2). No significant change in either taxonomic richness or total density of benthic macroinvertebrates was observed from 2005 to 2006 (Figure 6.1; Table 2.12.) for all three streams. Mean taxonomic richness increased from 8.1 ± 4.3 (2006) to 10.7 ± 4.4 (2013), which was significantly different to pre-flood richness (7.1 ± 5.1). Total density was significantly different from 2006 and 2013 with an increase from 1152 ± 1441 to 4282 ± 5195 inds m^{-2} and was also significantly different from pre-flood density (2604 ± 3778 inds m^{-2}). Community evenness and Shannon diversity were not significantly different between floods.

Following the 2014 floods (2013 to 2015) significant change in both mean density (4282 ± 5195 to 767 ± 825 inds m^{-2}) and mean taxa richness (10.7 ± 4.38 to 6.5 ± 2.6) of benthic macroinvertebrates were observed. By 2017, taxonomic richness was significantly different to other time periods. Mean richness was higher (12.9 ± 4.1) than during the first pre-flood period (7.1 ± 5.1; 2005). In contrast, total density had recovered to an average of 1733 ± 1736 inds m^{-2}, a similar level to that observed before both the 2005 and 2013 floods. No significant response was observed in Shannon diversity from 2013 to 2015, but a significant difference occurred in 2017 reaching 1.99 ± 0.30, the highest level during any year, with the previous high 1.53 ± 0.42 observed in 2013. No significant response in evenness was observed following the 2014 floods (Figure 6.1).

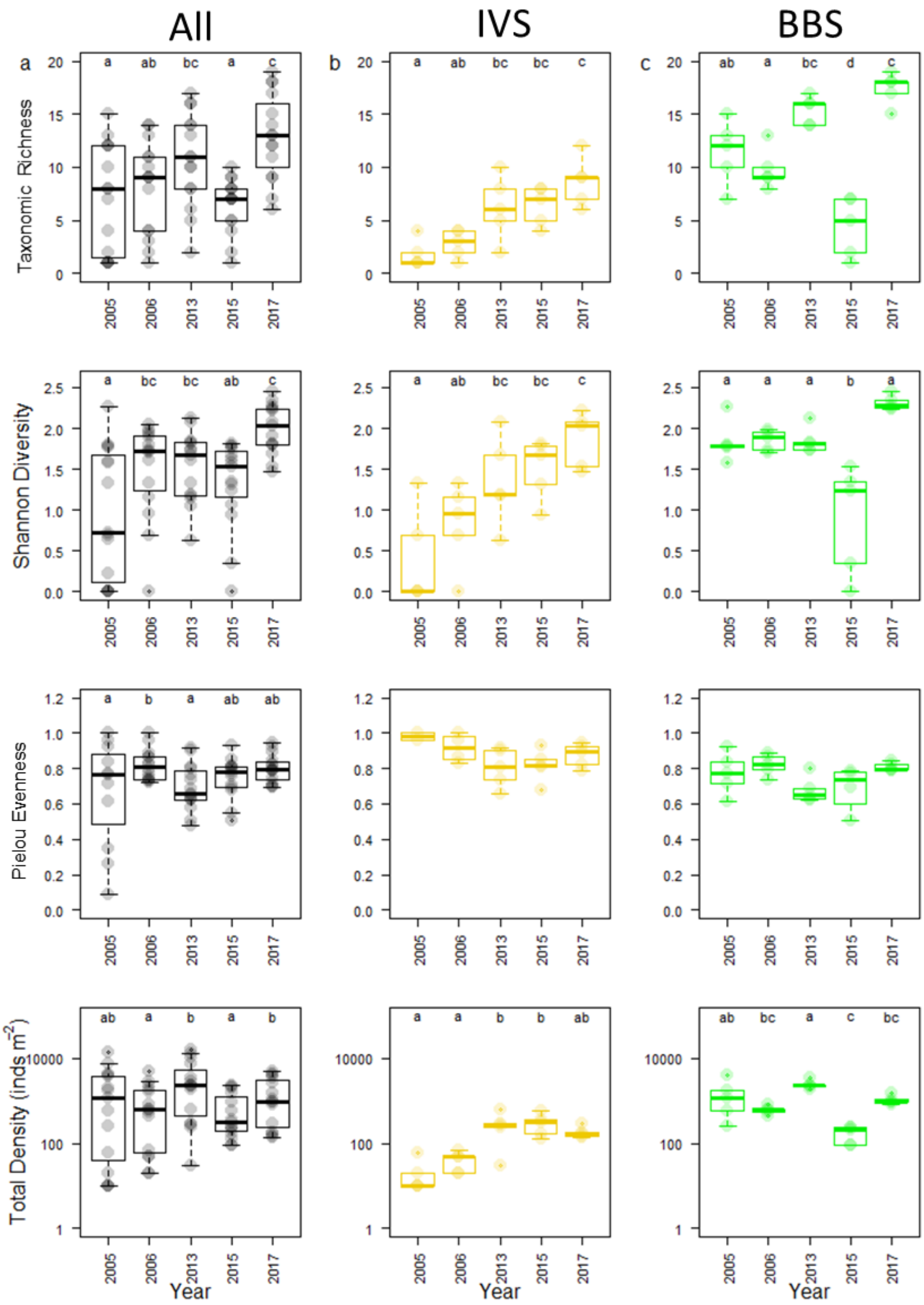

Figure 6.1. Taxonomic richness, Shannon diversity, Pielou evenness and total density of benthic macroinvertebrates through time. Different letters above boxes represent years, which are significantly different from one another at p < 0.05. a) All streams (black), b) IVS (gold), and c) BBS (green).

*Table 6.2. Model outputs for comparisons of taxonomic richness, Shannon diversity, Pielou evenness and total density of benthic macroinvertebrates through the study time periods. F statistics for overall comparisons and pairwise Tukey's test Z stats. $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***. GLMM = Generalized Linear Mixed Effects Model, AC = Autocorrelation, GLS = Generalized Lease Squares Regression. GLM (NB) = Generalized Linear Model with Negative Binomial error distribution.*

		Overall	**WPC**	**IVS**	**BBS**
Taxonomic Richness	Model	GLMM AC	GLS	GLS	GLS
	F	11.65***	3.03*	9.23***	25.90 ***
	05 to 06	-0.90	-2.29	-0.77	1.13
	05 to 13	-3.25*	-1.53	-3.38*	-2.83
	05 to 15	0.60	-0.26	-3.53*	4.96 ***
	05 to 17	-5.18***	-2.80	-5.22***	-4.25 **
	13 to 15	3.85**	1.27	-0.15	7.79 ***
	13 to 17	-1.93	-1.27	-1.84	-1.42
Shannon Diversity	Model	GLMM AC	GLS	GLS	GLS
	F	8.0 ***	9.77***	7.02**	11.71***
	05 to 06	-2.89*	-5.40***	-1.37	-0.06
	05 to 13	-3.06 *	-3.47*	-3.08 *	-0.03
	05 to 15	-1.93	-4.24**	-3.57*	4.42**
	05 to 17	-5.53***	-5.31***	-4.75***	-2.19
	13 to 15	1.14	-0.76	-0.49	4.45**
	13 to 17	-3.60**	-1.84	-1.67	-2.16
Pielou Evenness	Model	GLMM AC	GLS	GLS	GLS
	F	3.5*	5.80**	2.17	2.74
	05 to 06	-2.88*	-4.13**		
	05 to 13	-0.23	-2.49		
	05 to 15	-1.34	-3.96**		
	05 to 17	-2.37	-3.81**		
	13 to 15	-1.22	-1.56		
	13 to 17	-2.34	-1.40		
Total Density (inds m^{-2})	Model	GLMM AC	GLM (NB)	GLM (NB)	GLM (NB)
	F	5.94 ***	5.31 **	5.59 **	7.47 ***
	05 to 06	1.79	1.69	-0.25	2.05
	05 to 13	-2.07	-1.91	-3.26*	-1.97
	05 to 15	2.26	2.18	-3.63 *	3.03 *
	05 to 17	1.07	1.14	-2.04	1.04
	13 to 15	4.33 ***	4.09 **	-0.37	5.01 ***
	13 to 17	3.14 *	3.04 *	1.23	3.01 *

PERMANOVA analyses indicated a significant reduction in community diversity across the three study streams from 2005 to 2006 (Table 6.3), which did not recover before the 2014 floods (2013). Following the 2014 floods a further contraction of diversity of community composition across streams was observed by 2017 where ellipsoid size was the smallest during any time period in this study.

Intra-stream dissimilarity and turnover (metrics of beta-diversity) demonstrated no significant response to the 2005 floods. However, nestedness changed significantly, with mean decreasing from 0.22 ± 0.30 to 0.10 ± 0.08 in 2006 (Table 6.4), the lowest observed during any year. By 2017 dissimilarity and turnover decreased to the lowest observed levels for any year; 0.32 ± 0.19 and 0.22 ± 0.19 respectively.

Table 6.3. PERMANOVA analyses pseudo F stats for overalls and pairwise comparisons. Pairwise comparisons or adjusted for multiple testing using the Holm adjustment.

	All		**2005 - 2006**		**2005 - 2013**		**2005 - 2017**		**2013 - 2017**	
	Year	Stream	Year	Stream	Year	Stream	Year	Stream	Year	Stream
F	6.27	14.01	2.82	8.42	5.00	7.99	9.55	8.07	10.21	14.57
R^2	0.19	0.39	0.07	0.39	0.11	0.36	0.19	0.32	0.16	0.46
p	< 0.001	< 0.001	0.006	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

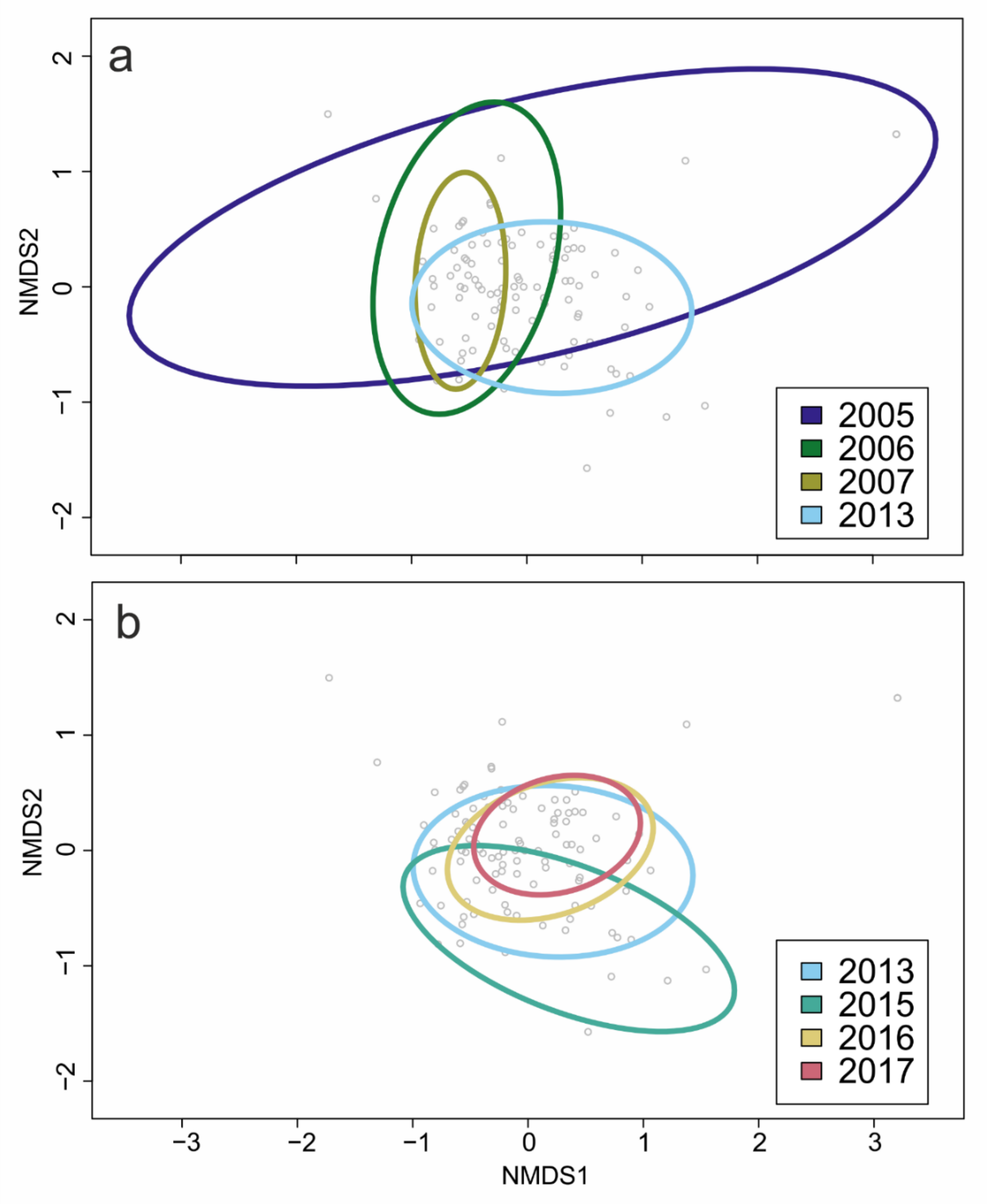

Figure 6.2. NMDS plot of benthic macroinvertebrate community composition, with overall analyses 95% confidence ellipsoids (standard deviation) of all streams combined for each year of the study a) 2005 to 2013 and b) 2013 to 2017

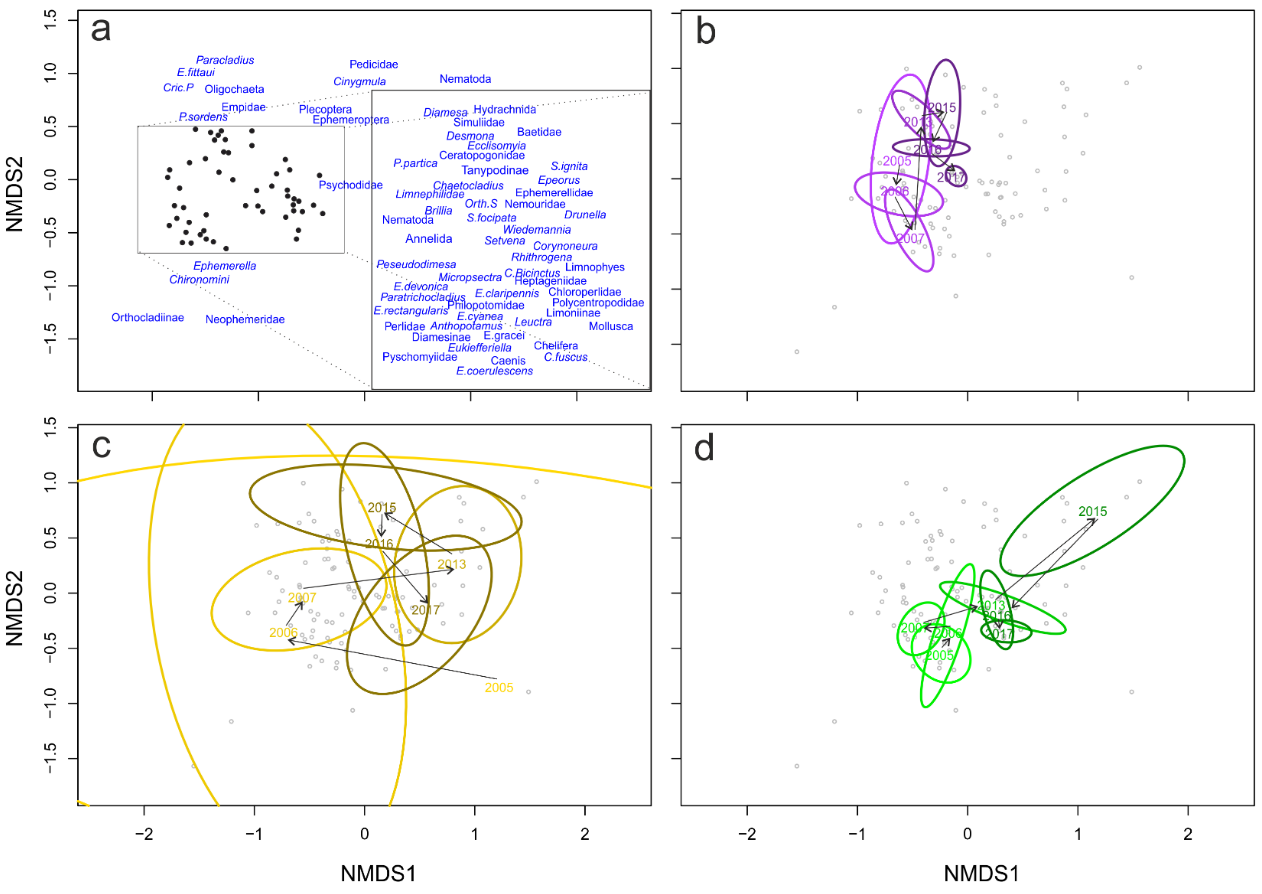

Figure 6.3. NMDS plots of (a) species, and years 2005 – 2017 for (b) WPC, (c) IVS and (d) BBS. Colours darken through time, i.e. 2005 is lightest and 2017 is darkest.

Inter-stream beta-diversity demonstrated consistent significant responses to both floods across the three streams (Figure 6.5). Following the 2005 floods, dissimilarity decreased from an average of 0.86 ± 0.17 (2005) to 0.72 ± 0.10 (2007), turnover decreased from 0.69 ± 0.34 (2005) to 0.49 ± 0.25 (2007) and nestedness increased 0.16 ± 0.28 (2005) to 0.23 ± 0.24 (2007). By 2013 (pre-2014 flood) these numbers recovered slightly to 0.82 ± 0.09, 0.68 ± 0.24 and 0.14 ± 0.21 respectively. Finally, by the end of the study period (2017) dissimilarity and turnover reached their lowest recorded averages (0.61 ± 0.10 and 0.40 ± 0.17 respectively), whilst nestedness increased to 0.21 ± 0.15.

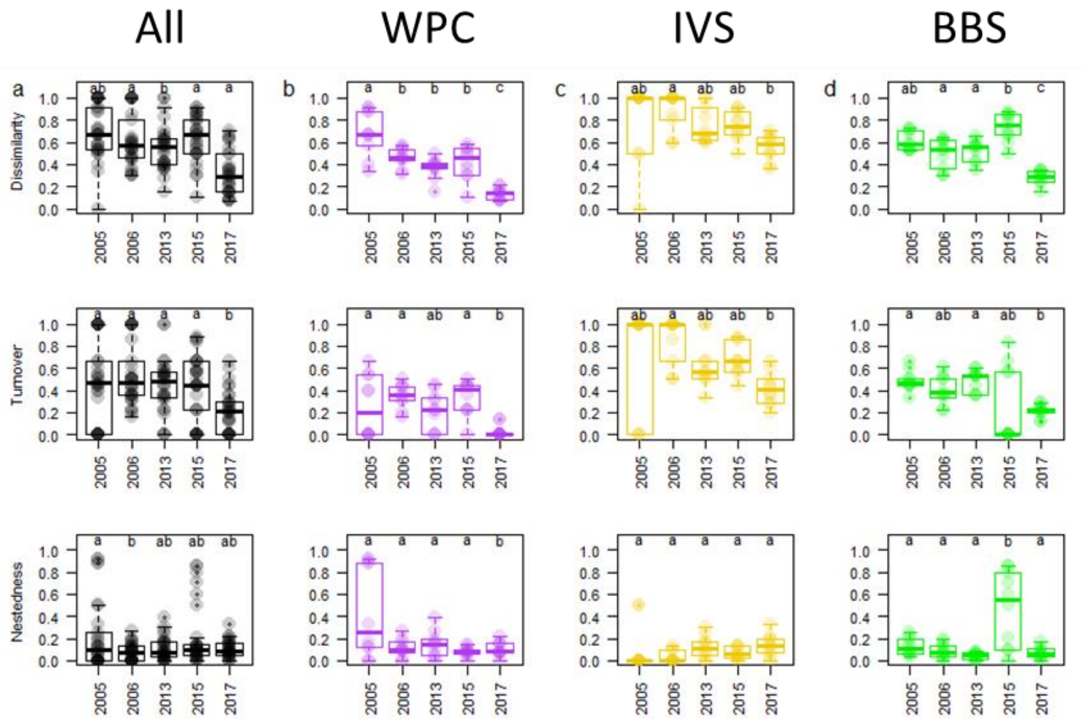

Figure 6.4. Intra-year beta-diversity for a) all streams (black), b) WPC (purple), c) IVS (gold) and d) BBS (green). Different letters above box-plots represent significantly different years.

*Table 6.4. Intra-stream beta-diversity measures for overall and individual analyses. Models type, F statistics and Tukeys pairwise Z statistics. p <0.05 *, p < 0.01 **, p < 0.001 ***. GLMM = Generalized Linear Mixed Effects Models, AC = Autocorrelation, GLS = Generalized Least Squares Regression.*

		Overall	**WPC**	**IVS**	**BBS**
Dissimilarity	Model	GLMM AC	GLS	GLS	GLS
	F	22.91 ***	23.07 ***	3.55 *	25.19 ***
	05 to 06	-1.96	3.81 **	-0.94	2.40
	05 to 13	-3.51 **	5.48 ***	0.45	1.84
	05 to 15	-1.56	4.64 ***	0.58	-2.70
	05 to 17	-8.79 ***	9.46 ***	2.69	6.96 ***
	13 to 15	1.95	-0.84	0.12	-4.53 ***
	13 to 17	-5.28 ***	3.98 ***	2.23	5.12 ***
Turnover	Model	GLMM AC	GLS	GLS AC	GLS
	F	9.41 ***	5.56 **	3.38 *	4.94 **
	05 to 06	1.01	-1.24	-1.26	1.00
	05 to 13	-0.63	0.52	0.53	0.01
	05 to 15	-1.01	-0.97	0.17	2.77
	05 to 17	-4.70 ***	2.95 *	2.35	3.40 *
	13 to 15	-0.38	-1.49	-0.36	2.75
	13 to 17	-3.69 ***	2.43	1.82	3.38 *
Nestedness	Model	GLMM AC	GLS	GLS	GLS AC
	F	3.51 *	5.45 **	1.32	12.00 ***
	05 to 06	-2.83 *	3.64 **		0.45
	05 to 13	-2.33	3.21 *		1.17
	05 to 15	-0.21	3.96 **		-4.81 ***
	05 to 17	-2.32	3.75 **		0.73
	13 to 15	2.12	0.75		-5.98 ***
	13 to 17	0.01	0.54		-0.45

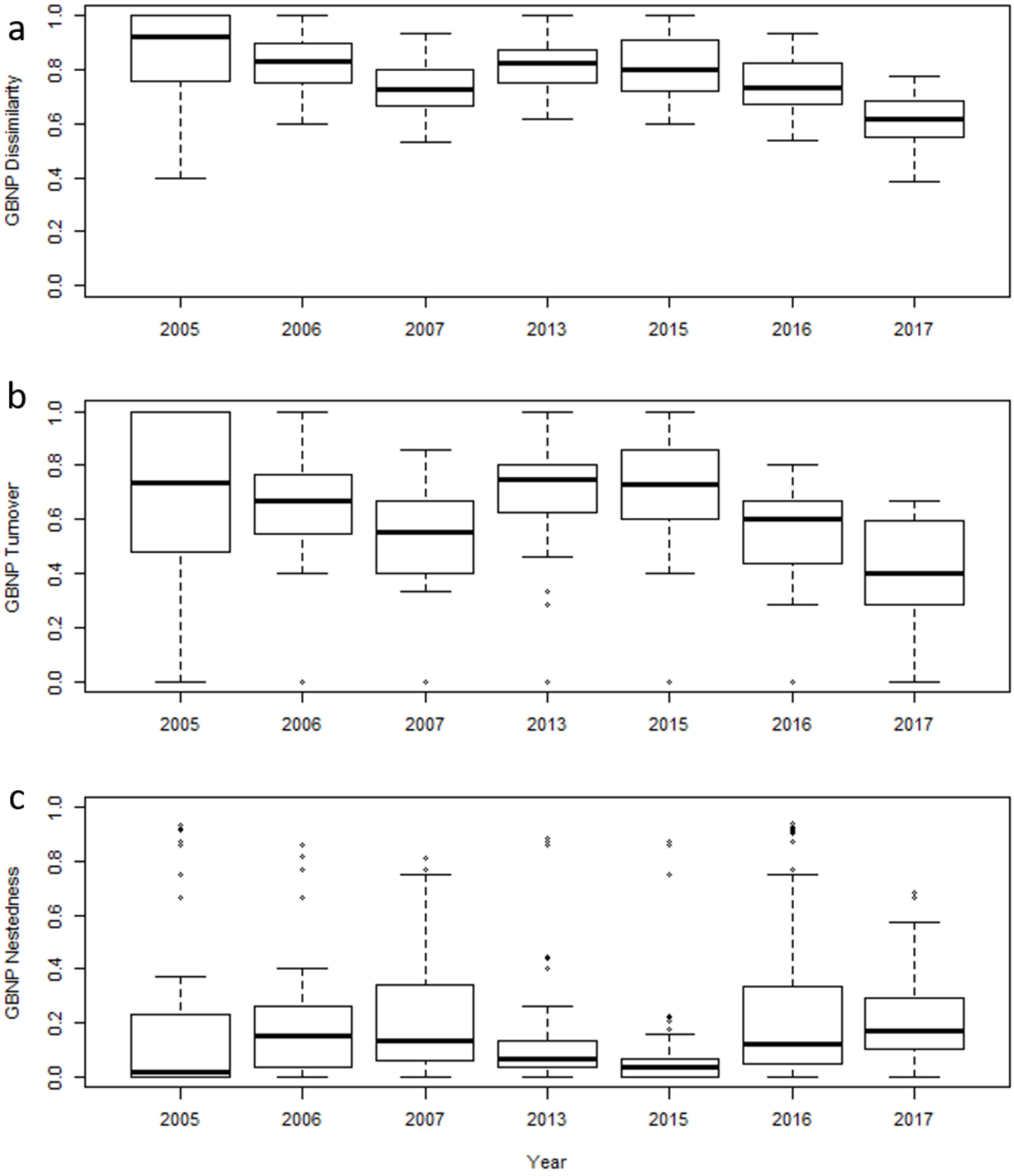

Figure 6.5. Between stream intra-year beta-diversity a = Jaccard's Dissimilarity, b = Turnover and c = Nestedness.

6.3.3 Dominance analyses

Before the 2005 floods, across the three study streams, all dominant taxa were members of the Chironomidae, with the exception of the Simuliidae (WPC, IVS and BBS) and the Nemouridae (BBS). This pattern persisted post-flood, in spite of an increase in evenness with the overall number of dominant taxa recorded across streams increasing (23 from 16) and the number of rare taxa decreasing (19 from 26). During this post-flood period the only dominant non-Chironomidae were the Simuliidae (WPC and BBS) and *Suwallia forcipata* (BBS). By 2013 (pre-2014 floods) the Chironomidae remained the group with the greatest proportion of dominant taxa (13 out of 21). However, an increasing number of Heptageniidae taxa were establishing at the core of communities including *Rithrogena* (BBS), *Cinygmula* sp. (IVS and BBS) and *Epeorus* sp. (IVS). The high-frequency summer floods of 2014 appeared to impact rare taxa reducing the total number across the three streams from 33 to 14, whereas little change was observed in the number of dominant taxa (21 to 22). All rare Diptera taxa were lost from communities post-2014 flood and only six of the 22 dominant taxa were members of the Chironomidae. In contrast a number of Ephemeroptera established as dominant taxa including *Serratella ignita* (WPC and IVS), *Drunella sp.* (BBS) and members of the Baetidae (WPC, IVS and BBS) in addition to members of the Plecoptera (IVS and BBS) including *Suwallia forcipata* (IVS). During the final sampling year (2017) the highest total number of dominant taxa was recorded across all streams (28) which were evenly spread across the three streams (WPC = 8, IVS = 10 and BBS = 10). This included the re-establishment of a number of taxa (*Orthocladius* Type S*, Paratrichocladius, Eukifferiella claripennis*) at the dominant core of the community at all streams. The only taxon that persisted as a dominant member of communities across all study years at all streams was *Orthocladius* Type S, with the exception of BBS in 2015 where it was recorded as a rare taxon.

Table 6.5. Dominant (Dom) and rare (Rar) taxa across the study. Streams are numbered 1 = WPC, 2 = IVS and 3 = BBS

Taxa	**2005**		**2006**		**2013**		**2015**		**2017**	
	Dom	**Rar**	**Dom**	**Rar**	**Dom**	**Rar**	**Dom**	**Rar**	**Dom**	**Rar**
Orthocladius Type S grp.	1,2,3		1,2,3		1,2,3		1,2	3	1,2,3	
Paracladius grp.							1	2		
Paratrichocladius	3	1	1,2	3	3				1,2,3	
Chaetocladius	3	1	1		1			2		2
C. bicinctus grp.					3				3	2
C. fuscus grp.										3
Crictopus TypeP						1				
E. claripennis grp.	3	1	2,3	1	3	2	1		1,2,3	
E. fittaui grp.						1				
E. devonica grp.		1,3	1							
E. rectangularis grp		1,3		1,3						
E. gracei grp.	3	1	1	3						
E. cyanea grp.		1		1						
Eukiefferiella	3			3						
Limnophyes					2,3				2,3	1
Corynoneura						2,3			3	1
Brillia		3		2						
Pagastia partica grp.	2	1,3	1,2,3		1,3		2	3	3	1,2
Diamesa		3	2	1,3			1			2
Pseudodimesa		1,2		1						
PolypSordens grp.						1				
Microspectra	2,3	1	1,3		1,3				1,3	
Tanypodinae						1				1
Orthocladiinae	2	1,3	2,3	1						
Chironomidae		3	3			2,3				
Cerapotogonidae		1		1,3		1,3		1	1	3
Wiedemannia sp.						3				
Chelifera sp.										2,3
Limoniinae						3				3
Pedicidae								2,3		
Simuliidae	1,2,3		1,3		2	1,3	1	2,3	1	3
Psychodidae						2,3				
Diptera			2							
Ephemeroptera					2	3	2,3			
Ephemerellidae						3	3			
Serratella ignita				3		1	1,2		1,2	3
Drunella sp.						3	3			3
Ephemerella		3								
Heptageniidae						3				
Rhithrogena					3					
Cinygmula sp.					2,3		2,3	1	2,3	1
Epeorus sp.		3			2				2	3
Baetidae		3		3		1,2,3	1,2,3		1,2	3
Neophemeridae		3								
Plecoptera				3		3	2,3			
Chloroperlidae					2				3	
Suwallia forcipata		1,3	3			1,2,3	2	1		1,3
Leuctra									2	3
Nemouridae	3			3					2	
Mollusca						3				
Hydrachnida						1,3		1		
Annelida				1						
Oligochaeta					1	2	2	1,3		

6.4 Discussion

This study contributes to our understanding of the importance of flood timing, form and the sequencing of events in driving change to benthic macroinvertebrate communities following disturbance. The two floods drove contrasting responses in benthic macroinvertebrate communities, with more extensive and significant declines in taxonomic richness and density being observed following the summer high-frequency floods (2014) compared to the winter high-magnitude flood (2005), with the exception of total density at WPC, potentially linked to flood timing and duration. Ongoing declines in beta-diversity both across and within streams were evident through time following the 2005 floods driven predominantly by changes in the years immediately after each flood.

6.4.1 Differences in flood timing and form

The contrasting responses contradict H_1 that both flooding regimes would drive significant declines in both total density and taxonomic richness. The smaller impacts of the 2005 flood was consistent with similar responses following high-magnitude winter flooding elsewhere (Herbst and Cooper, 2010). Such a contrast between the floods, could be linked to the natural flow regime of small rivers in southeast Alaska, which typically experience their lowest stream flow through the summer months (July and August) followed by increasing stream flows through to a peak during early winter (October/November), driven by increased precipitation, including rain on snow events (Neal et al., 2002). Floods occurring outside of this natural regime can be expected to impact communities more severely than impacts from atypically high magnitude events that occur in typical high flow periods consistent with high-magnitude floods occurring in summer (Woodward et al., 2015). These impacts arise from benthic macroinvertebrate community life history traits which demonstrate adaptation to a river's flow regime (Lytle and Poff, 2004, Poff et al., 1997). For instance, oviposition, which in some taxa can rely upon females accessing instream rocks, can be limited by high flows (Lancaster and Downes, 2010, Peckarsky et al., 2000). In addition, during high flows oviposition could still occur, on rocks at the edges of the high water wetted channel, which subsequently dry as water recedes leading to mass egg mortality. These findings suggest that flood form and timing, alongside antecedent conditions, could affect available niche space both during and after each flood event, by altering hydrological and geomorphological conditions with river channels reported in chapter 3 and within the literature (Milner et al., 2013, Robertson et al., 2015).

The greater impact of recurrent summer floods on taxonomic richness at both IVS and BBS is important evidence in support of H_2, that the summer 2014 high-frequency floods will have caused greater reductions in macroinvertebrate taxa density and richness than the 2005 winter high-magnitude flood. Taxa can be expected to be impacted significantly if they have: stream dwelling stages which cannot access refugia during floods, refugia access is limited by size and/or mobility (Lytle and Poff, 2004, Poff et al., 2018); adult life stages with short flight periods which coincided with floods, reducing overall oviposition; oviposited before high flows, which subsequently mobilised egg bearing sediments. This increased impact could therefore be the result of increased activity of benthic macroinvertebrate taxa during the summer which exposes more individuals to increased mortality risk caused by the floods, but this finding is, however, in contrast with evidence from WPC (Milner et al., 2018). This contrast between WPC and others could be the result of differences in community composition and geomorphological complexity. In addition the presence of an upstream lake at WPC could alter the hydrographs of high-magnitude and high-frequency floods compared to those observed at IVS and BBS, although further research would be necessary to evidence this.

Taxa with life histories that allowed them to generally avoid floods or recover rapidly could be expected to be the most successful in the post-flood community. For example following the summer 2014 floods *Cinygmula* sp., which typically demonstrate peak emergence in late September in cold water rivers, even under varying annual hydrographs (Finn and Poff, 2008), became a dominant member of post-2014-flood communities. This taxon’s highly mobile, flattened and small nymphs (Poff et al., 2006) are likely to have increased resistance to floods (Poff et al., 2018), compared to larger and less mobile taxa. Nemourid stoneflies represent another taxa with contrasting responses to the floods declining in abundance following the 2005 floods (Robertson et al., 2015) but increasing in abundance and colonising new streams (IVS) following the 2014 floods. Taxa in this family generally hatch during late spring and early summer (April and early June in cold water northern latitude streams; average summer stream temperatures <10^0C; Mutch and Pritchard, 1982; 1984, Stewart et al., 1990). Therefore, it can be expected that in GBNP nemourid adults have hatched from streams before the peak flows of the 2014 floods (mid-July to mid-August). Oviposition occurs up to two months later, which would have coincided with the first large floods of 2014. In addition, delayed egg hatching has been reported in members of the Nemouridae (*Zapada* sp.) in North American streams and is thought to be a trait which acts to limit the impacts of catastrophic disturbances (Harper, 1973a, Harper, 1973b). A trade-off is that the trait may expose nymphs to winter floods (2005) as they reach their peak sizes (early winter; Cather and Gaufin, 1976).

6.4.2 Community reassembly and flood sequences

In addition to the effects of contrasting flood form, biological responses may be a result of the compounded effects of multiple disturbance events (Buma, 2015). PERMANOVA analyses in this study indicated that overall communities across streams did not return to pre-2005 flood composition prior to the 2014 summer floods, with a constriction of ellipsoid area suggesting a loss of some rare taxa, consistent with the findings of Milner et al. (2013) at WPC. This temporally extended legacy effect of the high-magnitude flood could have altered ecological resilience to the subsequent high-frequency summer floods, by controlling how communities reform as demonstrated in drought experimental manipulations (Ledger et al., 2006). This observational and experimental evidence offers support to the model of ecological resilience following multiple flood events identified conceptually by Milner et al. (2018), at WPC. Under the conceptual model previous floods can (1) reduce (2) increase or (3) have no effect on ecological resilience to subsequent floods. In the current study the extended biotic legacy period, with significantly different community composition in 2013, suggested that the floods represent linked disturbances. These linked disturbances alter the ecological resilience of the biotic communities compared to that associated with the community prior to the 2005 flood. The greater declines in abundance and richness following the 2014 floods provides evidence in support of reduced ecological resilience in the communities that re-established at streams following the 2005 flood, despite smaller overall changes in composition observed in NMDS. However, to confidently identify how previous floods alter ecological resilience to subsequent events (i.e. reduce or increase) it will be necessary to experimentally test the model. Principally because greater declines in abundance and richness associated with the 2014 floods could be as a result of the contrasting timing and forms of the two flood disturbances compared in this chapter.

The NMDS and PERMANOVA findings here suggested that extreme floods may not drive the reassembly of communities dominated by taxa with traits previously considered to confer resilience to floods, such as high mobility and small size demonstrated in response to extreme floods elsewhere (Poff et al., 2018). This conclusion is put forth primarily because the high-frequency summer floods drove extensive and significant changes to total density, richness and community composition both at the individual stream and across/between all streams. These changes occurred in spite of a significant change in composition and a recovery of density in the benthic macroinvertebrate community from 2005 to 2013, such as Baetidae, Orthocladiinae and *Cinygmula* sp.. These findings are not consistent with a community of more resistant taxa being present before the 2014 floods; rather they suggest that the community which reassembled following the 2005 flood continues to lack resilience to future floods. Additionally, the observed reductions in intra- and inter-stream beta-diversity through both post-flood periods suggests that community form is more closely tied to the processes of community reassembly than the direct effect of the floods in driving community disassembly.

Over the 12 years of the study, a major reduction in inter-stream beta-diversity (dissimilarity) from an average of 0.92 (2005) to 0.59 (2017) offers support for H_3: the sequence of recurrent floods has driven declines in between stream beta-diversity. Reductions in inter-stream beta-diversity in the current study were driven predominantly by a decrease in the turnover of taxa with major responses observed following each flood. Low turnover of taxa between streams is linked to a greater number of shared taxa, predominantly from the Chironomidae, Baetidae and Heptagenidae. This may indicate a reduced capacity of post-disturbance communities to resist colonisation by taxa excluded from communities before the floods. Such increased susceptibility of communities to ‘invasion’ may be due to the availability of underutilised resources in the low density communities post-flood (Miller et al., 2002, Wright et al., 2015). Such alterations are regularly associated with changing dominance hierarchies and priority effects (Smith et al., 2004, Fraser et al., 2015). Further, this reduced turnover could be the result of the loss of taxa which are less able to recolonise such as non-insect taxa which are relatively ineffective dispersers and lack mobile adult stages. With observed increases in the frequency of extreme floods generally (Wouter et al., 2017) this homogenisation of communities can be expected to increase due to the more frequent occurrence of low density communities and the exclusion of flood intolerant taxa. Such homogenisation has significant implications for biodiversity at broader scales.

Between stream trends of decreasing beta-diversity observed in this study highlight the importance of dispersal capacity in facilitating recolonization and thus the role of both within and between stream dispersal to recovery of community’s post-flood (Anderson and Hayes, 2018, Tonkin et al., 2018). Dispersal has elsewhere been identified as a crucial element controlling community composition across a disturbance gradient (Brown et al., 2018), and the result of this study in Glacier Bay suggests its potential importance in response to sequences of disturbances. Dispersal is governed by a complex suite of processes, taxa’s life history traits and physical characteristics of catchments. Good drift dispersers may be able to disperse effectively where there are connected upstream populations that have not been significantly impacted by a set of extreme floods. However, where connectivity with upstream tributaries is low or where upstream populations have been significantly impacted by a disturbance, dispersal may not be as effective. Taxa with adults that are good dispersers between catchments may see effective recolonization of disturbed communities where wetted channels within two catchments are physically close to one another. When the physical distance between channels is great, or where barriers such as high mountains or powerful prevailing winds act against dispersal, source populations are effectively more isolated from disturbed systems.

Under future climate scenarios where extreme floods are more frequent components of flow regimes, the dispersal capacity of taxa will become increasingly important in controlling community composition across freshwater ecosystems. This has significant implications for historic approach of creating habitat and expecting colonisation of taxa associated with the created habitat. Where taxa are dispersal limited, colonisation may only occur at a low rate. Newly colonised low-density populations may not demonstrate resilience to future disturbances if they are yet to effectively colonise regions of the channel which could act as refugia from disturbance. This challenges one approach taken by policy makers and river managers when developing conservation strategies which increase the resilience of systems to future change. Crucially, systems may need to be developed which protect taxa with low dispersal capacity. This could be through the linkage of stream and river channels to marginal and standing freshwater habitats which could act as source populations and refugia during future disturbance events. Given ecological response to disturbance is governed by disturbance form and community composition and traits, it must be expected that solutions will require a considered approach that incorporates understanding from both the disturbance and restoration ecology fields.

6.5 Conclusions

The findings of this study highlight the complexities of ecological response to disturbances. Both high-magnitude and high-frequency floods drove significant changes to community composition within each stream and drove convergence of communities between streams. Together these findings demonstrate the threat that extreme disturbances pose to biodiversity across spatial scales. Furthermore, the significant effects of the 2014 floods on macroinvertebrate communities across streams suggests that extreme floods may not act as environmental drivers of increased resilience of communities to future disturbances; rather, the processes of re-assembly following disturbances simply favours taxa which can tolerate or rapidly colonise disturbed systems’ altered niche spaces, or who can disperse rapidly to disturbed systems. It is now necessary to more effectively incorporate ecological theory associated with the multiple processes controlling ecological response to disturbances, predominantly community reassembly, dispersal capacity and changing niche space, into disturbance theory.

6.6 References

ANDERSEN, T., CRANSTON, P. S. & EPLER, J. H. 2017. *Chironomidae of the Holarctic Region: Keys and Diagnoses, Part 1: Larvae*, Entomological Society of Lund, Sweden.

ANDERSON, K. E. & HAYES, S. M. 2018. The effects of dispersal and river spatial structure on asynchrony in consumer–resource metacommunities. *Freshwater Biology,* 63**,** 100-113.

ANDERSON, M. J. 2014. Permutational Multivariate Analysis of Variance (PERMANOVA). *Wiley StatsRef: Statistics Reference Online.*

ANDERSON, M. J., CRIST, T. O., CHASE, J. M., VELLEND, M., INOUYE, B. D., FREESTONE, A. L., SANDERS, N. J., CORNELL, H. V., COMITA, L. S., DAVIES, K. F., HARRISON, S. P., KRAFT, N. J. B., STEGEN, J. C. & SWENSON, N. G. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters,* 14**,** 19-28.

BASELGA, A. 2010. Partitioning the turnover and nestedness components of beta-diversity. *Global Ecology and Biogeography,* 19**,** 134-143.

BASELGA, A. & ORME, C. D. L. 2012. betapart: an R package for the study of beta-diversity. *Methods in Ecology and Evolution,* 3**,** 808-812.

BASELGA, A., ORME, D., VILLEGER, S., DE BORTOLI, J., LEPRIEUR, F. & 2018. betapart: Partitioning Beta-diversity into Turnover and Nestedness Components.

BERG, P., MOSELEY, C. & HAERTER, J. O. 2013. Strong increase in convective precipitation in response to higher temperatures. *Nature Geoscience,* 6**,** 181.

BOND, N. A., CRONIN, M. F., FREELAND, H. & MANTUA, N. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters,* 42**,** 3414-3420.

BOZELLI, R. L., THOMAZ, S. M., PADIAL, A. A., LOPES, P. M. & BINI, L. M. 2015. Floods decrease zooplankton beta-diversity and environmental heterogeneity in an Amazonian floodplain system. *Hydrobiologia,* 753**,** 233-241.

BROOKS, S., LANGDON, P. & HEIRI, O. 2008. *The Identification and Use of Palaearctic Chironomidae Larvae in Palaeoecology*.

BROWN, L. E., KHAMIS, K., WILKES, M., BLAEN, P., BRITTAIN, J. E., CARRIVICK, J. L., FELL, S., FRIBERG, N., FÜREDER, L., GISLASON, G. M., HAINIE, S., HANNAH, D. M., JAMES, W. H. M., LENCIONI, V., OLAFSSON, J. S., ROBINSON, C. T., SALTVEIT, S. J., THOMPSON, C. & MILNER, A. M. 2018. Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nature Ecology & Evolution,* 2**,** 325-333.

BUMA, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere,* 6**,** art70.

BUMA, B. & WESSMAN, C. A. 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere,* 2**,** art64.

BURGER, C. V., WILMOT, R. L. & WANGAARD, D. B. 1985. Comparison of Spawning Areas and Times for Two Runs of Chinook Salmon (Oncorhynchus tshawytscha) in the Kenai River, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences,* 42**,** 693-700.

CALDERON, M. R., BALDIGO, B. P., SMITH, A. J. & ENDRENY, T. A. 2017. Effects of extreme floods on macroinvertebrate assemblages in tributaries to the Mohawk River, New York, USA. *River Research and Applications,* 33**,** 1060-1070.

CATHER, M. R. & GAUFIN, A. R. 1976. Comparative Ecology of Three Zapada Species of Mill Creek, Wasatch Mountains, Utah (Plecoptera: Nemouridae). *The American Midland Naturalist,* 95**,** 464-471.

CRAWLEY, M. J. 2004. Timing of Disturbance and Coexistence in a Species-Rich Ruderal Plant Community. *Ecology,* 85**,** 3277-3288.

DIFFENBAUGH, N. S., SWAIN, D. L. & TOUMA, D. 2015. Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences,* 112**,** 3931-3936.

EKLÖF, J. S., MCMAHON, K. & LAVERY, P. S. 2009. Effects of multiple disturbances in seagrass meadows: shading decreases resilience to grazing. *Marine and Freshwater Research,* 60**,** 1317-1327.

FINN, D. S. & POFF, N. L. 2008. Emergence and Flight Activity of Alpine Stream Insects in Two Years with Contrasting Winter Snowpack. *Arctic, Antarctic, and Alpine Research,* 40**,** 638-646.

FLATHER, C. H. & SIEG, C. H. 2007. Species Rarity: Definition, Causes, and Classification. *In:* M.G;, R. & R, M. (eds.) *Conservation of Rare or Little-Known Species.* Washington, Covelo, London: Island Press.

FORD, M. J., FUSS, H., BOELTS, B., LAHOOD, E., HARD, J. & MILLER, J. 2006. Changes in run timing and natural smolt production in a naturally spawning coho salmon (Oncorhynchus kisutch) population after

60 years of intensive hatchery supplementation. *Canadian Journal of Fisheries and Aquatic Sciences,* 63**,** 2343-2355.

FOX, J. & WEISBERG, S. 2011. *An {R} Companion to Applied Regression,* Thousand Oaks CA, Sage.

FRASER, C. I., BANKS, S. C. & WATERS, J. M. 2015. Priority effects can lead to underestimation of dispersal and invasion potential. *Biological Invasions,* 17**,** 1-8.

GASTON, K. J. 1994. *Rarity,* London, Chapman and Hall.

GEORGE, S. D., BALDIGO, B. P., SMITH, A. J. & ROBINSON, G. R. 2015. Effects of extreme floods on trout populations and fish communities in a Catskill Mountain river. *Freshwater Biology,* 60**,** 2511-2522.

HARPER, P. P. 1973a. Emergence, Reproduction, and Growth of Setipalpian Plecoptera in Southern Ontario. *Oikos,* 24**,** 94-107.

HARPER, P. P. 1973b. *Life histories of Nemouridae and Leuctridae in Southern Ontario (Plecoptera)*.

HERBST, D. B. & COOPER, S. D. 2010. Before and after the deluge: rain-on-snow flooding effects on aquatic invertebrate communities of small streams in the Sierra Nevada, California. *Journal of the North American Benthological Society,* 29**,** 1354-1366.

JACCARD, P. 1912. The distribution of the flora in the alpine zone. *New Phytologist,* 11**,** 37-50.

KAPPES, H. & HAASE, P. 2012. Slow, but steady: dispersal of freshwater molluscs. *Aquatic Sciences,* 74**,** 1-14.

KLAAR, M. J., KIDD, C., MALONE, E., BARTLETT, R., PINAY, G., CHAPIN, F. S. & MILNER, A. 2015. Vegetation succession in deglaciated landscapes: implications for sediment and landscape stability. *Earth Surface Processes and Landforms,* 40**,** 1088-1100.

KLAAR, M. J., MADDOCK, I. & MILNER, A. M. 2009. The Development of Hydraulic and Geomorphic Complexity in Recently Formed Streams in Glacier Bay National Park, Alaska. *River Research and Applications,* 25**,** 1331-1338.

LAKE, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society,* 19**,** 573-592.

LANCASTER, J. & DOWNES, B. J. 2010. Linking the hydraulic world of individual organisms to ecological processes: Putting ecology into ecohydraulics. *River Research and Applications,* 26**,** 385-403.

LAPOINTE, M., EATON, B., DRISCOLL, S. & LATULIPPE, C. 2000. Modelling the probability of salmonid egg pocket scour due to floods. *Canadian Journal of Fisheries and Aquatic Sciences,* 57**,** 1120-1130.

LARSON, E. I., POFF, N. L., ATKINSON, C. L. & FLECKER, A. S. 2018. Extreme flooding decreases stream consumer autochthony by increasing detrital resource availability. *Freshwater Biology,* 0.

LEDGER, M., M L HARRIS, R., MILNER, A. & ARMITAGE, P. 2006. *Disturbance, biological legacies and community development in stream mesocosms*.

LEDGER, M. E. & MILNER, A. M. 2015. Extreme events in running waters. *Freshwater Biology,* 60**,** 2455-2460.

LI, S. & PENNINGS, S. C. 2017. Timing of disturbance affects biomass and flowering of a saltmarsh plant and attack by stem-boring herbivores. *Ecosphere,* 8**,** e01675.

LYTLE, D. A. & POFF, N. L. 2004. Adaptation to natural flow regimes. *Trends in Ecology & Evolution,* 19**,** 94-100.

MERRITT, R. W. & CUMMINS, K. W. 1996. *An introduction to the aquatic insects of North America*, Kendall Hunt.

MILAN, D. J. 2012. Geomorphic impact and system recovery following an extreme flood in an upland stream: Thinhope Burn, northern England, UK. *Geomorphology,* 138**,** 319-328.

MILLER, T. E., KNEITEL, J. M. & BURNS, J. H. 2002. Effect of community structure on invasion success rate *Ecology,* 83**,** 898-905.

MILNER, A. M. 1987. Colonization and ecological development of new streams in Glacier Bay National Park, Alaska. *Freshwater Biology,* 18**,** 53-70.

MILNER, A. M., KNUDSEN, E. E., SOISETH, C., ROBERTSON, A. L., SCHELL, D., PHILLIPS, I. T. & MAGNUSSON, K. 2000. Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences,* 57**,** 2319-2335.

MILNER, A. M., PICKEN, J. L., KLAAR, M. J., ROBERTSON, A. L., CLITHEROW, L. R., EAGLE, L. & BROWN, L. E. 2018. River ecosystem resilience to extreme flood events. *Ecology and Evolution,* 0.

MILNER, A. M., ROBERTSON, A. L., MCDERMOTT, M. J., KLAAR, M. J. & BROWN, L. E. 2013. Major flood disturbance alters river ecosystem evolution. *Nature Climate Change,* 3**,** 137-141.

NEAL, E. G., TODD WALTER, M. & COFFEEN, C. 2002. Linking the pacific decadal oscillation to seasonal stream discharge patterns in Southeast Alaska. *Journal of Hydrology,* 263**,** 188-197.

OKSANEN, J., BLANCHET, F. G., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGLINN, D., MINCHIN, P. R., O'HARA, R. B., SIMPSON, G. L., SOLYMOS, P., STEVENS, M. H. H., SZOECS, E. & WAGNER, H. 2018. vegan: Community Ecology Package. 2.5-2 ed.

PECKARSKY, B. L., TAYLOR, B. W. & CAUDILL, C. C. 2000. Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. *Oecologia,* 125**,** 186-200.

POFF, N. L., ALLAN, J. D., BAIN, M. B., KARR, J. R., PRESTEGAARD, K. L., RICHTER, B. D., SPARKS, R. E. & STROMBERG, J. C. 1997. The Natural Flow Regime. *BioScience,* 47**,** 769-784.

POFF, N. L., LARSON, E. I., SALERNO, P. E., MORTON, S. G., KONDRATIEFF, B. C., FLECKER, A. S., ZAMUDIO, K. R. & FUNK, W. C. 2018. Extreme streams: species persistence and genomic change in montane insect populations across a flooding gradient. *Ecology Letters,* 21**,** 525-535.

POFF, N. L., OLDEN, J. D., VIEIRA, N. K. M., FINN, D. S., SIMMONS, M. P. & KONDRATIEFF, B. C. 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society,* 25**,** 730-755.

POWER, M. E. & STEWART, A. J. 1987. Disturbance and Recovery of an Algal Assemblage Following Flooding in an Oklahoma Stream. *The American Midland Naturalist,* 117**,** 333-345.

R-CORE-TEAM 2017. R: A language and environment for statistical computing. . Vienna, Austria.: R Foundation for Statistical Computing.

RAHEL, F. J. & OLDEN, J. D. 2008. Assessing the Effects of Climate Change on Aquatic Invasive Species. *Conservation Biology,* 22**,** 521-533.

REICH, P. & DOWNES, B. J. 2004. Relating larval distributions to patterns of oviposition: evidence from lotic hydrobiosid caddisflies. *Freshwater Biology,* 49**,** 1423-1436.

ROBERTSON, A. L., BROWN, L. E., KLAAR, M. J. & MILNER, A. M. 2015. Stream ecosystem responses to an extreme rainfall event across multiple catchments in southeast Alaska. *Freshwater Biology,* 60**,** 2523-2534.

ROBINSON, C. T., SIEBERS, A. R. & ORTLEPP, J. 2018. Long-term ecological responses of the River Spöl to experimental floods. *Freshwater Science,* 37**,** 433-447.

ROGHAIR, C. N., DOLLOFF, C. A. & UNDERWOOD, M. K. 2002. Response of a Brook Trout Population and Instream Habitat to a Catastrophic Flood and Debris Flow. *Transactions of the American Fisheries Society,* 131**,** 718-730.

SCRIMGEOUR, G. J. & WINTERBOURN, M. J. 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia,* 171**,** 33-44.

SEIDL, R., RAMMER, W. & SPIES, T. A. 2014. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. *Ecological Applications,* 24**,** 2063-2077.

SMITH, M. D., WILCOX, J. C., KELLY, T. & KNAPP, A. K. 2004. Dominance not richness determines invasibility of tallgrass prairie. *Oikos,* 106**,** 253-262.

STANLEY, E. H., POWERS, S. M. & LOTTIG, N. R. 2010. The evolving legacy of disturbance in stream ecology: concepts, contributions, and coming challenges. *Journal of the North American Benthological Society,* 29**,** 67-83.

SZCZERKOWSKA-MAJCHRZAK, E., LIK, J. & LESZCZYŃSKA, J. 2014. Resistance of riverine macroinvertebrate assemblages to hydrological extremes. *Oceanological and Hydrobiological Studies.*

THORP, J. H. & COVICH, A. P. 2009. *Ecology and classification of North American freshwater invertebrates*, Academic press.

TONKIN, J. D., ALTERMATT, F., FINN, D. S., HEINO, J., OLDEN, J. D., PAULS, S. U. & LYTLE, D. A. 2018. The role of dispersal in river network metacommunities: Patterns, processes, and pathways. *Freshwater Biology,* 63**,** 141-163.

TRENBERTH, K. E. 2011. Changes in precipitation with climate change. *Climate Research,* 47**,** 123-138.

VIEIRA, N. K. M., CLEMENTS , W. H., GUEVARA, L. S. & JACOBS, B. F. 2004. Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire. *Freshwater Biology,* 49**,** 1243-1259.

WILSON, S. K., GRAHAM, N. A. J., PRATCHETT, M. S., JONES, G. P. & POLUNIN, N. V. C. 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology,* 12**,** 2220-2234.

WOODWARD, G., BONADA, N., FEELEY, H. B. & GILLER, P. S. 2015. Resilience of a stream community to extreme climatic events and long-term recovery from a catastrophic flood. *Freshwater Biology,* 60**,** 2497-2510.

WOUTER, R. B., EMMA, E. A., JOSHUA, R. L., RALPH, T. & ROSS, A. W. 2017. Recent changes in extreme floods across multiple continents. *Environmental Research Letters,* 12**,** 114035.

WRIGHT, A. J., EBELING, A., DE KROON, H., ROSCHER, C., WEIGELT, A., BUCHMANN, N., BUCHMANN, T., FISCHER, C., HACKER, N., HILDEBRANDT, A., LEIMER, S., MOMMER, L., OELMANN, Y., SCHEU, S., STEINAUER, K., STRECKER, T., WEISSER, W., WILCKE, W. & EISENHAUER, N. 2015. Flooding disturbances increase resource availability and productivity but reduce stability in diverse plant communities. *Nature Communications,* 6**,** 6092.

7. Macroinvertebrate community compositional stability and extreme floods

7.1 Introduction

Ecosystems are under threat from a range of external factors (Chapin et al., 2000) including land use change (Postel et al., 1996), pollution (Vörösmarty et al., 2010, Tai et al., 2014), and climate change (Vitousek et al., 1997). The increasing frequency and magnitude of disturbance events (Classen et al., 2008, Wouter et al., 2017) represent another significant threat to biodiversity. Together these factors, are driving a biodiversity crisis globally (Butchart et al., 2010) with unprecedented rates of extinction predicted for this century (Pimm and Raven, 2000). One significant question which remains intensely debated is: Do these anthropogenic pressures and associated biodiversity declines alter the stability of ecosystems (May, 1973, Tilman, 1996, McCann, 2000, Tilman et al., 2006) and thus threaten ecosystem function (Bengtsson, 1998, Zak et al., 2003)?

Ecological stability captures temporal and spatial ecosystem dynamics and importantly ecosystem response to perturbation (Odum, 1953, May, 1972, Pimm, 1984). Stability is an emergent property of an ecosystem (Saint-Béat et al., 2015) which captures the persistence of an ecosystem in its current form. Theoretical research has taken a mathematical approach typically using random interaction models and focusing on asymptotic resilience (May, 1972, May, 1973, Pimm, 1984, Neubert and Caswell, 1997, Allesina and Tang, 2012). The asymptotic resilience of a biological community is defined as the asymptotic rate of return to equilibrium post-perturbation and is based on asymptotic stability, a binary measure (Arnoldi et al., 2016). Ecosystems, however, do not always demonstrate a return to a previous state following perturbation (Petersen et al., 2008, Milner et al., 2013), for two reasons: (1) the potential for multiple stable states in ecosystems (Sutherland, 1974, Simenstad et al., 1978, Blindow et al., 1993) or (2) periodic/continued perturbation of the system (Paine, 1977, Hubbell, 1979, Sousa, 1979). The former reason falls within an intensely debated field and its validity continues to be questioned (Beisner et al., 2003, Sayer et al., 2010, Capon et al., 2015). Empirical research on the other hand, typically focuses on temporal variability of a community or population feature (of an adjusted form of biomass or abundance) or resilience (Jiang and Pu, 2009, Tilman et al., 2006, Campbell et al., 2011).

Although there is a broad range of metrics describing various components (or dimensions) of stability, empirical studies generally include only a single or occasionally a pair of components (Murry and Farrell, 2014, Dunne et al., 2002, Kratina et al., 2012, Mari et al., 2014, Bogan et al., 2015, Woodward et al., 2015). Where multiple components have been measured, for instance temporal and spatial variability of biomass and resistance, they have been treated separately in subsequent analysis and discussions (France and Duffy, 2006, O'Gorman and Emmerson, 2009, Stanley et al., 1994, Knapp et al., 2001). Experimental manipulations have demonstrated a significant coupling of stability components during periods without major perturbation, indicating that there are relationships between components (Harrison, 1979, Pimm, 1984, Donohue et al., 2013). Donohue et al. (2013) demonstrated this coupling and dependence of six commonly used components of ecological stability experimentally, in a tidal ecosystem. Importantly if all components of stability capture information regarding the same processes it would be expected that this coupling and associated low dimensionality would persist following perturbation and would limit the need to apply multiple components of stability in a given study.

Selective species removal manipulation experiments, mimicking species loss following perturbations in tidal shoreline ecosystems, indicate that this low dimensionality of ecological stability does not necessarily persist following perturbation (Donohue et al., 2013). This decoupling of relationships highlights the potential role of a number of different processes and mechanisms in driving an ecological stability response. If a variety of processes govern stability it will be necessary to include multiple components of ecological stability into analyses when a study aims to infer variation in ecological stability following a perturbation from a subset of components (Pennekamp et al., 2018). This dimensionality approach has now been applied in freshwater mesocosms (Hillebrand et al., 2018) and modelling studies (Yang et al., 2019) with consistent and increasing dimensionality of ecological stability components observed following significant disturbances to systems. Modelling evidence has suggested that disturbance form, linked to its timing, magnitude, duration and frequency, is likely to have a greater effect on how dimensionality is altered than changes in magnitude (Radchuk et al., 2019). This is important given the changing timings, frequencies and durations of climate driven extreme events now being observed globally (Trenberth, 2011, Berg et al., 2013, Wouter et al., 2017). However, there has yet been no attempt to apply the theory to ecological stability response following real-world disturbances. Further, the approach has only been applied to spatially replicated data sets and no attempts have been undertaken to apply the methodologies to time-series data. Given the importance of time in governing response to perturbation, it will be necessary to develop ways to adjust the approach to consider stability through time post-perturbation.

The historic approach of analysing individual components of stability in studies of perturbation may be in part a result of an assumption that an individual component’s response may be descriptive of/ consistent with the response of other components of stability. A consistent response could be expected were all components governed by the same processes or if all processes respond in the same manner to perturbation, or when an ecosystem is stable and there is little change in the relative importance of any one underlying process, for instance inter-specific competition. In such a case, were multiple ecological stability components are to be studied simultaneously, low dimensionality would be observed with strong relationships/correlations between all components. However, if this is not the case and components respond differently to any given perturbation, i.e. if they are governed by separate processes, it could be expected that ecological stability could demonstrate higher dimensionality with weaker relationships/ correlations between components. Developing such an understanding of the potential for high dimensionality of ecological stability is important if we hope to establish how perturbations influence fundamental processes which govern ecosystem form, assembly and function.

The dimensionality of ecological stability can be visualised in hypothetical multidimensional stability space, where the number of dimensions equates to the number of components of stability (Donohue et al., 2013). In multidimensional stability space, an ecosystem or community's stability is described by an ellipsoid, whose form is dictated by the relationships between stability components. The orientation, shape and volume of ellipsoids provides information regarding the extent of these relationships between components (Donohue et al., 2013). Where all components have significant relationships with one another this ellipsoid has a 'multidimensional cigar' like shape, with one axis dominating relative axis length, as observed in unperturbed communities in Donohue et al. (2013). In such a case, a change in one metric is matched by a consistent response in other components. If components decouple and relationships become less significant this ellipsoid can begin to resemble a 'multidimensional sphere', where no individual axis dominates relative axis length. Where ellipsoids are more spherical, components respond differently to one another, following the same perturbation, which may suggest changes in the processes which are driving responses between components. Under a multidimensional sphere model, studies which utilise a single stability metric may not capture the processes and patterns which underlie this complex property of ecosystems and communities.

Understanding changes in the dimensionality of ecological stability following extreme disturbance events is becoming increasingly important as these events become more frequent components of environmental variability (Berg et al., 2013, Wouter et al., 2017) and management struggles to keep pace. Whilst ecological stability concepts have been applied to community disassembly (e.g. Bogan et al., 2015), multi-dimensional approaches were not applied until Donohue et al. (2013). Few attempts have been made to understand how ecological stability varies during primary succession (community assembly; Yarranton and Morrison, 1974, Martínez et al., 2001, Tscherko et al., 2003) or secondary succession (community reassembly). Rather studies only address a subset of components, for instance the resistance or resilience of community composition (Fritz and Dodds, 2004, Anderson and Ferrington, 2013, Bêche et al., 2009, Woodward et al., 2015) or the variability of abundance, density or biomass (Flecker and Feifarek, 1994, Martínez et al., 2001, Mathers et al., 2018) following perturbations. Importantly there are no examples which consider multiple components of ecological stability in any long-term observational approaches. The temporal variability of stability is highly relevant given the directional changes now observed in both average weather patterns and extreme events. Further, following the increasing frequency and co-occurrence of disturbances (Buma, 2015, Wouter et al., 2017) it will become necessary to establish how ecological stability responds to co-occurring and sequences of disturbances. The dimensionality approach to understanding ecological stability can be applied to these challenges and provides a framework within which to consider the changing processes which govern stability following perturbations.

This study examines how the dimensionality of stability (Donohue et al., 2013, Hillebrand et al., 2018) varies in a time-series data set of a river macroinvertebrate community in response to flood disturbances. Such application of the dimensionality of ecological stability approach has yet to be undertaken in a time-series data set. Here, the dimensionality of benthic macroinvertebrate community compositional stability was assessed during community reassembly, following an extreme high-magnitude winter flood and subsequent high-frequency summer floods in a sub-Arctic stream ecosystem. The study tested four hypotheses;

> H_1 Stability components demonstrate low dimensionality during the relatively stable pre-flood period with negligible environmental or biotic perturbations and limited niche space available for colonizing species (Naeem and Li, 1997, Kiessling, 2005), because underlying ecological processes remain consistent during unperturbed periods.
>
> H_2 Community reassembly following the floods increased dimensionality when compared to the pre-flood period, because processes driving stability may decouple or change in their strength and nature following the physical

disruption of communities (Donohue et al., 2013, Hillebrand et al., 2018, Radchuk et al., 2019).

H_3 Each flood altered the dimensionality of community compositional stability in different ways because of differences in disturbance form (Radchuk et al., 2019). For instance, a flood occurring during a period prior to the maturation of a keystone taxa within an ecosystem could greatly impact its density post-flood which could alter inter-specific competition, ecosystem invaisability (susceptibility to invasion) and ecosystem function through time post-flood. Likewise, a flood or series of floods which persist for significantly longer than another flood may impact a greater number of taxa altering inter-specific competition, extinction rates and ecosystem resistance to perturbations.

H_4 Sequences of floods increased dimensionality of stability in steps by increasingly decoupling components which cannot recover before subsequent disturbances occur (Milner et al., 2018; Chapter 6).

7.2 Methods

7.2.1 Study site

Since approximately 1700 AD, glacial retreat has exposed a 150 km long tidal fjord in what is now Glacier Bay National Park and Preserve located in southeast Alaska, USA. This retreat released environments under which proglacial and subsequently paraglacial processes (Bormann and Sidle, 1990, Hall et al., 1995, Klaar et al., 2015) and ecological succession have occurred (Lawrence et al., 1967, Walker et al., 1993, Chapin et al., 1994, Buma et al., 2017,). In these landscapes, aquatic systems have also formed and undergone physical and ecological development (Fritz et al., 2004, Milner et al., 2007, Milner et al., 2008, Klaar et al., 2009). This aquatic research began in the late 1970's on a newly formed stream, Wolf Point Creek (WPC; Milner, 1987) and has continued with few interruptions to the modern day (Robertson et al., 2015, Milner et al., 2018). The catchment is 29.8 km^2 and in 2017 was dominated by cottonwood (*Populus trichocarpa*) and a few Sitka spruce with alder (*Alnus sinuata*) along the river margins (Klaar et al., 2015). The mouth of WPC was uncovered in the 1940s and the stream is fed by Lawrence Lake which developed in the 1970s. The stream is approximately 2 km in length and 10 m in width (Milner et al., 2008). The stream's benthic macroinvertebrate community has been a central focus of past research and has been studied through the processes of primary succession (Milner and Gloyne-Phillips, 2005, Brown and Milner, 2012, Milner et al., 2008) and more recently, following extreme floods, secondary succession (Klaar et al., 2015, Robertson et al., 2015, Milner et al., 2018).

7.2.2 Macroinvertebrate sampling and identification

Benthic macroinvertebrate samples were collected from 1999 to 2017. Typically, 10 samples were collected annually in August or September using a Surber sampler (330 µm mesh) from a long-standing survey reach approximately 1 km from the tidal limit, selected originally to be representative of the wider river network. Samples were preserved in 70 % ethanol and were then sorted and identified within a year of collection. Individual specimens were identified under a binocular microscope to the lowest possible taxonomic level, using up to date versions of keys available for North America (e.g. Merritt and Cummins, 1996, Thorp and Covich, 2009 for 2015 onward samples). Oligochaeta were identified to class. Chironomidae larvae were identified to species group using Wiederholm (1983), Brooks et al. (2008), and Andersen et al. (2017) under a light microscope. The study stream experienced an extreme high-magnitude flood in the winter of 2005 (Milner et al., 2013), although the summer of 2002 was the second wettest on record (following 2014) and consequently some floods were likely to have occurred during this time period. Subsequently during the summer of 2014 high-frequency floods occurred across streams within GBNP (Milner et al., 2018).

7.2.3 Data analysis

Analyses were undertaken in R studio version 1.1.456 (R version 3.5.1) NMDS was undertaken of $\log_{10}$(original taxa data+1) for all years samples included in this study, using metaMDS in the vegan package (Oksanen et al., 2018), and summary statistics of communities were calculated for each year. Five components of stability were calculated: *Temporal Variability, Extinctions, Invasions, Turnover and Resilience* (Table 7.2). Turnover (Jaccard's dissimilarity) was calculated using the vegdist function in the Vegan package (Oksanen et al., 2018). These measures were calculated using annual average taxa density data based on *n* samples (where *n* = number of samples collected in a given year) between pairs of years in either pre- or post-flood time periods. Four time periods were established (Figure 7.1; Table 7.1).

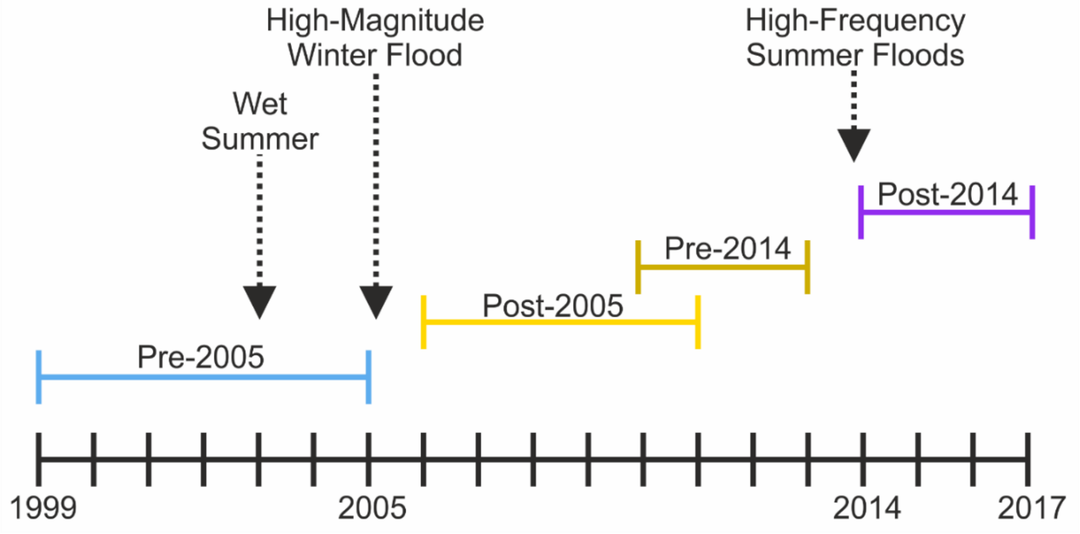

Figure 7.1. Timeline of flood events and sampling time periods applied in this study.

Table 7.1. Time periods of focus in this study, the years they encompass and the number of pairwise comparisons in each time period (number of data points)

Time Period	Years	Number of pairwise comparisons
Pre-2005	1999 - 2005	9
Post-2005	2006 - 2011	9
Pre-2014	2010 - 2013	6
Post-2014	2014 - 2017	6

Pairwise Pearson's correlation coefficients were calculated for components in each time period to assess relationships between individual pairs of components, following tests for normality. Ellipsoids of stability were produced using Principal Components Analysis (PCA) of standardised stability components data.

The orientation, volume and shape of ellipsoids for each time period were compared to a null distribution (sensu Donohue et al., 2013) using permutation analyses and associated permutation tests. Permutation analyses reassigned stability components (observations) year pairs randomly without replacement in the pre-2005 time period. In this study 1000 random permutation based ellipsoids were created. Information regarding the form of a given ellipsoid was then calculated to identify the dimensionality of stability during both pre- and post-flood time periods. Semi-axis lengths were calculated for all ellipsoids based on their axis eigenvalues, where a semi-axis length was calculated by:

$$Semi\ axis\ length = (\lambda \mathrm{i}\ )^{0.5} \qquad \text{Equation 1}$$

Where λ_i is the *i*th eigenvalue of the given covariance matrix of each time period. Relative semi-axis length was calculated by controlling all semi-axis lengths by the longest axis length. This measure allows comparisons to be made about the overall shape of an ellipsoid compared to the null distribution. Differences in relative semi-axis length of pre- and post-flood ellipsoids and pairs of permuted ellipsoids were calculated and tested for significance using permutation tests.

Table 7.2. Components of stability utilised in this study and the method for their quantification

Measure of stability	Description	Quantification method
Number of extinctions (*Extinctions*)	Represents the number of extinctions between a pair of years (Pimm, 1991, Solé and Montoya, 2001)	Quantified as the number of individual taxa identified in the earliest year, of each pair of years in the matrix, not present in the later year.
Number of invasions (*Invasions*)	Follows from the concept of ecological persistence. Persistent communities are hard to invade whilst non-persistent communities are easy to invade (Pimm, 1984)	Quantified as the number of individual taxa identified in the latest year, of each pair of years in the matrix, not present in the early year.
Compositional turnover (*Turnover*)	Change in species' composition of a community through time. This measure incorporates invasion, extinction resistance and temporal variability. Compositional turnover is the reciprocal of persistence (Pimm, 1984)	Quantified as the Jaccard dissimilarity (1-Jaccard similarity) between each pair of years in the matrix. Jaccard dissimilarity was calculated from presence/ absence data.
Resilience	Change in community structure through time. Incorporates species abundances as opposed to presence/ absence only. MacArthur (1955) 'stability' and Orians (1975) 'inertia'. A more resilient community shows lower structural change between samples than a less resilient community	Inverse distance between each pair of years in the matrix. Calculated from Bray-Curtis dissimilarity matrices of log(x+1) macroinvertebrate density data.
Temporal Variability	Variability of community abundance, density or biomass in space (Ives and Carpenter, 2007). Higher levels of temporal variability equate to lower ecological stability.	Quantified as the variation of total macroinvertebrate density among samples for each pair of years (Pimm, 1984, O'Gorman and Emmerson, 2009, Tilman et al., 2006).

Ellipsoid volume describes the overall amount of space occupied in multidimensional stability space with a greater volume indicating weaker relationships between components. Volume was calculated for separate time periods and the permutated ellipsoid data set using the formula:

$$V = \frac{\pi^{n/2}}{\Gamma\left(\frac{n}{2}+1\right)} \prod_{i=1}^{n} (\lambda_i^{0.5}) \qquad \text{Equation 2}$$

Where λ_i is the ith eigenvalue of the given covariance matrix of each time period and where n is the number of different stability components. Differences in calculated volumes will be statistically compared using the null distribution of permuted data sets. Change in the orientation of multidimensional ellipsoids may indicate a shift in the form of dominant relationships between stability components when compared between time periods. Orientation was measured through the identification of the angle (θ) between dominant eigenvectors (V_{1i} and V_{1j}) of each time period. The angle (θ) between these vectors was calculated from their dot products using the equation:

$$\theta = \cos^{-1} \frac{(V\_1i.V\_1j)}{||V_{1i}||\,||V_{1j}||} \qquad \text{Equation 3}$$

Where the magnitude of the dominant eigenvectors are |(|V_1i|)| and ||V_1j||respectively. Difference in angles were compared to a null distribution.

7.3 Results

Forty-six taxa were identified as members of the benthic macroinvertebrate community at WPC from 1999 to 2017 in this study. NMDS analyses associated pre-2005 flood samples with the Gammaridae, Daphniidae, Dytiscidae, *Suwallia forcipata*, *Limnophila* and *Tanyopteryx* (Figure 7.2). All these taxa were eliminated during the 2005 floods and were not recorded in subsequent years, with the exception of *S. forcipata* and *Limnophila,* which recolonized in the post-2014 time period. Post-flood time periods were heavily associated with *Cinygmula* sp., *Serratella ignita*, Oligochaeta and members of the Chironomidae including *Micropsectra, Limnophyes, Cheatocladius*, *Pagastia partica.* Taxonomic richness increased from pre- to post-2005 and then declined during each subsequent time period (Figure 7.3). In contrast total density was highest during the two pre-flood time periods and markedly lower during the post-flood time periods (Figure 7.3). The varied responses between summary statistics and time periods contrasts with the consistent increasing dimensionality of stability reported below.

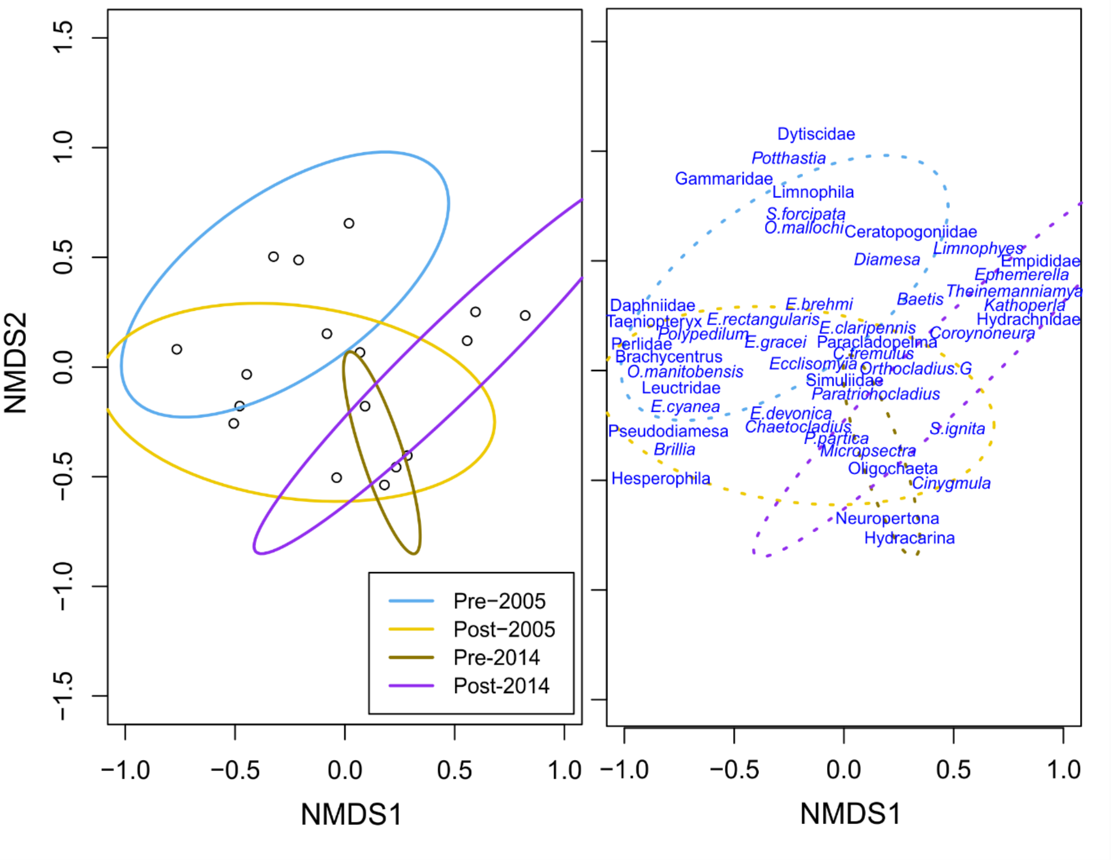

Figure 7.2. NMDS of original species data with a) 95% (standard deviation) confidence ellipsoids of centroid of each time period and b) species positions

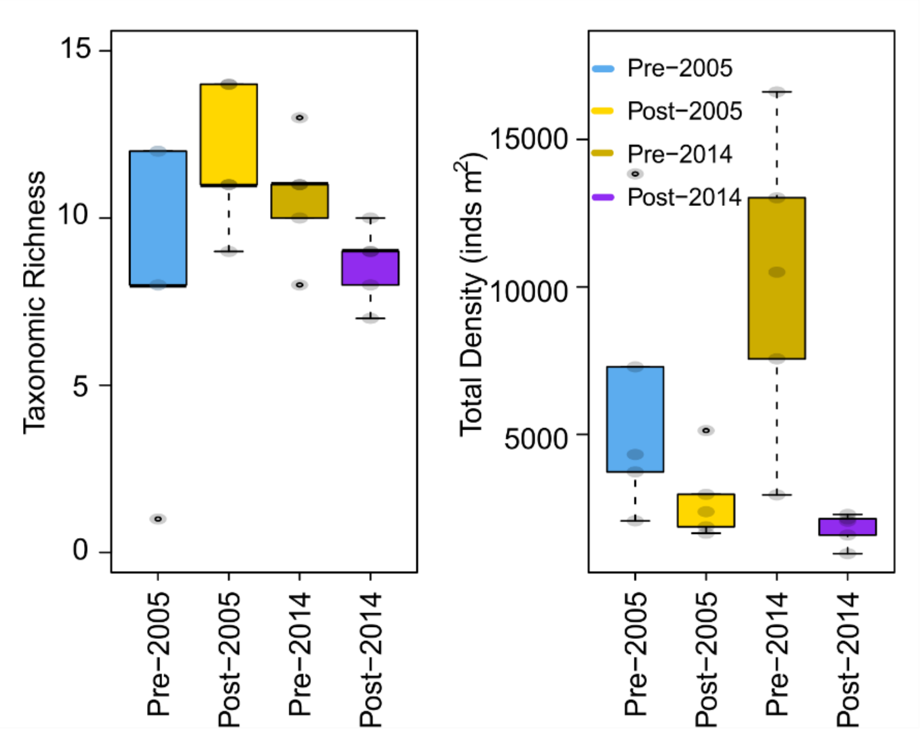

Figure 7.3. Boxplots of taxonomic richness and total density and line plots of semi axis relative length during pre-2005, post-2005, pre-2014 and post-2014 time periods.

Before the first extreme flood disturbance (pre-2005 time period) *Temporal Variability* was high (288 ± 137, Figure 7.4), more than double the next highest value (132 ± 81, post-2014) and *Resilience* between years was low (1.6 ± 0.7). Overall stability components were generally correlated with one another (Figure 7.5), however in a number of cases (four out of 10) these correlations were not significant, in part due to small sample sizes. Often relationships were strong (> ± 0.7, five out of 10; Figure 7.5), with *Turnover, Temporal Variability, Extinctions and Invasions* being positively correlated with each other, with the exception being the weak correlation (0.22) between *Extinctions* and *Invasions*. *Resilience* was negatively correlated with *Turnover, Temporal Variability, Extinctions and Invasions,* although the relationship with *Invasions* was not significant. During this time period, PCA indicated that 72 % of total variance could be explained in a single dimension (Table 7.3) and 89 % explained in two dimensions (Table 7.3).

Following the extreme high-magnitude flood of 2005 a significant increase in the mean number of *Invasions* (4.8 ± 2.9 to 6.1 ± 2.8 taxa; Figure 7.4) and *Turnover* (0.4 ± 0.1 to 0.5 ± 0.2 taxa) was observed. In addition, *Resilience* in this time period increased from the pre-2005 time period to 3.12 ± 3.7. The magnitude of pairwise relationships between stability components decreased (seven out of 10 cases; Figure 7.5a) with fewer significant and less strong pairwise relationships (four out of 10; Figure 7.5b). The direction of relationships was consistent, with the exception of *Extinctions* and *Temporal Variability,* which became negative post-flood. Post-2005 flood the dimensionality of community compositional stability altered with less variation explained in the first dimension (65%) and more explained in two dimensions (93%).

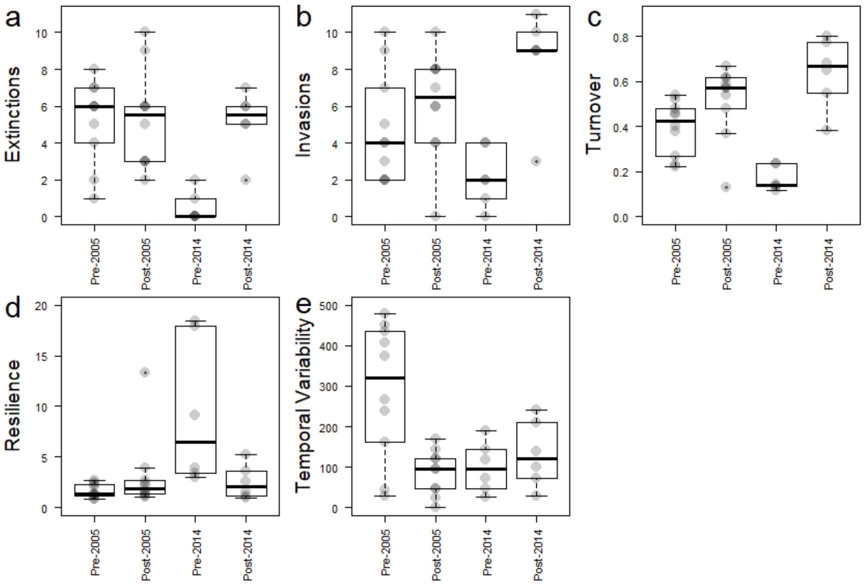

Figure 7.4. Boxplots of components of community compositional stability for each study time period.

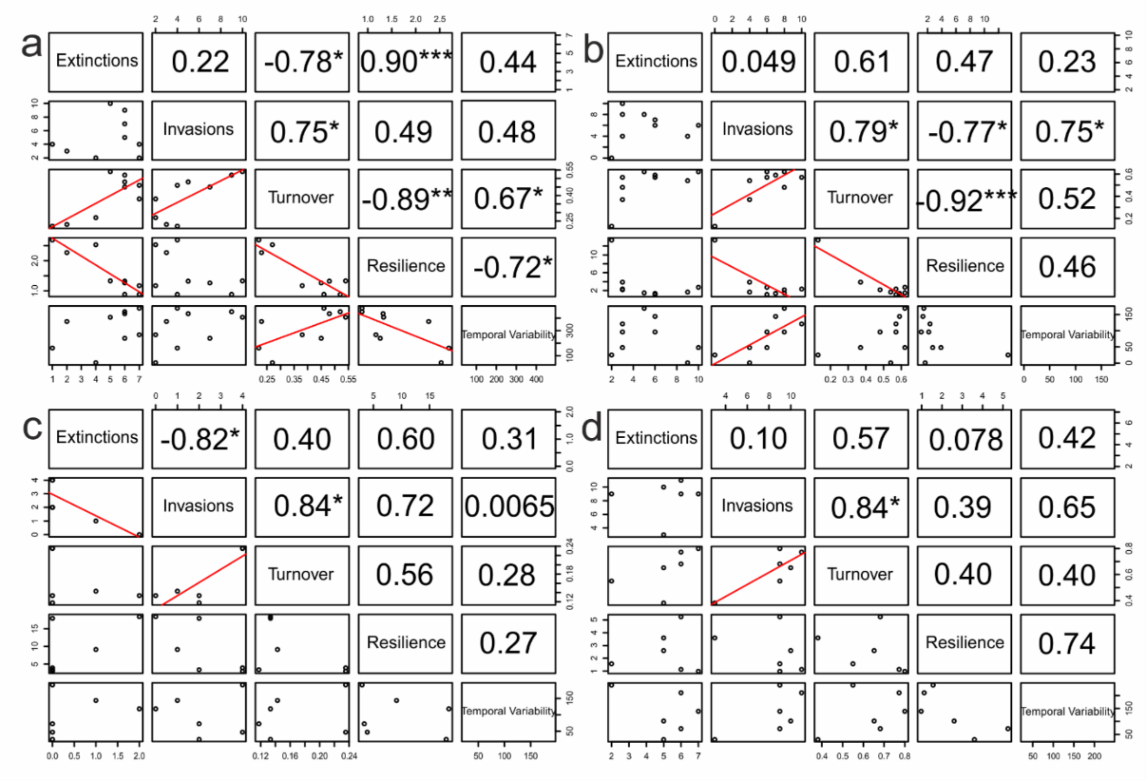

*Figure 7.5. Pairwise correlations for a) pre- and b) post- 2005 (top) and c) pre- and d) post- 2014 floods. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.*

Prior to the second floods (pre-2014), the number of *Extinctions* decreased from >5 during pre- and post-2005 time periods to a mean of 0.5 ± 0.8, whilst *Invasions* also declined, from a mean of >4.8 to 2.2 ± 1.6. *Resilience* during pre-2014 was the highest of any time period at 9.3 ± 7.2, a threefold increase from post-2005. Relationships between components of stability further degraded from earlier time periods with only three strong relationships pre-2014. One of these strong relationships, between *Extinctions* and *Invasions* (-0.82; Figure 7.5) developed from a previously non-significant relationship (pre-2005 and post-2005). The ellipsoid of community compositional stability suggested increased dimensionality during this time period, with 61 % of variation explained by PC1 and a total 86 % including PC2.

Following the extreme high-frequency floods (post-2014), *Invasions* and *Turnover* of taxa were the highest during any time period with means of 8.5 ± 2.8 (increasing fourfold from pre-2014) and 0.6 ± 0.2 respectively. Mean *Extinctions, Resilience* and *Temporal Variability* of density were intermediate between those of earlier time periods. The correlation analyses indicated components of stability decoupled further following the high-frequency floods of 2014, with only two out of 10 pairwise relationships (*Invasions* and *Turnover)* remaining strong. *Resilience*, which pre-2005 had the 2nd highest number of significant relationships and the two most powerful (with *Turnover* -0.89 and *Extinctions* -0.90), had no significant relationships with other components by the final time period (post-2014). This decoupling of components was seen in ellipsoid analyses, as dimensionality increased with only 54% of variation explained in a single dimension and 87% explained in two dimensions (Table 3). Both post-flood time periods saw decreased semi-axis 1 length and increased semi-axis 2 length compared to the respective pre-flood time periods (Figure 7.6).

These changes in the dimensionality of compositional stability are highlighted in the analyses of ellipsoid form. The volume of ellipsoids increased in each subsequent time period from 0.072 (pre-2005) to 0.290 (post-2014; Figure 7.7), with all time period ellipsoid volumes being significantly different to permutation analyses (all $p < 0.01$; **Error! Reference source not found.**). Semi-axis 1 length was significantly different to null models with a shorter length during pre-2005, post-2005 and pre-2014 time periods. Length decreased through each subsequent time period (Figure 7.7a), with the post-2014 axis being shortest; this axis length was not significantly different from those of null models. Semi-axis 2 length and relative length (Figure 7.7b) were significantly different to null models with shorter lengths inn pre-2005 and pre-2014 time periods; in contrast, during post-2005 and post-2014 time periods semi-axis two was not significantly different to null models. Importantly, no significant response was observed in differences in angle between the dominant semi-axes for either extreme flood event (Figure 7.7).

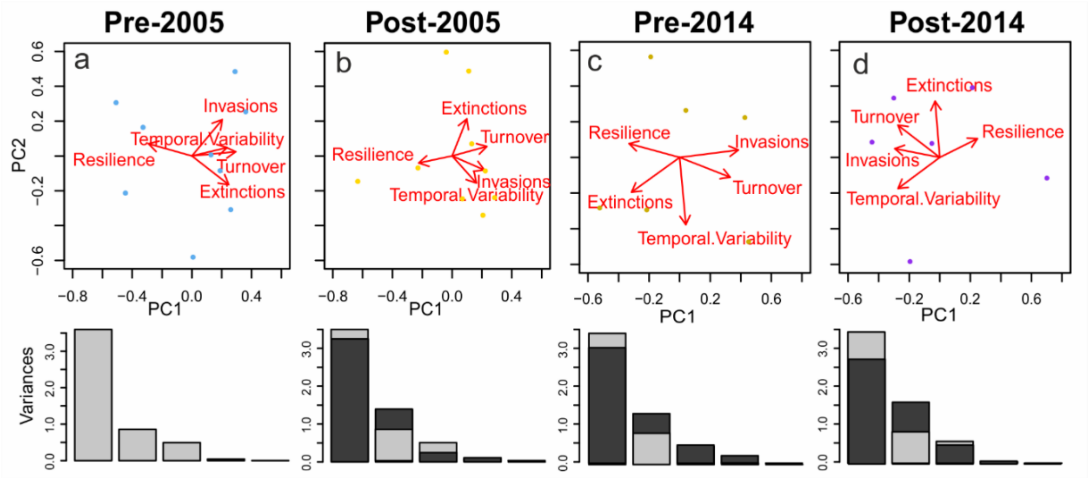

Figure 7.6. PCA biplots and barplots of variances for each axis for each time period in this study. Pre-2005 time period bars (light grey) are overlaid on subsequent time periods (dark grey) in barplots

Table 7.3. Proportions of total variation explained by each semi-axis for stability components during each time period. During all time periods 100% of variation was explained in four axes and thus semi-axis 4 and 5 are not shown.

Cumulative Proportion of Variation	Semi-axis 1	Semi-axis 2	Semi-axis 3
Pre-2005	0.72	0.89	0.99
Post-2005	0.65	0.93	0.98
Pre-2014	0.61	0.86	0.96
Post-2014	0.54	0.87	0.98

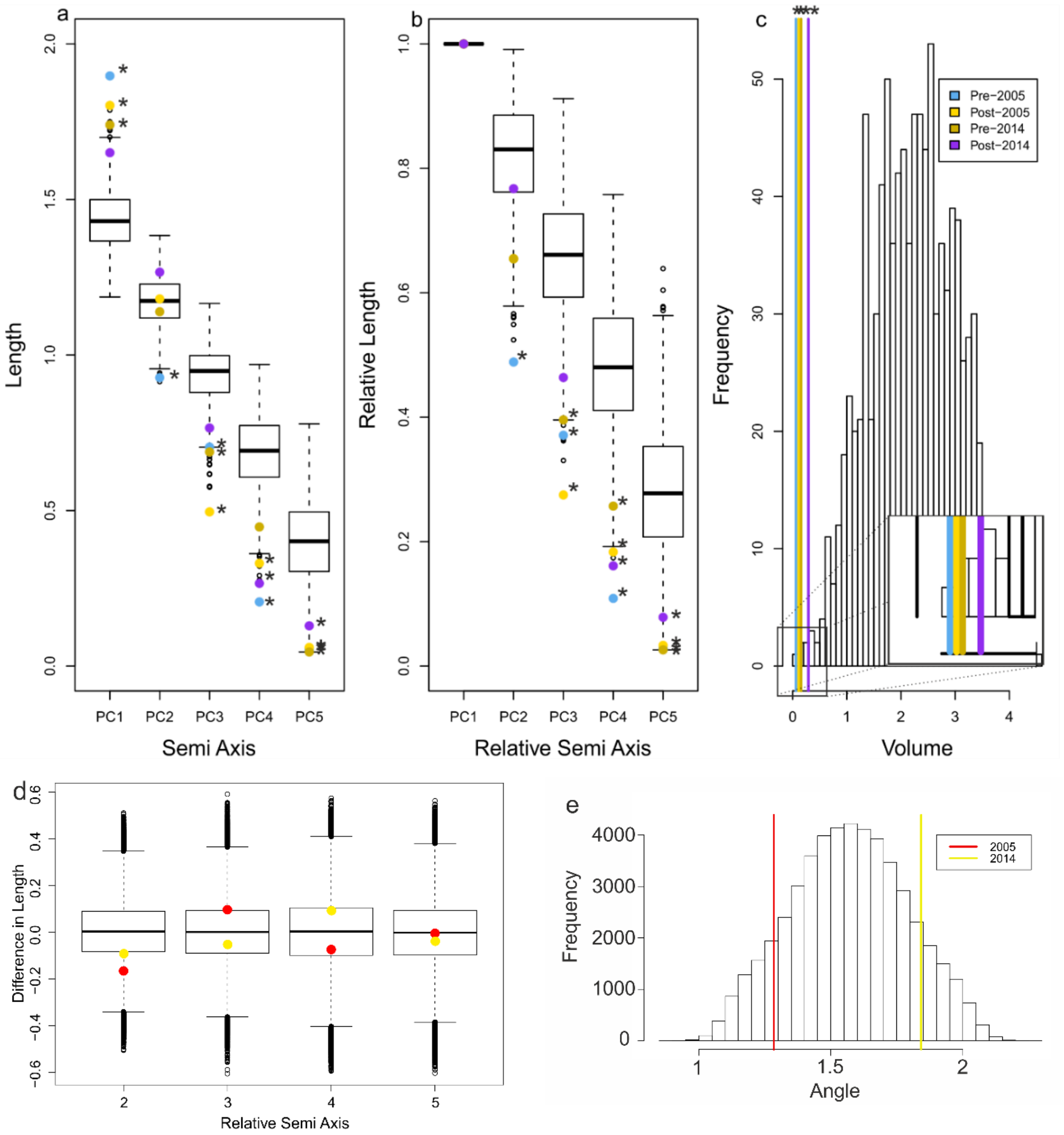

Figure 7.7. Boxplots of Semi-axis a) lengths b) relative lengths and c) histograms of ellipsoid volumes. * equals significant at $p < 0.05$. All study time periods volumes were significant at $p < 0.01$. Difference in relative axis length (bottom left) and angle between semi-axis 1 orientations (bottom right). Box plots and histograms represent permuted dataset and coloured points (see legend for colours) represent time periods in this study.

7.4 Discussion

The dimensionality of benthic macroinvertebrate community compositional stability in the pre-disturbance time period (pre-2005) was low compared to later time periods, a pattern consistent with experimental (Hillebrand et al., 2018) and modelling (Radchuk et al., 2019) studies. Both types of flood (high-magnitude and high-frequency) acted to increase the dimensionality of stability through pathways which appeared to be predominantly consistent. However, contrasting responses between *extinctions* and *turnover* were observed between the two sets of floods. These contrasting responses to such disturbances which occurred in sequence represent a new finding in the study of dimensionality of stability. In addition, the contrasting responses between *extinctions* and *turnover* between the two floods highlights the complexities of stability and thus the challenges associated with studying its response to extreme disturbances. The pair of floods in this study sequentially degraded the comparatively low dimensionality of benthic macroinvertebrate community compositional stability observed prior to the first flood in 2005, leading to increased dimensionality through time. This study represents the first example of the implementation of the concept of dimensionality of stability to long-term, real-world community data.

The lowest dimensionality of community compositional stability observed during the pre-2005 flood period offers the first evidence of this in an unmanipulated ecosystem, previously only reported in in-situ and ex-situ experiments (Donohue et al., 2013, Hillebrand et al., 2018) and modelling studies (Radchuk et al., 2019, Yang et al., 2019) and thus supports H_1. The dimensionality reported here during the pre-2005 flood time period is broadly consistent with that reported for controls in Donohue et al. (2013). This finding demonstrates that low dimensionality of stability can persist through some perturbations and disturbances that are typical of natural systems (Ives and Carpenter, 2007), for instance the particularly wet summer of 2002 (Milner et al., 2018).

Whilst at WPC the consistent monitoring of the benthic macroinvertebrate community since the stream was first colonised provides us with a clear record of the extent of disturbances to this community. The lack of substantial disturbances recorded during community assembly (to 2005) is not consistent with conditions observed in the majority of ecosystems. As a result, a fundamental question may need to be asked about how regularly you may be able to attribute the label ‘stable’ to a natural ecosystem. In the majority of ecosystems intermittent disturbance is a regular feature (Jenkins et al., 2010). In such systems periods of stability may represent relatively rare moments rather than representing the norm.

The extreme high-magnitude flood (2005) increased the dimensionality of benthic macroinvertebrate compositional stability in support of H_2. This increased dimensionality was driven by the reduced strength and in many cases the complete breakdown of relationships between *extinctions* and *turnover* with all other components, which highlights the broad reaching effect of disturbances on stability reported previously (Van Ruijven and Berendse, 2010, Donohue et al., 2013, Hillebrand et al., 2018). The decoupling of *extinctions* from invertebrate community *resilience* and *turnover* after the 2005 flood, increased further following the 2014 floods suggesting this may be a common feature of macroinvertebrate community response to flood events within this early successional stage stream ecosystem.

In contrast to the decoupling of *extinctions*, *invasions* became increasingly coupled with other stability components following the floods, in spite of increased dimensionality overall. This pattern is consistent with dispersal governed community reassembly as reported elsewhere (Jiang and Patel, 2008, Ferrenberg et al., 2013, Brown et al., 2018) where community composition is controlled by the capacity of taxa to access a disturbed system. This shift in relationships is indicative of community reassembly driven predominantly by the invasion of new taxa (e.g. *Serratella ignita, Cinygmula, Limnophyes* grp. and *Corynoneura* grp.), and recolonization of taxa (e.g. *Suwallia forcipata* and *Pagastia partica* grp.) previously present (Davis et al., 2000; Chapter 4). In addition, altered niche space post-flood (Chapter 5) may influence community compositional stability by controlling the success of future invasions through time. Release from inter-specific competition may have acted to limit the extent of extinctions post-flood (Bengtsson, 1989, Urban et al., 2012) and increased opportunities for colonization. Higher rates of invasion and lower rates of extinctions have been associated with reduced competition in ecosystems with available unused resources elsewhere (Davis et al., 2000), a pattern that must now be explored in GBNP to identify if it governs reassembly in the post-glacial streams.

The dimensionality of stability did not recover to its pre-2005 state before the high-frequency floods of 2014, a pattern consistent with the failure of community taxonomic composition to recover post-flood (Milner et al., 2018; Chapter 6). This was evident in five pairwise relationships which remained decoupled before the 2014 floods, but which had been coupled before the 2005 floods. Such a failure to recouple is expected to have left legacy effects in the community. Legacy effects are ongoing effects which persist temporally following a disturbance (Foster et al., 1998) altering ecosystems reassembly (Ledger et al., 2006) and response to future disturbances (Buma and Wessman, 2011, Stanley et al., 2010). These legacy effects lead to increased ellipsoid volume and reduced semi-axis 1 length following the 2005 floods. This failure of community compositional stability to recover its low dimensionality through almost a decade post-flood (2005 to 2013) possibly reflects disruption and/or alterations to the processes governing community assembly between time periods.

Before the first flood (pre-2005), where the community has developed over a period of 60 years following deglaciation, assembly had been linked to colonization by new species (Brown and Milner, 2012) and through later years (i.e. the pre-2005 time period) by biotic interactions between taxa and habitat availability (Flory and Milner, 1999, Milner and Gloyne-Phillips, 2005). In contrast, the processes of community reassembly following a disturbance are thought to be more closely controlled by alterations to the available niche space (Chapter 5) and dispersal capacity of potential colonizers (Brown et al., 2018; Chapter 4 and 6)**.** Such differences in controls of assembly have previously been reported in drought affected pond communities (Chase, 2007). In the current study, these differences may explain the increasingly severe response of pairwise interactions to the two floods, for instance between *extinctions* and *turnover* which began to be decoupled following the 2005 floods and then switched in direction completely following the 2014 floods. Such an exacerbated response highlights the threats multiple disturbances could pose to natural ecosystems and their community stability, whilst it also increases the challenges ecosystem managers will face when managing ecosystems which have prescribed end points, such as those set out under European Union and English Law (Special Areas of Conservation and Sites of Special Scientific Interest). To facilitate the successful management of ecosystems moving forward into an increasingly extreme and unstable future, it may be necessary to embrace dynamism in our managed ecosystems.

Benthic macroinvertebrate community composition is associated with important ecosystem functions in streams (Schäfer et al., 2007), including nutrient cycling and secondary productivity (Wallace and Webster, 1996, Cao et al., 2018). Decreased stability post-flood could increase the likelihood of drastic and/or unpredictable changes to community composition and thus ecosystem function (Grman et al., 2010). This is particularly pertinent given the disruption of natural processes and the pathways which govern community assembly observed here and in previous studies of dimensionality of ecological stability (Donohue et al., 2013, Hillebrand et al., 2018). Elsewhere such alterations to diversity and composition, associated with decreased stability, have been shown to drive reductions in numerous ecosystem functions as disturbed communities become assembled predominantly of taxa which are able to exploit the disturbed environment (Cao et al., 2018). Decreased community and more broadly ecosystem stability could increase the risk of such major changes in the capacity of ecosystems to provide important ecosystems functions in the future, and thus could threaten ecosystem services relied upon by human populations across the globe (Dodds et al., 2013).

This study highlights the capacity of a pair of floods with drastically different forms to sequentially degrade the low dimensionality of stability observed prior to flood events. A consistent increasing dimensionality of community compositional stability was observed from a relatively 'cigar' shaped hyperdimensional ellipsoid in which >70 % of variation was explained in a single dimension, consistent with the earlier research (Donohue et al., 2013, Hillebrand et al., 2018), to the dimensionality ellipsoid becoming more 'disk' shaped with only 50 % of variation explained in one axis and 87 % explained in two axes following the second extreme flood (2014). This is the first application of the concept of changing dimensionality of stability to multiple disturbance events and clearly highlights that multiple disturbances can sequentially degrade relationships between stability components. These findings are supported by the significant changes to community composition reported for the same study stream in Milner et al. (2018) during the same disturbance events. However, when comparing taxonomic richness, total density and stability in this study, it was apparent that summary metrics did not respond to the floods in the same manner as the dimensionality of stability. This may be because the powerful multidimensional approach to stability utilised here potentially captures a more diverse array of processes which govern ecological response than any individual summary statistic can alone or when analysed individually (Donohue et al. 2013). Understanding how community and more broadly ecological stability components respond together to a series of disturbances can only be expected to become more relevant as we experience more frequent disturbances under future climate scenarios.

The varied responses of individual components of stability through each time period further highlighted the limited utility of applying a single metric of community compositional stability to studies which attempt to elucidate the processes which govern community response and stability overall (Donohue et al., 2013, Donohue et al., 2016). This finding gives credence to the approach taken in chapters four and six in which a number of potential measures of community compositional stability were included: *resilience* (highlighted by Donohue et al. (2016) as an inherently multidimensional metric of stability), *temporal variability*, *persistence* (referred to as *turnover* in this chapter, to be consistent with the ecological stability literature (Donohue et al., 2013)) degraded into its metric parts - turnover and nestedness as well as consideration of dominance hierarchies which are important for the control of invasions (Hillebrand et al., 2008).

Given the evidence made available in this study, the diverse approach was necessary to capture community wide and stability responses to extreme floods given the significant increase in dimensionality of stability reported in this study.

This study represents the first attempt to apply dimensionality of ecological stability concepts developed experimentally to an unmanipulated natural system at larger spatial (10^1 m^2) and temporal (18 years) scale. The increasing dimensionality of stability observed here following flood disturbances is consistent with past manipulative small spatial and temporal scale work (Donohue et al., 2013, Barros et al., 2016, Hillebrand et al., 2018, Radchuk et al., 2019) and thus suggests that this theory may be pertinent to processes occurring in natural and unmanipulated ecosystems. Further, this study may offer evidence that disturbances with different forms (timing, duration, magnitude) can affect dimensionality in different ways consistent with Radchuk et al. (2019), although the dominant responses were largely consistent between the two floods observed in the current study. However, it is possible that differences in response could be driven by the sequential nature of the two disturbances and the failure of communities to recover completely before the 2014 floods.

An important next step is to scale up the in-situ approach taken here, to a more diverse range of ecosystems to further develop our understanding of responses of ecological stability to disturbance. The fundamental challenge in doing this is accessing sufficiently data rich data sets across a diverse array of systems. One possible opportunity to do this can be found in governmental monitoring databases, such as those which are collected under the Water Framework Directive in European law (European-Commission, 2000), or by compiling multiple long-term time-series originally collected for research purposes. Such data sets represent an invaluable resource within which to attempt to scale up the concepts developed experimentally in smaller scale studies into more consistent broad reaching theories. A future step would be the application of these concepts to open source global databases of terrestrial and aquatic ecosystems and evidencing responses to multiple forms of disturbance (e.g. fire, drought, ocean acidification, pollution) to establish if findings at these broadest levels are also consistent with current evidence.

7.5 Conclusion

This study has demonstrated the applicability of the dimensionality of ecological stability concept to detect clear effects of disturbance in a natural ecosystem. As such it corroborates the past findings of experimental and modelling studies. Two extreme floods occurring in sequence drove sequential degradation of the relatively low dimensionality of stability that was evident before disturbance. Generally, all components of stability were decoupled by the floods, however *invasions* demonstrated increased coupling to *resilience* and *temporal variability* during post-flood time periods. Increased association between invasion and other components of stability is thought to be consistent with community reassembly, driven predominantly by dispersal limitation of colonising taxa, rather than other possible assembly processes, such as priority effects or inter-specific competition. This study demonstrates the application of a multidimensional stability approach significantly enhances classical community response analyses. In this study, relatively variable responses in taxonomic richness and total density were observed following the floods in comparison to the directional decrease in stability. Future research is necessary to further develop and ground truth the theory of changing dimensionality of ecological and community stability in other natural systems.

7.6 References

ALLESINA, S. & TANG, S. 2012. Stability criteria for complex ecosystems. *Nature,* 483**,** 205-208.

ANDERSEN, T., CRANSTON, P. S. & EPLER, J. H. 2017. *Chironomidae of the Holarctic Region: Keys and Diagnoses, Part 1: Larvae*, Entomological Society of Lund, Sweden.

ANDERSON, A. M. & FERRINGTON, L. C. 2013. Resistance and resilience of winter-emerging Chironomidae (Diptera) to a flood event: implications for Minnesota trout streams. *Hydrobiologia,* 707**,** 59-71.

ARNOLDI, J. F., LOREAU, M. & HAEGEMAN, B. 2016. Resilience, reactivity and variability: A mathematical comparison of ecological stability measures. *Journal of Theoretical Biology,* 389**,** 47-59.

BARROS, C., THUILLER, W., GEORGES, D., BOULANGEAT, I. & MÜNKEMÜLLER, T. 2016. N-dimensional hypervolumes to study stability of complex ecosystems. *Ecology Letters,* 19**,** 729-742.

BÊCHE, L. A., CONNORS, P. G., RESH, V. H. & MERENLENDER, A. M. 2009. Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography,* 32**,** 778-788.

BEISNER, B. E., HAYDON, D. T. & CUDDINGTON, K. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment,* 1**,** 376-382.

BENGTSSON, J. 1989. Interspecific competition increases local extinction rate in a metapopulation system. *Nature,* 340**,** 713-715.

BENGTSSON, J. 1998. Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. *Applied Soil Ecology,* 10**,** 191-199.

BERG, P., MOSELEY, C. & HAERTER, J. O. 2013. Strong increase in convective precipitation in response to higher temperatures. *Nature Geoscience,* 6**,** 181.

BLINDOW, I., ANDERSSON, G., HARGEBY, A. & JOHANSSON, S. 1993. Long-term pattern of alternative stable states in two shallow eutrophic lakes. *Freshwater Biology,* 30**,** 159-167.

BOGAN, M. T., BOERSMA, K. S. & LYTLE, D. A. 2015. Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams. *Freshwater Biology,* 60**,** 2547-2558.

BORMANN, B. T. & SIDLE, R. C. 1990. Changes in Productivity and Distribution of Nutrients in a Chronosequence at Glacier Bay National Park, Alaska. *Journal of Ecology,* 78**,** 561-578.

BROOKS, S., LANGDON, P. & HEIRI, O. 2008. *The Identification and Use of Palaearctic Chironomidae Larvae in Palaeoecology*.

BROWN, L. E., KHAMIS, K., WILKES, M., BLAEN, P., BRITTAIN, J. E., CARRIVICK, J. L., FELL, S., FRIBERG, N., FÜREDER, L., GISLASON, G. M., HAINIE, S., HANNAH, D. M., JAMES, W. H. M., LENCIONI, V., OLAFSSON, J. S., ROBINSON, C. T., SALTVEIT, S. J., THOMPSON, C. & MILNER, A. M. 2018. Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nature Ecology & Evolution,* 2**,** 325-333.

BROWN, L. E. & MILNER, A. M. 2012. Rapid loss of glacial ice reveals stream community assembly processes. *Global Change Biology,* 18**,** 2195-2204.

BUMA, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere,* 6**,** art70.

BUMA, B., BISBING, S., KRAPEK, J. & WRIGHT, G. 2017. A foundation of ecology rediscovered: 100 years of succession on the William S. Cooper plots in Glacier Bay, Alaska. *Ecology,* 98**,** 1513-1523.

BUMA, B. & WESSMAN, C. A. 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere,* 2**,** art64.

BUTCHART, S. H. M., WALPOLE, M., COLLEN, B., VAN STRIEN, A., SCHARLEMANN, J. P. W., ALMOND, R. E. A., BAILLIE, J. E. M., BOMHARD, B., BROWN, C., BRUNO, J., CARPENTER, K. E., CARR, G. M., CHANSON, J., CHENERY, A. M., CSIRKE, J., DAVIDSON, N. C., DENTENER, F., FOSTER, M., GALLI, A., GALLOWAY, J. N., GENOVESI, P., GREGORY, R. D., HOCKINGS, M., KAPOS, V., LAMARQUE, J.-F., LEVERINGTON, F., LOH, J., MCGEOCH, M. A., MCRAE, L., MINASYAN, A., MORCILLO, M. H., OLDFIELD, T. E. E., PAULY, D., QUADER, S., REVENGA, C., SAUER, J. R., SKOLNIK, B., SPEAR, D., STANWELL-SMITH, D., STUART, S. N., SYMES, A., TIERNEY, M., TYRRELL, T. D., VIÉ, J.-C. & WATSON, R. 2010. Global Biodiversity: Indicators of Recent Declines. *Science,* 328**,** 1164-1168.

CAMPBELL, V., MURPHY, G. & ROMANUK, T. N. 2011. Experimental design and the outcome and interpretation of diversity–stability relations. *Oikos,* 120**,** 399-408.

CAO, X., CHAI, L., JIANG, D., WANG, J., LIU, Y. & HUANG, Y. 2018. Loss of biodiversity alters ecosystem function in freshwater streams: potential evidence from benthic macroinvertebrates. *Ecosphere,* 9**,** e02445.

CAPON, S. J., LYNCH, A. J. J., BOND, N., CHESSMAN, B. C., DAVIS, J., DAVIDSON, N., FINLAYSON, M., GELL, P. A., HOHNBERG, D., HUMPHREY, C., KINGSFORD, R. T., NIELSEN, D., THOMSON, J. R., WARD, K. & NALLY, R. M. 2015. Regime shifts, thresholds and multiple stable states in freshwater ecosystems; a critical appraisal of the evidence. *Science of The Total Environment,* 534**,** 122-130.

CHAPIN, F. S., WALKER, L. R., FASTIE, C. L. & SHARMAN, L. C. 1994. Mechanisms of Primary Succession Following Deglaciation at Glacier Bay, Alaska. *Ecological Monographs,* 64**,** 149-175.

CHAPIN, F. S., ZAVALETA, E. S., EVINER, V. T., NAYLOR, R. L., VITOUSEK, P. M., REYNOLDS, H. L., HOOPER, D. U., LAVOREL, S., SALA, O. E., HOBBIE, S. E., MACK, M. C. & DÍAZ, S. 2000. Consequences of changing biodiversity. *Nature,* 405**,** 234-242.

CHASE, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences,* 104**,** 17430-17434.

CLASSEN, A. T., KNAPP, A. K., SMITH, B., BEIER, C., BRISKE, D. D., WENG, E., HEISLER, J. L., BELL, J. E., REICHSTEIN, M., SMITH, M. D., FAY, P. A., SHERRY, R., SMITH, S. D., LEAVITT, S. W. & LUO, Y. 2008. Consequences of More Extreme Precipitation Regimes for Terrestrial Ecosystems. *BioScience,* 58**,** 811-821.

DAVIS, M. A., GRIME, J. P. & THOMPSON, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology,* 88**,** 528-534.

DODDS, W. K., PERKIN, J. S. & GERKEN, J. E. 2013. Human Impact on Freshwater Ecosystem Services: A Global Perspective. *Environmental Science & Technology,* 47**,** 9061-9068.

DONOHUE, I., HILLEBRAND, H., MONTOYA, J. M., PETCHEY, O. L., PIMM, S. L., FOWLER, M. S., HEALY, K., JACKSON, A. L., LURGI, M., MCCLEAN, D., O'CONNOR, N. E., O'GORMAN, E. J. & YANG, Q. 2016. Navigating the complexity of ecological stability. *Ecology Letters,* 19**,** 1172-1185.

DONOHUE, I., PETCHEY, O. L., MONTOYA, J. M., JACKSON, A. L., MCNALLY, L., VIANA, M., HEALY, K., LURGI, M., O'CONNOR, N. E. & EMMERSON, M. C. 2013. On the dimensionality of ecological stability. *Ecology Letters,* 16**,** 421-429.

DUNNE, J. A., WILLIAMS, R. J. & MARTINEZ, N. D. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters,* 5**,** 558-567.

EUROPEAN-COMMISSION 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy Official Journal L 327 , 22/12/2000 P. 0001 - 0073. *In:* PARLIAMENT, E. (ed.).

FERRENBERG, S., O'NEILL, S. P., KNELMAN, J. E., TODD, B., DUGGAN, S., BRADLEY, D., ROBINSON, T., SCHMIDT, S. K., TOWNSEND, A. R., WILLIAMS, M. W., CLEVELAND, C. C., MELBOURNE, B. A., JIANG, L. & NEMERGUT, D. R. 2013. Changes in assembly processes in soil bacterial communities following a wildfire disturbance. *The Isme Journal,* 7**,** 1102.

FLECKER, A. S. & FEIFAREK, B. 1994. Disturbance and the temporal variability of invertebrate assemblages in two Andean streams. *Freshwater Biology,* 31**,** 131-142.

FLORY, E. A. & MILNER, A. M. 1999. The role of competition in invertebrate community development in a recently formed stream in Glacier Bay National Park, Alaska. *Aquatic Ecology,* 33**,** 175-184.

FOSTER, D. R., KNIGHT, D. H. & FRANKLIN, J. F. 1998. Landscape Patterns and Legacies Resulting from Large, Infrequent Forest Disturbances. *Ecosystems,* 1**,** 497-510.

FRANCE, K. E. & DUFFY, J. E. 2006. Diversity and dispersal interactively affect predictability of ecosystem function. *Nature,* 441**,** 1139-43.

FRITZ, K. M. & DODDS, W. K. 2004. Resistance and Resilience of Macroinvertebrate Assemblages to Drying and Flood in a Tallgrass Prairie Stream System. *Hydrobiologia,* 527**,** 99-112.

FRITZ, S. C., ENGSTROM, D. R. & JUGGINS, S. 2004. Patterns of early lake evolution in boreal landscapes: a comparison of stratigraphic inferences with a modern chronosequence in Glacier Bay, Alaska. *Holocene,* 14**,** 828-840.

GRMAN, E., LAU, J. A., SCHOOLMASTER JR., D. R. & GROSS, K. L. 2010. Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecology Letters,* 13**,** 1400-1410.

HALL, D. K., BENSON, C. S. & FIELD, W. O. 1995. Changes of Glaciers in Glacier Bay, Alaska, Using Ground and Satellite Measurements. *Physical Geography,* 16**,** 27-41.

HARRISON, G. W. 1979. Stability under Environmental Stress: Resistance, Resilience, Persistence, and Variability. *The American Naturalist,* 113**,** 659-669.

HILLEBRAND, H., BENNETT, D. M. & CADOTTE, M. W. 2008. Consequences of Dominance: A Review of Evenness Effects on Local and Regional Ecosystem Proceses *Ecology,* 89**,** 1510-1520.

HILLEBRAND, H., LANGENHEDER, S., LEBRET, K., LINDSTRÖM, E., ÖSTMAN, Ö. & STRIEBEL, M. 2018. Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters,* 21**,** 21-30.

HUBBELL, S. P. 1979. Tree Dispersion, Abundance, and Diversity in a Tropical Dry Forest. *Science,* 203**,** 1299-1309.

IVES, A. R. & CARPENTER, S. R. 2007. Stability and Diversity of Ecosystems. *Science,* 317**,** 58-62.

JIANG, L. & PATEL, S. N. 2008. COMMUNITY ASSEMBLY IN THE PRESENCE OF DISTURBANCE: A MICROCOSM EXPERIMENT. *Ecology,* 89**,** 1931-1940.

JIANG, L. & PU, Z. 2009. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *Am Nat,* 174**,** 651-9.

KIESSLING, W. 2005. Long-term relationships between ecological stability and biodiversity in Phanerozoic reefs. *Nature,* 433**,** 410-413.

KLAAR, M. J., KIDD, C., MALONE, E., BARTLETT, R., PINAY, G., CHAPIN, F. S. & MILNER, A. 2015. Vegetation succession in deglaciated landscapes: implications for sediment and landscape stability. *Earth Surface Processes and Landforms,* 40**,** 1088-1100.

KLAAR, M. J., MADDOCK, I. & MILNER, A. M. 2009. The Development of Hydraulic and Geomorphic Complexity in Recently Formed Streams in Glacier Bay National Park, Alaska. *River Research and Applications,* 25**,** 1331-1338.

KNAPP, R. A., MATTHEWS, K. R. & SARNELLE, O. 2001. RESISTANCE AND RESILIENCE OF ALPINE LAKE FAUNA TO FISH INTRODUCTIONS. *Ecological Monographs,* 71**,** 401-421.

KRATINA, P., GREIG, H. S., THOMPSON, P. L., CARVALHO-PEREIRA, T. S. A. & SHURIN, J. B. 2012. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology,* 93**,** 1421-1430.

LAWRENCE, D. B., SCHOENIKE, R. E., QUISPEL, A. & BOND, G. 1967. The Role of Dryas Drummondii in Vegetation Development Following Ice Recession at Glacier Bay, Alaska, with Special Reference to Its Nitrogen Fixation by Root Nodules. *Journal of Ecology,* 55**,** 793-813.

LEDGER, M., M L HARRIS, R., MILNER, A. & ARMITAGE, P. 2006. *Disturbance, biological legacies and community development in stream mesocosms*.

MACARTHUR, R. H. 1955. Fluctuation of Animal Populations and a Measure of Community Stability. *Ecology,* 36**,** 533-536.

MARI, L., CASAGRANDI, R., BERTUZZO, E., RINALDO, A. & GATTO, M. 2014. Metapopulation persistence and species spread in river networks. *Ecology Letters,* 17**,** 426-434.

MARTÍNEZ, M. L., VÁZQUEZ, G. & SÁNCHEZ COLÓN, S. 2001. Spatial and temporal variability during primary succession on tropical coastal sand dunes. *Journal of Vegetation Science,* 12**,** 361-372.

MATHERS, K. L., RICE, S. P. & WOOD, P. J. 2018. Temporal variability in lotic macroinvertebrate communities associated with invasive signal crayfish (Pacifastacus leniusculus) activity levels and substrate character. *Biological Invasions,* 20**,** 567-582.

MAY, R. M. 1972. Will a Large Complex System be Stable? *Nature,* 238**,** 413-414.

MAY, R. M. 1973. *Stability and complexity in model ecosystems.,* Princeton N. J., Princeton University Press.

MCCANN, K. S. 2000. The diversity–stability debate. *Nature,* 405**,** 228-233.

MERRITT, R. W. & CUMMINS, K. W. 1996. *An introduction to the aquatic insects of North America*, Kendall Hunt.

MILNER, A. M. 1987. Colonization and ecological development of new streams in Glacier Bay National Park, Alaska. *Freshwater Biology,* 18**,** 53-70.

MILNER, A. M., FASTIE, C. L., CHAPIN, F. S., ENGSTROM, D. R. & SHARMAN, L. C. 2007. Interactions and linkages among ecosystems during landscape evolution. *Bioscience,* 57**,** 237-247.

MILNER, A. M. & GLOYNE-PHILLIPS, I. T. 2005. The role of riparian vegetation and woody debris in the development of macroinvertebrate assemblages in streams. *River Research and Applications,* 21**,** 403-420.

MILNER, A. M., PICKEN, J. L., KLAAR, M. J., ROBERTSON, A. L., CLITHEROW, L. R., EAGLE, L. & BROWN, L. E. 2018. River ecosystem resilience to extreme flood events. *Ecology and Evolution,* 0.

MILNER, A. M., ROBERTSON, A. L., MCDERMOTT, M. J., KLAAR, M. J. & BROWN, L. E. 2013. Major flood disturbance alters river ecosystem evolution. *Nature Climate Change,* 3**,** 137-141.

MILNER, A. M., ROBERTSON, A. L., MONAGHAN, K. A., VEAL, A. J. & FLORY, E. A. 2008. Colonization and development of an Alaskan stream community over 28 years. *Frontiers in Ecology and the Environment,* 6**,** 413-419.

MURRY, B. A. & FARRELL, J. M. 2014. Resistance of the size structure of the fish community to ecological perturbations in a large river ecosystem. *Freshwater Biology,* 59**,** 155-167.

NAEEM, S. & LI, S. 1997. Biodiversity enhances ecosystem reliability. *Nature,* 390**,** 507-509.

NEUBERT, M. G. & CASWELL, H. 1997. Alternatives to Resilience for Measuring the Responses of Ecological Systems to Perturbations. *Ecology,* 78**,** 653-665.

O'GORMAN, E. J. & EMMERSON, M. C. 2009. Perturbations to trophic interactions and the stability of complex food webs. *Proc Natl Acad Sci U S A,* 106**,** 13393-8.

ODUM, E. 1953. *Fundamentals of Ecology,* Philadelphia, PA, Saunders.

OKSANEN, J., BLANCHET, F. G., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGLINN, D., MINCHIN, P. R., O'HARA, R. B., SIMPSON, G. L., SOLYMOS, P., STEVENS, M. H. H., SZOECS, E. & WAGNER, H. 2018. vegan: Community Ecology Package. 2.5-2 ed.

ORIANS, G. H. 1975. Diversity, stability and maturity in natural ecosystems. *In:* VAN DOBBEN, W. H. & LOWE-MCCONNELL, R. H. (eds.) *Unifying Concepts in Ecology: Report of the plenary sessions of the First international congress of ecology, The Hague, the Netherlands, September 8–14, 1974.* Dordrecht: Springer Netherlands.

PAINE, R. Controlled manipulations in the marine intertidal zone and their contributions to ecological theory. Academy of Natural Sciences, 1977. 245-270.

PENNEKAMP, F., PONTARP, M., TABI, A., ALTERMATT, F., ALTHER, R., CHOFFAT, Y., FRONHOFER, E. A., GANESANANDAMOORTHY, P., GARNIER, A., GRIFFITHS, J. I., GREENE, S., HORGAN, K., MASSIE, T. M., MÄCHLER, E., PALAMARA, G. M., SEYMOUR, M. & PETCHEY, O. L. 2018. Biodiversity increases and decreases ecosystem stability. *Nature,* 563**,** 109-112.

PETERSEN, J. K., HANSEN, J. W., LAURSEN, M. B., CLAUSEN, P., CARSTENSEN, J. & CONLEY, D. J. 2008. REGIME SHIFT IN A COASTAL MARINE ECOSYSTEM. *Ecological Applications,* 18**,** 497-510.

PIMM, S. L. 1984. The complexity and stability of ecosystems. *Nature,* 307**,** 321-326.

PIMM, S. L. 1991. *The balance of nature? ,* Chicago, University of Chicago Press.

PIMM, S. L. & RAVEN, P. 2000. Extinction by numbers. *Nature,* 403**,** 843-845.

POSTEL, S. L., DAILY, G. C. & EHRLICH, P. R. 1996. Human Appropriation of Renewable Fresh Water. *Science,* 271**,** 785-788.

RADCHUK, V., LAENDER, F. D., CABRAL, J. S., BOULANGEAT, I., CRAWFORD, M., BOHN, F., RAEDT, J. D., SCHERER, C., SVENNING, J.-C., THONICKE, K., SCHURR, F. M., GRIMM, V. & KRAMER-SCHADT, S. 2019. The dimensionality of stability depends on disturbance type. *Ecology Letters,* 0.

ROBERTSON, A. L., BROWN, L. E., KLAAR, M. J. & MILNER, A. M. 2015. Stream ecosystem responses to an extreme rainfall event across multiple catchments in southeast Alaska. *Freshwater Biology,* 60**,** 2523-2534.

SAINT-BÉAT, B., BAIRD, D., ASMUS, H., ASMUS, R., BACHER, C., PACELLA, S. R., JOHNSON, G. A., DAVID, V., VÉZINA, A. F. & NIQUIL, N. 2015. Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review. *Ecological Indicators,* 52**,** 458-471.

SAYER, C. D., BURGESS, A. M. Y., KARI, K., DAVIDSON, T. A., PEGLAR, S., YANG, H. & ROSE, N. 2010. Long-term dynamics of submerged macrophytes and algae in a small and shallow, eutrophic lake: implications for the stability of macrophyte-dominance. *Freshwater Biology,* 55**,** 565-583.

SCHÄFER, R. B., CAQUET, T., SIIMES, K., MUELLER, R., LAGADIC, L. & LIESS, M. 2007. Effects of pesticides on community structure and ecosystem functions in agricultural streams of three biogeographical regions in Europe. *Science of The Total Environment,* 382**,** 272-285.

SIMENSTAD, C. A., ESTES, J. A. & KENYON, K. W. 1978. Aleuts, sea otters, and alternate stable-state communities. *Science,* 200**,** 403-411.

SOLÉ, R. V. & MONTOYA, J. M. 2001. Complexity and fragility in ecological networks. *Proceedings of the Royal Society B: Biological Sciences,* 268**,** 2039-2045.

SOUSA, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology,* 60**,** 1225-1239.

STANLEY, E. H., BUSCHMAN, D. L., BOULTON, A. J., GRIMM, N. B. & FISHER, S. G. 1994. Invertebrate Resistance and Resilience to Intermittency in a Desert Stream. *The American Midland Naturalist,* 131**,** 288-300.

STANLEY, E. H., POWERS, S. M. & LOTTIG, N. R. 2010. The evolving legacy of disturbance in stream ecology: concepts, contributions, and coming challenges. *Journal of the North American Benthological Society,* 29**,** 67-83.

SUTHERLAND, J. P. 1974. Multiple Stable Points in Natural Communities. *The American Naturalist,* 108**,** 859-873.

TAI, A. P. K., MARTIN, M. V. & HEALD, C. L. 2014. Threat to future global food security from climate change and ozone air pollution. *Nature Climate Change,* 4**,** 817.

THORP, J. H. & COVICH, A. P. 2009. *Ecology and classification of North American freshwater invertebrates*, Academic press.

TILMAN, D. 1996. Biodiversity: Population Versus Ecosystem Stability. *Ecology,* 77**,** 350-363.

TILMAN, D., REICH, P. B. & KNOPS, J. M. H. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature,* 441**,** 629-632.

TRENBERTH, K. E. 2011. Changes in precipitation with climate change. *Climate Research,* 47**,** 123-138.

TSCHERKO, D., RUSTEMEIER, J., RICHTER, A., WANEK, W. & KANDELER, E. 2003. Functional diversity of the soil microflora in primary succession across two glacier forelands in the Central Alps. *European Journal of Soil Science,* 54**,** 685-696.

URBAN, M. C., TEWKSBURY, J. J. & SHELDON, K. S. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B: Biological Sciences,* 279**,** 2072-2080.

VAN RUIJVEN, J. & BERENDSE, F. 2010. Diversity enhances community recovery, but not resistance, after drought. *Journal of Ecology,* 98**,** 81-86.

VITOUSEK, P. M., MOONEY, H. A., LUBCHENCO, J. & MELILLO, J. M. 1997. Human Domination of Earth's Ecosystems. *Science,* 277**,** 494-499.

VÖRÖSMARTY, C. J., MCINTYRE, P. B., GESSNER, M. O., DUDGEON, D., PRUSEVICH, A., GREEN, P., GLIDDEN, S., BUNN, S. E., SULLIVAN, C. A., LIERMANN, C. R. & DAVIES, P. M. 2010. Global threats to human water security and river biodiversity. *Nature,* 467**,** 555.

WALKER, L. R., CHAPINI, F. S. I., FASTIE, C. L. & SHARMAN, L. 1993. Mechanisms of primary succession at Glacier Bay, Alaska. *Bulletin of the Ecological Society of America,* 74**,** 475-475.

WALLACE, J. B. & WEBSTER, J. R. 1996. The Role of Macroinvertebrates in Stream Ecosystem Function. *Annual Review of Entomology,* 41**,** 115-139.

WIEDERHOLM, T. 1983. *Chironomidae of the Holarctic region : keys and diagnoses. Pt. 1, Larvae,* Borgströms Tryckeri, Motala

WOODWARD, G., BONADA, N., FEELEY, H. B. & GILLER, P. S. 2015. Resilience of a stream community to extreme climatic events and long-term recovery from a catastrophic flood. *Freshwater Biology,* 60**,** 2497-2510.

WOUTER, R. B., EMMA, E. A., JOSHUA, R. L., RALPH, T. & ROSS, A. W. 2017. Recent changes in extreme floods across multiple continents. *Environmental Research Letters,* 12**,** 114035.

YANG, Q., FOWLER, M. S., JACKSON, A. L. & DONOHUE, I. 2019. The predictability of ecological stability in a noisy world. *Nature Ecology & Evolution,* 3**,** 251-259.

YARRANTON, G. A. & MORRISON, R. G. 1974. Spatial Dynamics of a Primary Succession: Nucleation. *Journal of Ecology,* 62**,** 417-428.

ZAK, D. R., HOLMES, W. E., WHITE, D. C., PEACOCK, A. D. & TILMAN, D. 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? . *Ecology,* 84**,** 2042-2050.

8. Synthesis

8.1 Thesis overview

The multidisciplinary approach outlined in this thesis examined ecosystem response to high-frequency floods on the physical environment (Chapter 3), habitat availability (Chapters 3 and 5), biotic communities (Chapter 4, 5 and 6) and associated trophic interactions (Chapter 5). This approach elucidated complex interactions between components of stream ecosystems following disturbance (Chapters 5 and 7). Legacy effects were identified following the high-frequency summer floods in 2014 (Chapter 3 to 5) and an earlier extreme high-magnitude winter flood in 2005 (Chapter 6). Extended legacy effects and persistent alterations to community composition followed the 2005 winter floods (Chapter 6). In spite of these changes to composition, communities across streams demonstrated low resilience to the high-frequency summer floods which occurred in the summer of 2014.

Extreme high-frequency summer floods caused major changes in stream channel morphology. In spite of high rates of channel change observed at all streams, varying patterns of resilience in total habitat heterogeneity were observed across the chronosequence, which has not previously been reported. This variation in resilience of habitat availability is thought to be associated with changing instream wood and sediment availability post-flood. The floods increased the short-term availability of sediment (silt, sand, gravel and cobble) within streams, which benefitted streams in later paraglacial condition (older streams) to a greater event, driving renewed habitat development post-flood. Alterations in stream habitat heterogeneity may significantly influence the composition, size structure and resilience of biotic communities to future disturbances through the changing availability of habitat, trophic resources and refugia.

The high-frequency summer floods of 2014 significantly altered benthic macroinvertebrate community composition at the four streams, irrespective of their pre-flood geomorphological and habitat heterogeneity. Taxa loss was the main driver at more geomorphologically complex systems whereas taxa turnover dominated at lower complexity streams. Low resilience of communities was observed at all streams with no return to pre-flood composition observed during the study period from 2015 to 2017; rather a consistent directional response was observed across streams through time post-flood. This directional response was associated with colonisation by the same taxa at each stream through time post-flood, leading to a homogenisation of communities and an associated decline in beta-diversity between streams by 2017. Directional colonisation was driven by members of the Heptageniidae (*Cinygmula*), Baetidae (*Acentrella)* and Chironomidae (*Paratrichocladius*, *Eukifferella* and *Pagastia*). This pathway suggests that resilience is governed by indirect effects of disturbance (i.e. post-flood dispersal and/or altered available niche space) rather than the direct effects of mortality and displacement of individuals and their resistance during the floods.

Juvenile salmon altered their feeding behaviour following the high-frequency summer floods, in response to changing benthic macroinvertebrate prey availability. A significant decline in terrestrial subsidies was observed for juvenile coho salmon potentially indicative of altered feeding behaviour or flood driven impacts to multidirectional subsidies associated with invertebrates which utilise the stream as immature stages and the terrestrial biome as mature adults. Changing prey selection occurred alongside significant declines in average fish condition and a shift in community size structure across study streams across both juvenile coho salmon and Dolly Varden. Post-flood communities were dominated by smaller individuals and size structure had not recovered three years after the floods, suggesting persistent post-flood impacts to instream recruitment, which could have impacted subsequent stream escapement. Modelling approaches suggested time since flood and total freshwater prey availability were the best predictors of community size structure of juvenile salmon. In contrast habitat availability, which increased at the majority of streams following the floods, was not an effective predictor of community size structure. Evidence from juvenile salmon communities identified the importance of both direct and indirect (niche space) effects on community response to floods.

Legacy effects of past disturbance were identified in the benthic macroinvertebrate community following the extreme high-magnitude winter flood of 2005. These persistent changes in community composition indicate that recovery of communities did not occur over almost a decade following the initial flood disturbance. Despite the presence of such legacy effects, the extreme floods may not function as environmental filters, selecting for taxa resistant to floods. Rather, the processes of reassembly following the floods simply favours taxa which can rapidly colonise and/or tolerate conditions within disturbed systems’ altered niche space. Indeed, consistent patterns of declining beta-diversity between streams following each flood suggests similarities in the pathway of response to these contrasting extreme flood events, irrespective of observed differences in response within some taxa (e.g. *Cinygmula* sp. and some Nemouridae taxa).

Community stability at Wolf Point Creek (Chapter 7) over two decades demonstrated floods of contrasting forms drove ongoing declines in the relationships between stability metrics leading to an increase in the overall dimensionality of stability through time. An increasingly significant relationship between invasions and resilience was observed following each of the two extreme flooding events in 2005 and 2014. The value of the multidimensionality approaches to ecological stability measurements in exploring response to disturbance is demonstrated, with a clear and consistent response observed following each flood where contrasting responses were observed in simple metrics of community structure including total density and richness.

8.2 The *perturbation pathway* extending the pulse, press, ramp model through intermediary processes

To better predict the impact of disturbance regimes (Parry et al., 2013, Diffenbaugh et al., 2015, Wouter et al., 2017) to ecosystems, the theoretical framework within which we consider their effects should be enhanced. Here the disturbance 'cause' and biotic response 'effect' model of Lake (2000) has been recast as a *perturbation pathway*. In the proposed *perturbation pathway* model, 'cause' and 'effect' remain but are reframed as the 'input' and 'output' and intermediary processes can be assembled, which may be associated with (in however small or large a degree) the biological response to all disturbances, in this case floods. The processes highlighted here are not an exclusive list, rather they are a subset of possible processes based on the empirical findings of this research and evidence from the literature.

Here it is argued that biological response to a given disturbance is driven by two principal mechanisms: (1) changes in the available niche space through time which incorporate the direct (displacement and mortality of individuals) and indirect (post-disturbance alterations to resource availability (e.g. Larson et al., 2018)) effects and (2) the rates of post-disturbance dispersal of the taxa present in the regional species pool. These mechanisms can both individually and together take the form of pulse, press and ramp processes which govern the form of biological response observed. Through this simplistic approach a framework is established to elucidate the diverse array of biological responses (Table 8.1) observed to disturbances, which may appear to have similar forms (Figure 8.1). Without such a framework, developing a systematic understanding of how disturbances control ecological processes is more challenging, threatening to reduce our ability to predict the ongoing threat of and prepare for increased future disturbances associated with continued land use and climate change (Turner, 2010).

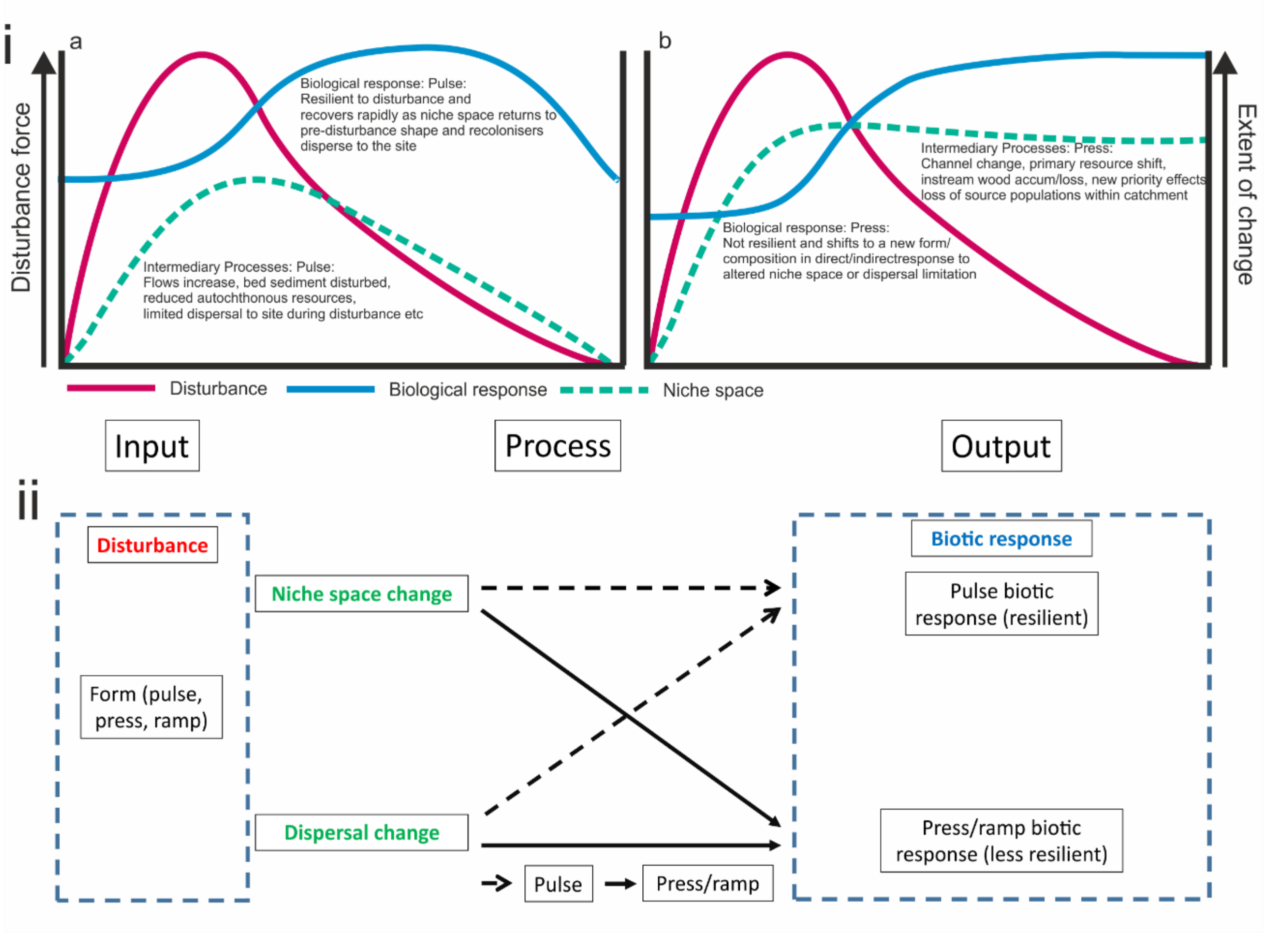

Figure 8.1. (i) Pulse disturbance with two associated biological responses (a) pulse or (b) press with the associated intermediary processes. (ii) A conceptual model of how niche space and dispersal change links disturbance to biological response. The sections in blue dashed boxes are the original Lake (2000) model.

Table 8.1. Examples of disturbance events and associated biological responses

	Biological Pulse	
Pulse Disturbance	Flood (1 in 50 year event) summer	Recovery of benthic macroinvertebrate community composition (6 Years post-flood) (Woodward et al. 2015)
	Flood (100 times average discharge)	Recovery of diatom assemblages within one year post-flood (Tornés et al. 2015)
	Flood (1 in 100 year event) summer	Recovery of salmonid communities within two years post-flood (George et al. 2015)
	Flood (record magnitude event)	Recovery of benthic macroinvertebrate community composition one year post-flood (Mundahl and Hunt 2011)
	Flood (1 in 2000 year event)	Recovery of benthic macroinvertebrate community composition (Herbst and Cooper 2010)
	Flood (1 in 100 year event)	Recovery of fish community - 2 months (Lojkásek et al. 2005)
	Flood (return interval not specified)	Recovery of salmonid community - 3 years (Roghair et al. 2002)
	Biological Press	
	Flood (magnitude not specified)	Increased dominance of crawlers (*Epeorus sp*.) and swimmers (*Baetis sp*.) in macroinvertebrate community Bae and Park (2016)
	Flood (100 times average discharge)	Significant reset in community composition toward earlier successional stage (Milner et al. 2013)
Press Disturbance	**Biological Pulse**	
	Diffuse pollution	Resilience of zooplankton community to the addition of pollutants to ponds (Kanehl et al. 1997)
	Biological Press	
	Diffuse pollution	Persistent shifts in fish community composition despite theoretical variation in pollution tolerance (Whitney et al. 2019)
	Diffuse pollution	Diffuse pollution metrics were effective predictors of benthic macroinvertebrate community summary statistics (Berger et al. 2017)
Ramp Disturbance	**Biological Pulse**	
	Drought	Wetland bird distributions predicted by extent of drought occurrence (Wen et al. 2016)
	Biological Press	
	Heatwave (> 1 in 1000 year event)	Failure of mollusc communities to recover post-drought in spite of abiotic conditions favouring recolonization (Mouthon and Daufresne 2015)
	Biological Ramp	
	Drought (5 year event)	Low fish and macroinvertebrate resilience and drought facilitated colonization by invasive fish species (Bêche et al. 2009)

Changing niche space can elicit a biological response through two processes: (1) direct effects of reduced survival and displacement of individuals during the disturbance and (2) indirect effects as a result of alterations to the habitat, energy and biotic interactions following disturbance (Roghair et al., 2002). These direct and indirect processes should be expected to interact during a given disturbance event, such interactions could be synergistic (exacerbating the impact of one other) or antagonistic (reducing the impact of one other) and could be associated with additive effects.

Dispersal is a fundamental aspect of meta community dynamics and has received significant attention (Howell et al., 2018, Terui et al., 2018) and its role in ecological response to climate change disturbance is established (Brown et al., 2018). Niche space and dispersal are inherently intertwined. For example, a given taxa may not establish for two reasons, one they strongly disperse to disturbed watersheds, but suitable niche space is unavailable post-disturbance (species sorting; Vanschoenwinkel et al., 2010), or two, if niche space is suitable but individuals are unable to disperse to the site (dispersal limitation; Shurin et al., 2009). These are the two simplest versions of a highly complex set of interactions (including the potential for changing priority effects amongst others), which are beyond the scope of this synthesis to address. The *perturbation pathway* provides a potential approach to conceptually explore the significance of disturbance by providing a simple next step in developing our understanding of the processes which govern response.

8.3 Linking biotic response and resilience

Biotic responses also affect the resilience of an ecosystem or community to disturbance. Communities across streams in Glacier Bay expressed consistent ongoing low resilience following divergent initial drivers of resilience. Apparent differences in the initial resilience are thought to be associated with meta-population processes and dispersal at varying spatial scales. Differences in benthic macroinvertebrate response and thus ecological resilience across streams are described in a new conceptual model (Figure 8.2).

In this model pre-flood riffle communities (c), represent the local species pool (b) under meta-population processes working at the riffle/patch scale (Hanski, 2001, Heino et al., 2004). These communities can persist through time where no major disturbance events occur. However, following significant floods, local species pools and individual riffle communities demonstrate changes to composition dependent upon their pre-flood composition. In higher complexity streams the local species pool and thus riffle communities are more diverse (Milner et al., 2000), change is dominated by the loss of taxa less tolerant of disturbance. In such streams the floods acted as a significant environmental filter allowing only resilient taxa to persist, although generally at reduced densities. In such a system the immediate community response to the floods may be driven by **species sorting**, based upon the traits of both extinct and persistent taxa. In contrast, at lower complexity streams, floods are potentially less effective environmental filters, and thus species sorting is less effective, due to the dominance of disturbance tolerant taxa in pre-flood communities. Rather the response is predominantly driven by local **patch dynamics** and **dispersal capacity/limitation**. However, definitive conclusions should not be drawn here before further research is conducted, in part due to smaller sample sizes presented in this thesis. R-selected traits possessed by most persisting species may allow them to rapidly exploit disrupted patches in post-flood ecosystems (Langton and Casas, 1998). Under this model, community reassembly depends upon both the taxa able to persist within a given patch (irrespective of their perceived resilience; a direct effect of the floods) and the order in which new/recolonizing species arrive and establish within the community (dispersal and indirect niche space changes) post-flood. These intermediate processes could lead to lower riffle habitat alpha- and beta-diversity, where a small group of taxa are capable of exploiting post-flood conditions in all streams. Contrasts in dominant intermediate processes have previously been alluded to, (e.g. Szczerkowska-Majchrzak et al., 2014), although not yet described conceptually in relation to observed biological response to floods across patches, or streams with varying geomorphological complexities.

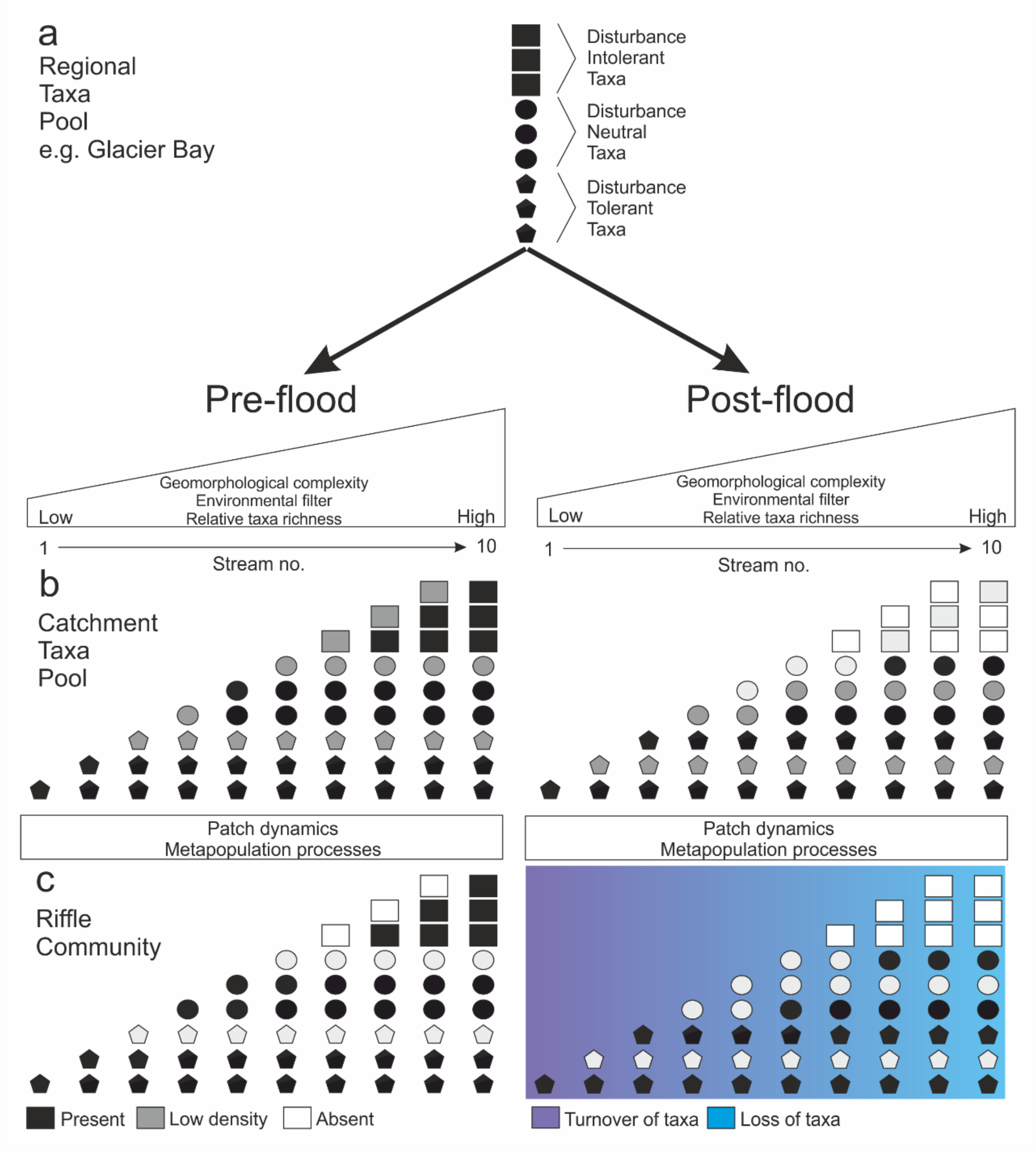

Figure 8.2. Conceptual model of stream ecological resilience in macroinvertebrate communities following floods across a series of 10 hypothetical streams with a gradient of increasing geomorphological complexity (1 low to 10 high). a – the regional taxa pool is composed of taxa which are disturbance intolerant, neutral or tolerant. b – catchment taxa pools develop from taxa which can pass through the environmental filter of stream geomorphological complexity. c – riffle communities represent the catchment taxa pool under meta-population processes. Following floods b sees the loss of some disturbance intolerant taxa, whilst c sees the turnover within the available 'tolerant' taxa at low complexity streams and the loss of intolerant taxa at higher complexity stream. High density represents densities at which it would be expected that a taxon would be recorded under standard sampling procedures Low density represents densities which at the catchment scale indicate the taxon is not successful relative to other taxa in communities. Absent represents occasions where a taxon is not physically present at a given spatial scale and therefore will not be sampled no matter the sampling effort.

8.4 Ecological resilience and linked disturbances

With ever increasing anthropogenic and climate pressures facing ecosystems (Wouter et al., 2017, Whitney et al., 2019), the threat of multiple disturbances occurring concurrently or in close temporal sequence are ever increasing (Buma, 2015). Crucially, feedback between the direct and indirect effects of a disturbance event has the capacity to drive non-linear alterations to the biotic impact of subsequent disturbance events (e.g. Kulakowski and Jarvis, 2013 in terrestrial systems). The pathways underlying these legacy effects (Johnstone et al., 2016) have not yet been explored intensively for stream systems, but it could be predicted that such a failure to recover in the time period of the research could exacerbate the effects of each individual disturbance event (Milner et al., 2018).

The temporal extension of altered niche space post-flood (Chapter 5), alongside delays in the recovery of biotic communities or populations (Chapters 4 to 6) associated with recolonization, acts to extend the duration of legacy effects in ecosystems. This research offers evidence for the potential importance of legacy effects in creating linked flood disturbances during the summer of 2014. Under the *perturbation pathway* model these individual floods (pulse hydrological disturbances) can become linked by their relaxation stages (Chapter 3) and possible disruptions to resource availability (Chapter 5). These combined effects could have driven a ramp disruption of available niche space (Figure 8.3) over a significant period (minimum 3 months) of the benthic macroinvertebrate community (which in GBNP are typically univoltine; Milner pers. comms.) and juvenile salmon life cycles.

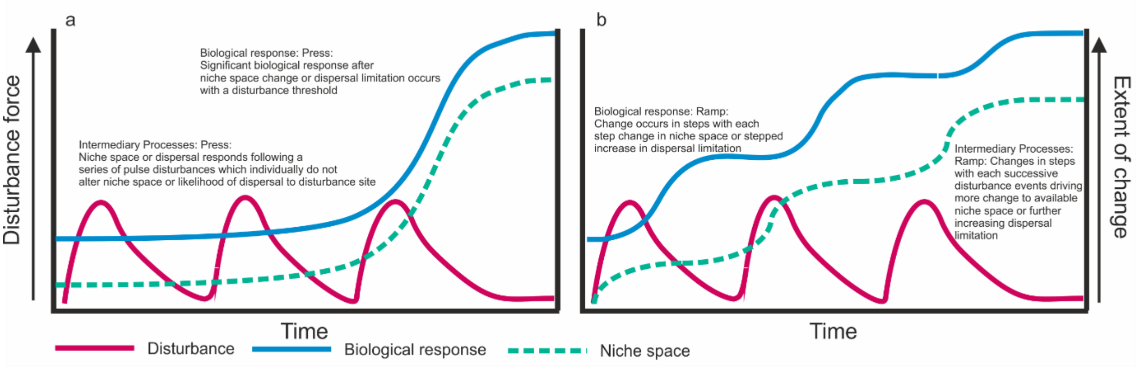

Figure 8.3. Conceptual models of the response of biological units to a series of pulse disturbances. a) a series of pulse disturbances drive a press change in niche space and a subsequent press biological response as reported by Villnäs et al. (2013). b) a series of pulse disturbances drive a stepped ramp response in niche space and a subsequent ramp biological response as proposed as the underlying processes for the 2014 floods in GBNP streams (Chapter 4, Chapter 5).

An experimental study of hypoxia pulses in sedimentary communities (Villnäs et al., 2013) demonstrated that each individual pulse of hypoxia decreased ecological resistance. Through a series of such decreases a tipping point was met, leading to a press response without an obvious or persistent shift in niche space either between pulses or following them (Figure 8.3a). Both the results outlined in this thesis and Villnäs et al. (2013) offer evidence for the presence of disturbance legacies, which act to link disturbances and can affect ecological resilience to subsequent disturbances. This evidence suggests that high-frequency floods impact communities as a series of steps (stepped ramp) with earlier disturbances destabilising biological units and reducing their subsequent resilience to further disturbance events.

8.5 Implications of linked disturbances for biodiversity

Increasingly frequent disturbance events, including but not exclusively floods, appear to pose a significant threat to freshwater biodiversity at both the local (individual catchment) and regional (multiple catchment) scales. The convergence of macroinvertebrate community composition between and within streams following the 2005 and then 2014 floods is outlined in Chapter 6. With increasingly regular disturbance it can be expected that taxa lacking traits that confer resilience to disturbance in communities will go extinct. These losses will lead to reduced freshwater biodiversity locally. In turn, these continued local losses could significantly modify regional meta-population dynamics (Harrison, 2008), as more source populations are lost following each disturbance, further reducing the likelihood of a given taxa successfully recolonising a site.

Under such a system, it is possible that a rise in the regional dominance of some resilient r-selected taxa could occur although this was not directly evidenced in this research. Such dominance would be consistent with the homogenisation of communities between streams reported here (Chapter 4) and evidence from the literature (Mundahl and Hunt, 2011, Ming-Chih and Mei-Hwa, 2012, Poff et al., 2018). In contrast populations of K-selected and less resilient taxa will potentially become more isolated in catchments that have by chance avoided disturbance. Such isolated populations often experience higher rates of extinction than widespread species (Harrison, 2008) and therefore one cannot expect their persistence to continue in the long-term at the regional scale. Equally populations of K-selected taxa may only persist where densities are sufficient to ensure some individuals are able to access flow refugia during the floods. These findings have crucial implications for river managers and policy makers globally who are responsible for preserving biodiversity. It will be necessary to identify new approaches to establishing refugia to disturbance and stable source populations which can recolonise disturbed ecosystems.

8.6 Limitations of research and challenges of studying unpredictable disturbance events

The value of a multidisciplinary approach to studying disturbance events has been outlined in this thesis. Indeed, one of the major strengths of this research, in comparison to other studies of extreme floods (e.g. Herbst and Cooper, 2010, Mundahl and Hunt, 2011, Bae and Park, 2016, George et al., 2015), has been in the diverse range of data sets available for exploration. These data sets enabled a broad range of novel analyses to be undertaken. Nevertheless, some areas of investigation were hindered by the lack of relevant data regarding the changing niche space and dispersal rate following the floods which are clear limitations of the work. The collection of pre-flood data sets, focussed on primary production and macroinvertebrate habitat availability would have further extended this body of work. The importance of collecting such data pre-disturbance was emphasised in Chapter 5 but knowledge gaps must be identified in understanding the biological response to disturbance events. Such knowledge gaps can then be used to identify future research opportunities and the pre-disturbance data sets necessary to explore these questions.

In addition, our understanding of how freshwater macroinvertebrates occupy benthic habitat, one element of niche space, remains in its infancy (Lancaster and Downes, 2010). More in depth data about the niche space in streams should be collected, principally the localised bed sediment composition and hydrology (e.g. Gayraud and Philippe, 2003) and the availability of primary (autochthonous and allochthonous) resources (e.g. Power and Stewart, 1987, Grimm and Fisher, 1989). Such steps may require more extensive collaborations between geomorphologists, hydrologists, aquatic botanists, microbiologists and disturbance ecologists as the challenges associated with developing understanding of local bed hydrology and instream production are complex (e.g. Ceola et al., 2013).

Through the study of multiple sampling reaches within stream networks it would be possible to develop a more thorough understanding of recolonisation within streams following disturbances. Identifying the rates and extent of within and between water body/catchment dispersal (Anderson and Hayes, 2018, Schmera et al., 2018, Tonkin et al., 2018) will be invaluable in developing our understanding of the risk extreme disturbances, occurring over various spatial scales, pose to ecosystems. Further trait based analyses, which have now been undertaken in a handful of studies (Ming-Chih and Mei-Hwa, 2012, Brown et al., 2018, Larson et al., 2018, Poff et al., 2018), will allow us to enrich our understanding of impacts to ecosystem function and the pathway of resilience.

The analyses undertaken in Chapter 5 highlighted the significance of niche space changes in predicting salmonid community size structure and condition, yet there remains a great deal more that could be done. Principally, the more thorough inclusion of alterations to bioenergetics via the inclusion of prey biomass, only raised at BBS post-flood in this thesis, is necessary to further elucidate the role of different freshwater and terrestrial taxa in trophic interactions. This could also be enhanced by the inclusion of stable isotope analysis, as has been implemented in studies of change driven by invasive species (Vander Zanden et al., 1999). Finally, it would be valuable to utilise behavioural studies, either instream or ex-situ in experimental mesocosms, to identify the response of feeding behaviour to altered abundance and species of prey items in the drift and benthos. This would enable researchers to establish if shifts in feeding behaviour can be driven by extreme floods, as reported following experimental suppression of prey availability in the drift in some salmon taxa (Nakano, 1995, Nakano et al., 1999).

The exploration of changing dimensionality of ecological stability following floods outlined in this thesis, represents an important first step in extending theoretical (Donohue et al., 2013), experimental (Hillebrand et al., 2018) and modelling (Radchuk et al., 2019, Yang et al., 2019) approaches into a real-world dataset. To further enhance this analysis, it is necessary to apply the approach to more observation rich data sets. This would allow ellipsoids with better fits to be created for pre- and post-disturbance time periods and thus more reliable interpretations would be possible. Meta-analyses of ecological stability across biomes and disturbance types, was beyond the scope of this research project, but would represent another valuable addition to the literature. Together these suggested extensions of the approaches utilised in this thesis, represent exciting opportunities to further develop our understanding of ecological stability and thus resilience of streams to disturbance.

8.7 Future efforts to develop evidence and guide hydrological disturbance theory

With increasing anthropogenic influence pressurising our lotic environments globally (Friberg, 2010), as well as an increasing risk of drought (Diffenbaugh et al., 2015), occurrence of extreme rainfall events (Berg et al., 2013) and resulting flood (Wouter et al., 2017) disturbances are expected to play an ever more powerful role in structuring lotic ecosystems. Therefore, understanding the processes which govern biotic responses will continue to grow in importance.

Of particular value will be the exploration of how varying forms of disturbance actively alter niche space, to support the limited examples which indirectly explore this premise already (Ming-Chih and Mei-Hwa, 2012, Bae and Park, 2016 , Larson et al., 2018, Poff et al., 2018). Further, meta-analyses of the current literature can help identify where disturbances were likely to have driven changes to niche space or likelihood of recolonization, and if these changes persisted. Such evidence when considered within the context of the *perturbation pathway* would be of value to help disentangle the broadly varying responses to similar types of disturbances reported to date (Herbst and Cooper, 2010, Mundahl and Hunt, 2011, Milner et al., 2013, Milner et al., 2018, Robinson et al., 2018).

The *perturbation pathway* can provide a framework within which to enhance our understanding of how linked disturbances affect freshwater ecosystems. We must also extend and increase the available evidence of linked disturbances currently found in the literature (Woodward et al., 2015, Milner et al., 2018). Experimental work will be necessary to identify the processes underlying changing ecological resilience. Mesocosm studies offer a controlled approach to directly explore varying responses of communities to different forms of disturbances both alone and in sequence. Such studies can then be used to identify if previously disturbed communities become more or less resilient to future disturbances. Following the model of Milner et al. (2018), it would be possible to explore how novel sequences of disturbances can impact ecological stability more generally. Such evidence will enable the advancement of models grounded in ecological theory. Such grounded models are particularly important given the cross-biome effects possible in extreme hydrological events which can drive change in both terrestrial and aquatic systems (Boulton and Lake, 2008, Parmesan et al., 2000).

Finally, further efforts should be made to continue to develop our understanding of how co-occurring disturbances affect ecosystems. Crucially with ever increasing global land use change and other anthropogenic impacts such as global mean temperature rise (Hawkins et al., 2017) and increased spread of invasive species (Neubert and Parker, 2004), press disturbances, such as fine sediment deposition (Lane et al., 2006), diffuse pollution from agriculture and mining (Pulley et al., 2016), water abstraction (Arroita et al., 2017) and water temperature rises (van Vliet et al., 2013) are all likely to continue to pressurise lotic systems. These press disturbances are relatively contiguous across human influenced landscapes. The consideration of how these changes interact with more unpredictable hydrological disturbances has been negligible but can be major drivers of change (Milner et al., 2018, Aspin et al., 2019). A new focus is necessary to identify how such press disturbances alter the resilience of communities to future disturbances. The development of a conceptual understanding of these processes will facilitate a greater capacity to predict how our actions are likely to alter future system resilience to hydrological disturbance.

8.8 Conclusions

Stream benthic macroinvertebrate and fish community resilience to high-frequency summer floods was generally low. Streams demonstrated significant geomorphological responses leading to recruitment of instream wood and increased post-flood sediment availability across all but the lowest complexity stream. Benthic macroinvertebrate and juvenile salmon communities failed to recover to pre-flood composition, size structure and condition three years post-flood. Community composition and thus resilience may have been impacted by legacy effects which linked an earlier high-magnitude flood (2005) to the high-frequency floods (2014). Evidence suggested that these linked disturbances sequentially degraded relationships between metrics of community stability, leading to a dominant role of invasions through time. The complex indirect effects of floods appear to be crucial in attempting to understand the processes which govern biotic response and resilience to floods. To further develop our understanding of disturbances we must incorporate these complex intermediary processes into analytical approaches. This synopsis has offered new conceptual approaches to assist in this process. The increasing frequency and magnitude of floods predicted under climate change will only increase their importance in governing community assembly/reassembly processes in the future.

8.9 References

ANDERSON, K. E. & HAYES, S. M. 2018. The effects of dispersal and river spatial structure on asynchrony in consumer–resource metacommunities. *Freshwater Biology,* 63**,** 100-113.

ARROITA, M., FLORES, L., LARRAÑAGA, A., MARTÍNEZ, A., MARTÍNEZ-SANTOS, M., PEREDA, O., RUIZ-ROMERA, E., SOLAGAISTUA, L. & ELOSEGI, A. 2017. Water abstraction impacts stream ecosystem functioning via wetted-channel contraction. *Freshwater Biology,* 62**,** 243-257.

ASPIN, T. W. H., KHAMIS, K., MATTHEWS, T. J., MILNER, A. M., O'CALLAGHAN, M. J., TRIMMER, M., WOODWARD, G. & LEDGER, M. E. 2019. Extreme drought pushes stream invertebrate communities over functional thresholds. *Global Change Biology,* 25**,** 230-244.

BAE, M.-J. & PARK, Y.-S. 2016 Responses of the functional diversity of benthic macroinvertebrates to floods and drought at small streams with different flow permanence. *Inland Waters,* 6**,** 461-475.

BÊCHE, L. A., CONNORS, P. G., RESH, V. H. & MERENLENDER, A. M. 2009. Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography,* 32**,** 778-788.

BERG, P., MOSELEY, C. & HAERTER, J. O. 2013. Strong increase in convective precipitation in response to higher temperatures. *Nature Geoscience,* 6**,** 181.

BERGER, E., HAASE, P., KUEMMERLEN, M., LEPS, M., SCHÄFER, R. B. & SUNDERMANN, A. 2017. Water quality variables and pollution sources shaping stream macroinvertebrate communities. *Science of The Total Environment,* 587-588**,** 1-10.

BOULTON, A. J. & LAKE, P. S. 2008. Effects of drought on stream insects and its ecological consequences. *In:* LANCASTER, J. & BRIERS, R. A. (eds.) *Aquatic insects: challenges to populations.* . London: Royal Entomological Society of London.

BROWN, L. E., KHAMIS, K., WILKES, M., BLAEN, P., BRITTAIN, J. E., CARRIVICK, J. L., FELL, S., FRIBERG, N., FÜREDER, L., GISLASON, G. M., HAINIE, S., HANNAH, D. M., JAMES, W. H. M., LENCIONI, V., OLAFSSON, J. S., ROBINSON, C. T., SALTVEIT, S. J., THOMPSON, C. & MILNER, A. M. 2018. Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. *Nature Ecology & Evolution,* 2**,** 325-333.

BUMA, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere,* 6**,** art70.

CEOLA, S., HÖDL, I., ADLBOLLER, M., SINGER, G., BERTUZZO, E., MARI, L., BOTTER, G., WARINGER, J., BATTIN, T. J. & RINALDO, A. 2013. Hydrologic Variability Affects Invertebrate Grazing on Phototrophic Biofilms in Stream Microcosms. *PLOS ONE,* 8**,** e60629.

DIFFENBAUGH, N. S., SWAIN, D. L. & TOUMA, D. 2015. Anthropogenic warming has increased drought risk in California. *Proceedings of the National Academy of Sciences,* 112**,** 3931-3936.

DONOHUE, I., PETCHEY, O. L., MONTOYA, J. M., JACKSON, A. L., MCNALLY, L., VIANA, M., HEALY, K., LURGI, M., O'CONNOR, N. E. & EMMERSON, M. C. 2013. On the dimensionality of ecological stability. *Ecology Letters,* 16**,** 421-429.

FRIBERG, N. 2010. Pressure-response relationships in stream ecology: introduction and synthesis. *Freshwater Biology,* 55**,** 1367-1381.

GAYRAUD, S. & PHILIPPE, M. 2003. Influence of Bed-Sediment Features on the Interstitial Habitat Available for Macroinvertebrates in 15 French Streams. *International Review of Hydrobiology,* 88**,** 77-93.

GEORGE, S. D., BALDIGO, B. P., SMITH, A. J. & ROBINSON, G. R. 2015. Effects of extreme floods on trout populations and fish communities in a Catskill Mountain river. *Freshwater Biology,* 60**,** 2511-2522.

GRIMM, N. B. & FISHER, S. G. 1989. Stability of Periphyton and Macroinvertebrates to Disturbance by Flash Floods in a Desert Stream. *Journal of the North American Benthological Society,* 8**,** 293-307.

HANSKI, I. 2001. Spatially realistic theory of metapopulation ecology. *Naturwissenschaften,* 88**,** 372-381.

HARRISON, S. 2008. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society,* 42**,** 73-88.

HAWKINS, E., ORTEGA, P., SUCKLING, E., SCHURER, A., HEGERL, G., JONES, P., JOSHI, M., OSBORN, T. J., MASSON-DELMOTTE, V., MIGNOT, J., THORNE, P. & OLDENBORGH, G. J. V. 2017. Estimating Changes in Global Temperature since the Preindustrial Period. *Bulletin of the American Meteorological Society,* 98**,** 1841-1856.

HEINO, J., LOUHI, P. & MUOTKA, T. 2004. Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure. *Freshwater Biology,* 49**,** 1230-1239.

HERBST, D. B. & COOPER, S. D. 2010. Before and after the deluge: rain-on-snow flooding effects on aquatic invertebrate communities of small streams in the Sierra Nevada, California. *Journal of the North American Benthological Society,* 29**,** 1354-1366.

HILLEBRAND, H., LANGENHEDER, S., LEBRET, K., LINDSTRÖM, E., ÖSTMAN, Ö. & STRIEBEL, M. 2018. Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters,* 21**,** 21-30.

HOWELL, P. E., MUTHS, E., HOSSACK, B. R., SIGAFUS, B. H. & CHANDLER, R. B. 2018. Increasing connectivity between metapopulation ecology and landscape ecology. *Ecology,* 99**,** 1119-1128.

JOHNSTONE, J. F., ALLEN, C. D., FRANKLIN, J. F., FRELICH, L. E., HARVEY, B. J., HIGUERA, P. E., MACK, M. C., MEENTEMEYER, R. K., METZ, M. R., PERRY, G. L., SCHOENNAGEL, T. & TURNER, M. G. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment,* 14**,** 369-378.

KANEHL, P. D., LYONS, J. & NELSON, J. E. 1997. Changes in the Habitat and Fish Community of the Milwaukee River, Wisconsin, Following Removal of the Woolen Mills Dam. *North American Journal of Fisheries Management,* 17**,** 387-400.

KULAKOWSKI, D. & JARVIS, D. 2013. Low-severity fires increase susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado. *Forest Ecology and Management,* 289**,** 544-550.

LANCASTER, J. & DOWNES, B. J. 2010. Linking the hydraulic world of individual organisms to ecological processes: Putting ecology into ecohydraulics. *River Research and Applications,* 26**,** 385-403.

LANE, P. N. J., SHERIDAN, G. J. & NOSKE, P. J. 2006. Changes in sediment loads and discharge from small mountain-catchments following wild-fire in south eastern Australia. *Journal of Hydrology,* 331**,** 495-510.

LANGTON, P. H. & CASAS, J. 1998. Changes in chironomid assemblage composition in two Mediterranean mountain streams over a period of extreme hydrological conditions. *Hydrobiologia,* 390**,** 37-49.

LARSON, E. I., POFF, N. L., ATKINSON, C. L. & FLECKER, A. S. 2018. Extreme flooding decreases stream consumer autochthony by increasing detrital resource availability. *Freshwater Biology,* 0.

LOJKÁSEK, B., LUSK, S., HALAČKA, K., LUSKOVÁ, V. & DROZD, P. 2005. The Impact of the Extreme Floods in July 1997 on the Ichthyocenosis of the Oder Catchment Area (Czech Republic). *Hydrobiologia,* 548**,** 11-22.

MILNER, A. M., KNUDSEN, E. E., SOISETH, C., ROBERTSON, A. L., SCHELL, D., PHILLIPS, I. T. & MAGNUSSON, K. 2000. Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences,* 57**,** 2319-2335.

MILNER, A. M., PICKEN, J. L., KLAAR, M. J., ROBERTSON, A. L., CLITHEROW, L. R., EAGLE, L. & BROWN, L. E. 2018. River ecosystem resilience to extreme flood events. *Ecology and Evolution,* 0.

MILNER, A. M., ROBERTSON, A. L., MCDERMOTT, M. J., KLAAR, M. J. & BROWN, L. E. 2013. Major flood disturbance alters river ecosystem evolution. *Nature Climate Change,* 3**,** 137-141.

MING-CHIH, C. & MEI-HWA, K. 2012. Application of r/K selection to macroinvertebrate responses to extreme floods. *Ecological Entomology,* 37**,** 145-154.

MINSHALL, G. W. 2003. Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management,* 178**,** 155-161.

MOUTHON, J. & DAUFRESNE, M. 2015. Resilience of mollusc communities of the River Saone (eastern France) and its two main tributaries after the 2003 heatwave. *Freshwater Biology,* 60**,** 2571-2583.

MUNDAHL, N. D. & HUNT, A. M. 2011. Recovery of stream invertebrates after catastrophic flooding in southeastern Minnesota, USA. *Journal of Freshwater Ecology,* 26**,** 445-457.

NAKANO, S. 1995. Competitive interactions for foraging microhabitats in a size-structured interspecific dominance hierarchy of two sympatric stream salmonids in a natural habitat. *Canadian Journal of Zoology,* 73**,** 1845-1854.

NAKANO, S., FAUSCH, K. D. & KITANO, S. 1999. Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *Journal of Animal Ecology,* 68**,** 1079-1092.

NEUBERT, M. G. & PARKER, I. M. 2004. Projecting Rates of Spread for Invasive Species. *Risk Analysis,* 24**,** 817-831.

PARMESAN, C., ROOT, T. L. & WILLIG, M. R. 2000. Impacts of Extreme Weather and Climate on Terrestrial Biota. *Bulletin of the American Meteorological Society,* 81**,** 443-450.

PARRY, S., MARSH, T. & KENDON, M. 2013. 2012: from drought to floods in England & Wales. *Weather* 68**,** 268-274.

POFF, N. L., LARSON, E. I., SALERNO, P. E., MORTON, S. G., KONDRATIEFF, B. C., FLECKER, A. S., ZAMUDIO, K. R. & FUNK, W. C. 2018. Extreme streams: species persistence and genomic change in montane insect populations across a flooding gradient. *Ecology Letters,* 21**,** 525-535.

POWER, M. E. & STEWART, A. J. 1987. Disturbance and Recovery of an Algal Assemblage Following Flooding in an Oklahoma Stream. *The American Midland Naturalist,* 117**,** 333-345.

PULLEY, S., FOSTER, I. & ANTUNES, P. 2016. The dynamics of sediment-associated contaminants over a transition from drought to multiple flood events in a lowland UK catchment. *Hydrological Processes,* 30**,** 704-719.

RADCHUK, V., LAENDER, F. D., CABRAL, J. S., BOULANGEAT, I., CRAWFORD, M., BOHN, F., RAEDT, J. D., SCHERER, C., SVENNING, J.-C., THONICKE, K., SCHURR, F. M., GRIMM, V. & KRAMER-SCHADT, S. 2019. The dimensionality of stability depends on disturbance type. *Ecology Letters,* 0.

ROBINSON, C. T., SIEBERS, A. R. & ORTLEPP, J. 2018. Long-term ecological responses of the River Spöl to experimental floods. *Freshwater Science,* 37**,** 433-447.

ROGHAIR, C. N., DOLLOFF, C. A. & UNDERWOOD, M. K. 2002. Response of a Brook Trout Population and Instream Habitat to a Catastrophic Flood and Debris Flow. *Transactions of the American Fisheries Society,* 131**,** 718-730.

SCHMERA, D., ÁRVA, D., BODA, P., BÓDIS, E., BOLGOVICS, Á., BORICS, G., CSERCSA, A., DEÁK, C., KRASZNAI, E. Á., LUKÁCS, B. A., MAUCHART, P., MÓRA, A., SÁLY, P., SPECZIÁR, A., SÜVEGES, K., SZIVÁK, I., TAKÁCS, P., TÓTH, M., VÁRBÍRÓ, G., VOJTKÓ, A. E. & ERŐS, T. 2018. Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshwater Biology,* 63**,** 74-85.

SHURIN, J. B., COTTENIE, K. & HILLEBRAND, H. 2009. Spatial autocorrelation and dispersal limitation in freshwater organisms. *Oecologia,* 159**,** 151-159.

SZCZERKOWSKA-MAJCHRZAK, E., LIK, J. & LESZCZYŃSKA, J. 2014. Resistance of riverine macroinvertebrate assemblages to hydrological extremes. *Oceanological and Hydrobiological Studies.*

TERUI, A., ISHIYAMA, N., URABE, H., ONO, S., FINLAY, J. C. & NAKAMURA, F. 2018. Metapopulation stability in branching river networks. *Proceedings of the National Academy of Sciences,* 115**,** E5963-E5969.

TONKIN, J. D., ALTERMATT, F., FINN, D. S., HEINO, J., OLDEN, J. D., PAULS, S. U. & LYTLE, D. A. 2018. The role of dispersal in river network metacommunities: Patterns, processes, and pathways. *Freshwater Biology,* 63**,** 141-163.

TORNÉS, E., ACUÑA, V., DAHM, C. N. & SABATER, S. 2015. Flood disturbance effects on benthic diatom assemblage structure in a semiarid river network. *Journal of Phycology,* 51**,** 133-143.

TURNER, M. G. 2010. Disturbance and landscape dynamics in a changing world1. *Ecology,* 91**,** 2833-2849.

VAN VLIET, M. T. H., FRANSSEN, W. H. P., YEARSLEY, J. R., LUDWIG, F., HADDELAND, I., LETTENMAIER, D. P. & KABAT, P. 2013. Global river discharge and water temperature under climate change. *Global Environmental Change,* 23**,** 450-464.

VANDER ZANDEN, M. J., CASSELMAN, J. M. & RASMUSSEN, J. B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature,* 401**,** 464.

VANSCHOENWINKEL, B., WATERKEYN, A., JOCQUÉ, M., BOVEN, L., SEAMAN, M. & BRENDONCK, L. 2010. Species sorting in space and time—the impact of disturbance regime on community assembly in a temporary pool metacommunity. *Journal of the North American Benthological Society,* 29**,** 1267-1278.

VILLNÄS, A., NORKKO, J., HIETANEN, S., JOSEFSON, A. B., LUKKARI, K. & NORKKO, A. 2013. The role of recurrent disturbances for ecosystem multifunctionality. *Ecology,* 94**,** 2275-2287.

WEN, L., SAINTILAN, N., REID, J. R. W. & COLLOFF, M. J. 2016. Changes in distribution of waterbirds following prolonged drought reflect habitat availability in coastal and inland regions. *Ecology and Evolution,* 6**,** 6672-6689.

WHITNEY, J. E., HOLLOWAY, J. A., SCHOLES, D. T. & KING, A. D. 2019. Long-Term Change of Fish Communities in a Polluted Watershed: Does Cleaner Water “Act” on Fishes? *Transactions of the American Fisheries Society,* 148**,** 191-206.

WOODWARD, G., BONADA, N., FEELEY, H. B. & GILLER, P. S. 2015. Resilience of a stream community to extreme climatic events and long-term recovery from a catastrophic flood. *Freshwater Biology,* 60**,** 2497-2510.

WOUTER, R. B., EMMA, E. A., JOSHUA, R. L., RALPH, T. & ROSS, A. W. 2017. Recent changes in extreme floods across multiple continents. *Environmental Research Letters,* 12**,** 114035.

YANG, Q., FOWLER, M. S., JACKSON, A. L. & DONOHUE, I. 2019. The predictability of ecological stability in a noisy world. *Nature Ecology & Evolution,* 3**,** 251-259.

9. Appendices

9.1 Chapter 3

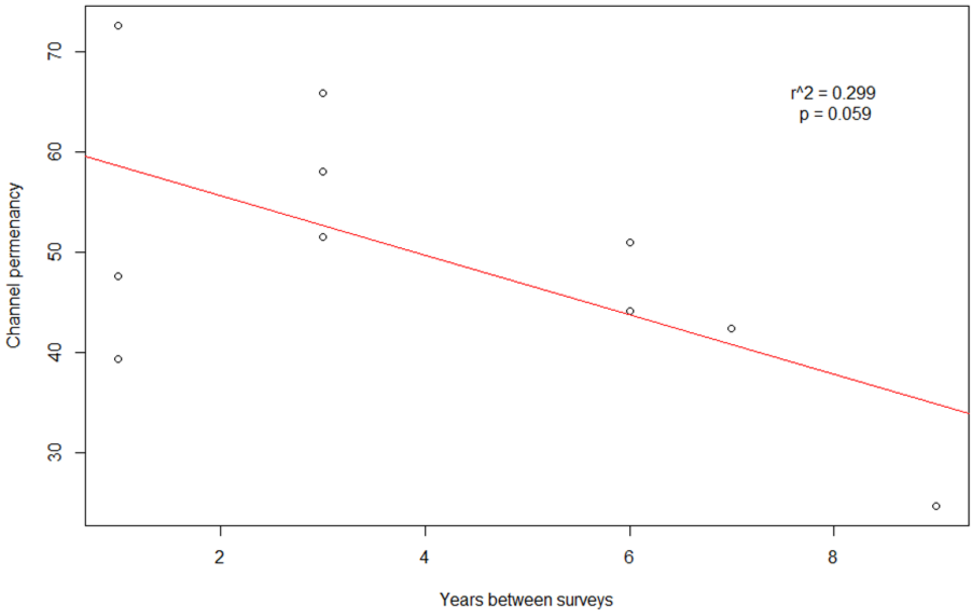

Figure 9.1. Scatterplot of number of years between samples and channel permanency/persistence scores across all sites for pre-, across and post-flood periods. Generalised linear model r^2 *= 0.299 and p value = 0.059. Non-significant relationship between the number of years between samples and the level of channel permanency.*

Table 9.1. Results of tests for differences backwaters depth, velocity and Froude numbers between sites. Anova - Analysis of variance (post hoc tukeys tests), (SQRT) - Square root transformed data, KW - Kruskall Wallis test, MU - Mann-Whitney U post hoc comparisons. All values Bonferroni adjusted. *** = p<0.001, ** = p<0.05, * =p<0.01, n/s = not significant, / data not available.

Backwater				
Depth cm Anova (SQRT)	WPC	IVS	BBS	RPC
WPC	-	/	/	/
IVS	/	-	***	***
BBS	/	***	-	n/s
RPC	/	***	n/s	-
Velocity m2/s KW MU	WPC	IVS	BBS	RPC
WPC	-	/	/	/
IVS	/	-	n/s	*
BBS	/	n/s	-	***
RPC	/	*	***	-
Froude number KW MU	WPC	IVS	BBS	RPC
WPC	-	/	/	/
IVS	/	-	n/s	n/s
BBS	/	n/s	-	***
RPC	/	n/s	***	-

*Table 9.2. . Results of tests for differences pool depth, velocity and Froude numbers between sites. Anova - Analysis of variance (post hoc tukeys tests), (SQRT) - Square root transformed data, KW - Kruskall Wallis test, MU - Mann-Whitney U post hoc comparisons. All values Bonferroni adjusted. *** = p<0.001, ** = p<0.05, * =p<0.01, n/s = not significant, / data not available.*

Pool				
Depth cm Anova	WPC	IVS	BBS	RPC
WPC	-	n/s	***	***
IVS	n/s	-	***	***
BBS	***	***	-	n/s
RPC	***	***	n/s	-
Velocity m2/s ANOVA(SQRT)	WPC	IVS	BBS	RPC
WPC	-	n/s	n/s	n/s
IVS	n/s	-	n/s	n/s
BBS	n/s	n/s	-	n/s
RPC	n/s	n/s	n/s	-
Froude number ANOVA(SQRT)	WPC	IVS	BBS	RPC
WPC	-	n/s	n/s	n/s
IVS	n/s	-	n/s	n/s
BBS	n/s	n/s	-	n/s
RPC	n/s	n/s	n/s	-

*Table 9.3. Results of tests for differences glide depth, velocity and Froude numbers between sites. Anova - Analysis of variance, KW - Kruskall Wallis test. All values Bonferroni adjusted. *** = p<0.001, n/s = not significant, / data not available*

Glide				
Depth cm ANOVA	WPC	IVS	BBS	RPC
WPC	-	/	/	/
IVS	/	-	/	/
BBS	/	/	-	***
RPC	/	/	***	-
Velocity m2/s KW	WPC	IVS	BBS	RPC
WPC	-	/	/	/
IVS	/	-	/	/
BBS	/	/	-	*
RPC	/	/	*	-
Froude number ANOVA	WPC	IVS	BBS	RPC
WPC	-	/	/	/
IVS	/	-	/	/
BBS	/	/	-	***
RPC	/	/	***	-

*Table 9.4. Results of tests for differences in run depth, velocity and Froude numbers between sites. Anova - Analysis of variance (post hoc tukeys tests), , KW - Kruskall Wallis test, MU - Mann-Whitney U post hoc comparisons. All values Bonferroni adjusted. *** = p<0.001, ** = p<0.05, * =p<0.01, n/s = not significant, / data not available.*

Run				
Depth cm ANOVA	WPC	IVS	BBS	RPC
WPC	-	***	***	n/s
IVS	***	-	n/s	***
BBS	***	n/s	-	***
RPC	n/s	***	***	-
Velocity m2/s ANOVA	WPC	IVS	BBS	RPC
WPC	-	***	***	***
IVS	***	-	n/s	n/s
BBS	***	n/s	-	**
RPC	***	n/s	**	-
Froude number KW MU	WPC	IVS	BBS	RPC
WPC	-	n/s	***	**
IVS	n/s	-	*	n/s
BBS	***	*	-	n/s
RPC	**	n/s	n/s	-

*Table 9.5. Results of tests for differences riffles depth, velocity and Froude numbers between sites. KW - Kruskall Wallis test, MU - Mann-Whitney U post hoc comparisons. All values Bonferroni adjusted. *** = p<0.001, ** = p<0.05, * =p<0.01, n/s = not significant, / data not available.*

		Riffle		
Depth cm KW MU	WPC	IVS	BBS	RPC
WPC	-	***	***	**
IVS	***	-	***	***
BBS	***	***	-	***
RPC	**	***	***	-
Velocity m2/s KW MU	WPC	IVS	BBS	RPC
WPC	-	***	***	n/s
IVS	***	-	*	***
BBS	***	*	-	n/s
RPC	n/s	***	n/s	-
Froude number KW MU	WPC	IVS	BBS	RPC
WPC	-	n/s	n/s	n/s
IVS	n/s	-	***	n/s
BBS	n/s	***	-	n/s
RPC	n/s	n/s	n/s	-

*Table 9.6. Results of tests for differences rapids depth, velocity and Froude numbers between sites. Anova - Analysis of variance (post hoc tuckeys tests), (SQRT) - Square root transformed data, KW - Kruskall Wallis test, MU - Mann-Whitney U post hoc comparisons. All values Bonferroni adjusted. *** = p<0.001, ** = p<0.05, * =p<0.01, n/s = not significant, / data not available.*

Rapid

Depth cm KW MU	WPC	IVS	BBS	RPC
WPC	-	***	***	/
IVS	***	-	***	/
BBS	***	***	-	/
RPC	/	/	/	-

Velocity m2/s ANOVA	WPC	IVS	BBS	RPC
WPC	-	***	***	/
IVS	***	-	n/s	/
BBS	***	n/s	-	/
RPC	/	/	/	-

Froude number ANOVA	WPC	IVS	BBS	RPC
WPC	-	***	n/s	/
IVS	***	-	n/s	/
BBS	n/s	n/s	-	/
RPC	/	/	/	-

9.2 Chapter 4

Table 9.7. Final regression models selected for overall and individual stream analyses

Stream	Test Comparison	Taxa Richness	Shannon's diversity	Total density (ind/m^2)	Sorenson's Dissimilarity	Simpson's Turnover	Sorenson's Nestedness	Ephemoptera (ind/m^2)	Heptagenidae (ind/m^2)	*Cinygmula* sp. (ind/m^2)	Chironimidae (ind/m^2)	*Orthocladius* Type *S* grp (ind/m^2)	*Eukifferella Claripennis* grp (ind/m^2)
All	Model	GLMM	GLMM	GLMM PQL	GLMM	GLMM	GLMM	GLMM Glmer	GLMM PQL	GLMM Glmer	GLMM PQL	GLMM Glmer	GLMM PQL
	Error distribution	Normal	Normal	NegBin	Normal	Normal	Normal	NegBin	NegBin	NegBin	NegBin	NegBin	NegBin
WPC	Model	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM
	Error distribution	Normal	Normal	NegBin	Normal	Normal	Normal	GEE quasiPoiss	NegBin	NegBin	NegBin	NegBin	NegBin
IVS	Model	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM
	Error distribution	Normal	Normal	NegBin	Normal	Normal	Normal	NegBin	NegBin	NegBin	NegBin	NegBin	Poisson
BBS	Model	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM
	Error distribution	Normal	Normal	NegBin	Normal	Normal	Normal	NegBin	NegBin	NegBin	NegBin	NegBin	NegBin
RPC	Model	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM	GLM
	Error distribution	Normal	Normal	GEE quasiPoiss	Normal	Normal	Normal	NegBin	NegBin	NegBin	GEE quasiPoiss	NegBin	GEE quasiPoiss

9.3 Chapter 5

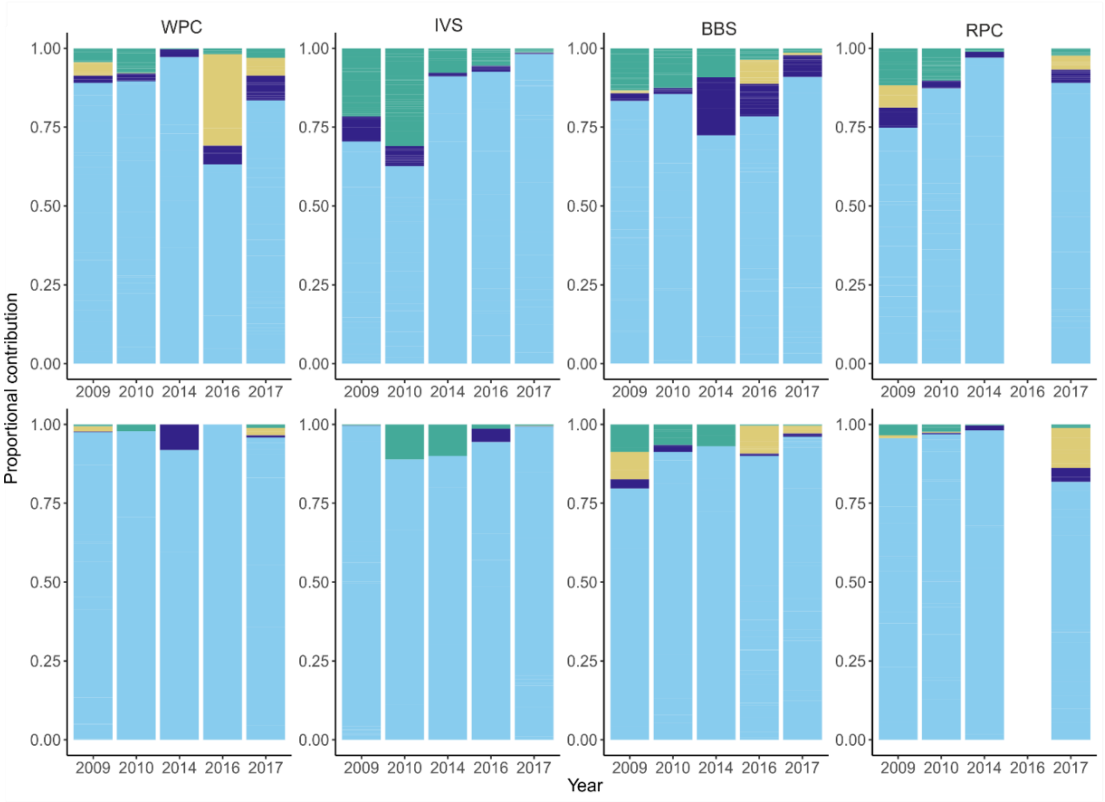

Figure 9.2. Proportion of guts containing items from resource groups (top) coho salmon, (bottom) Dolly Varden. freshwater = light blue, freshwater aerial stage = dark blue, marine = gold and terrestrial = green.

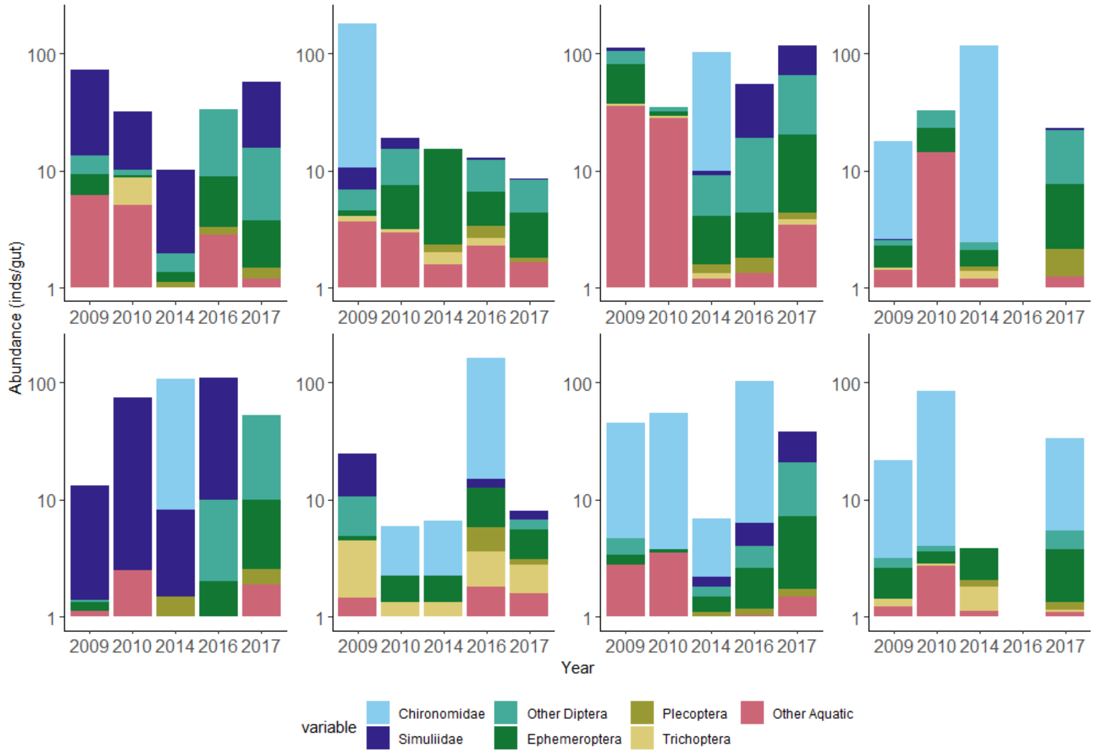

Figure 9.3. Mean abundance of freshwater resources in juvenile salmon guts (top) coho salmon, (bottom) Dolly Varden.

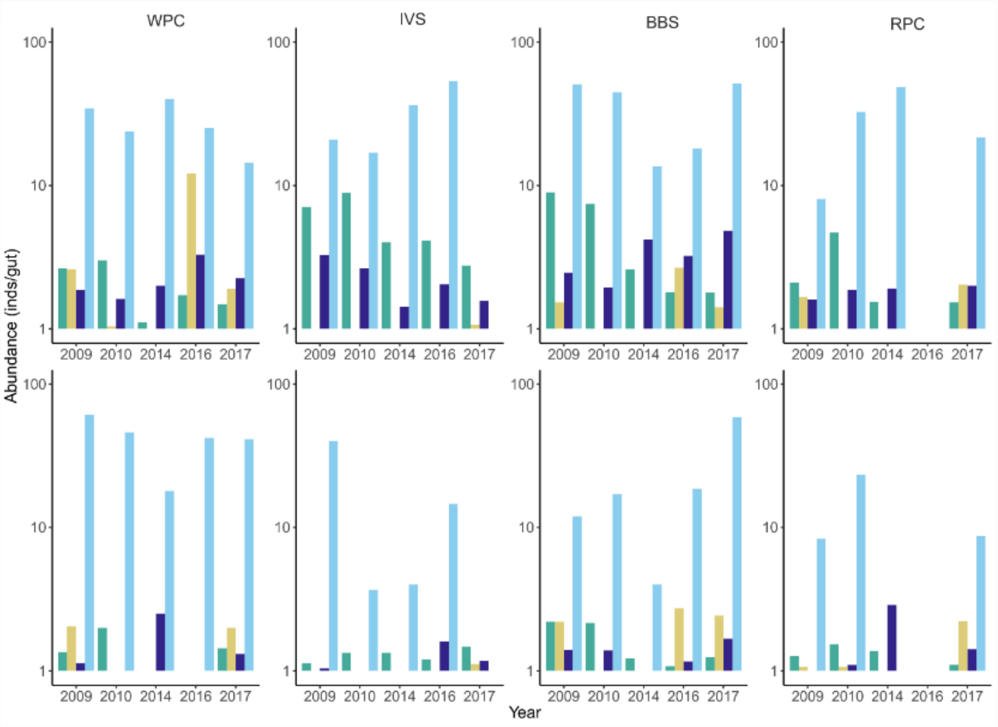

Figure 9.4. Mean abundance of gut contents items from resource groups. (top) coho salmon, (bottom) Dolly Varden. Light Blue = freshwater, Dark Blue = freshwater aquatic stage, Gold = marine, Green = terrestrial.

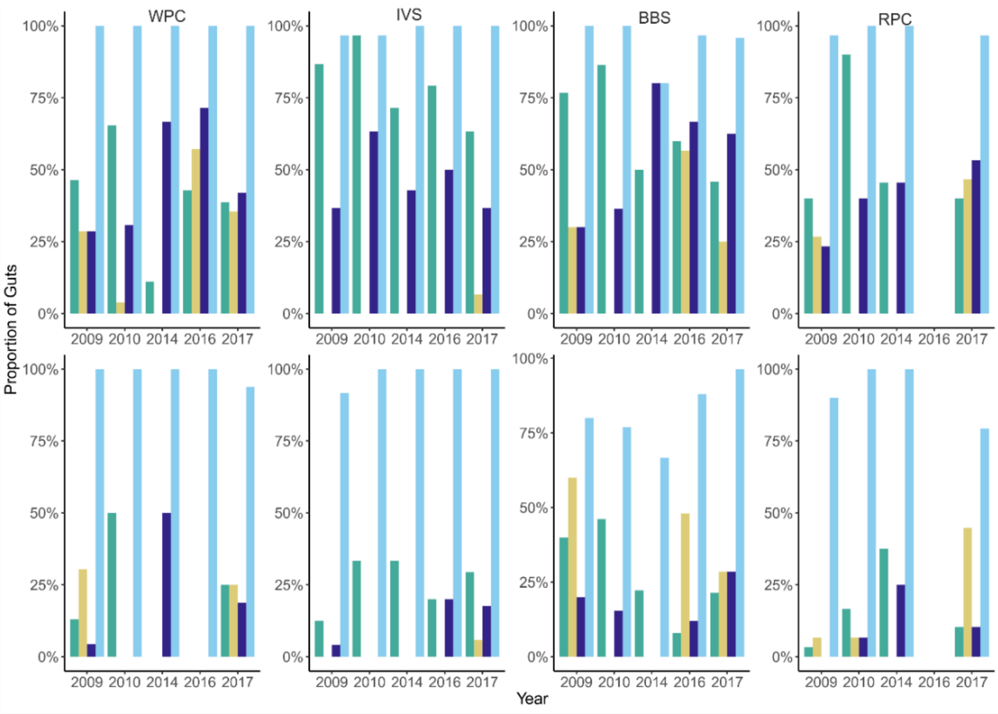

Figure 9.5. Percentage of guts containing prey resources from each source (top) coho salmon, (bottom) Dolly Varden. Columns left to right - WPC, IVS, BBS, RPC. Light Blue = freshwater, Dark Blue = freshwater aquatic stage, Gold = marine, Green = terrestrial.

Table 9.8. Coho salmon odds ratios for larvae of abundant freshwater benthic macroinvertebrate taxa.

Site	Year	Chironomidae	Simuliidae	Cerapotogonidae	Empididae	Ephemeroptera	Plecoptera	Trichoptera	Hydrachnidia
WPC	2009	-0.76	0.77	0.71	0.00	1.35	0.96	0.19	0.93
	2014	1.68	2.53	0.29		-3.36	-2.64	-17.20	-21.81
	2016	-0.44	1.93	-0.72	6.21	-0.48	1.60	-23.32	-21.83
	2017	-1.38	1.64	-2.64		0.83	1.29		4.97
IVS	2009	0.31	0.00	0.00	0.79	0.03	0.00	0.65	0.00
	2014	3.31	-0.17		2.14	-3.08	-2.50	3.77	3.54
	2016	3.62	-3.56		-2.44	-4.06	-3.15	1.77	3.77
	2017	3.30	-3.86		-3.45	-3.22	-4.49		2.39
BBS	2009	-1.33	0.36	0.00	0.13	0.48	0.48	0.00	2.98
	2014	1.27	3.87	3.46	-0.24	-0.96	-2.41	3.46	-0.94
	2016	-1.02	1.04	4.31	3.13	0.59	-0.80		2.35
	2017	0.51	0.23	-1.91	-1.14	0.50	-3.63	3.52	3.16
RPC	2009	-0.56	0.13	0.00	0.21	0.51	0.44	0.57	2.75
	2014	3.93	3.04		-2.87	-3.91	-4.34	3.04	1.94
	2016								
	2017	1.29		0.14	1.25	-0.99	-1.33	-21.95	4.94

Table 9.9. Dolly Varden odds ratios for larvae of abundant freshwater benthic macroinvertebrate taxa.

Site	Year	Chironomidae	Simuliidae	Cerapotogonidae	Empididae	Ephemeroptera	Plecoptera	Trichoptera	Hydrachnidia
WPC	2009	-0.76	1.07	0.11	0.00	1.90	1.25	0.17	0.00
	2014	0.79	3.19	-21.44		-1.10	-0.69	-17.05	0.69
	2016	0.17	1.74	-22.53		-1.81	-2-.21	-24.04	-22.55
	2017	-1.09	1.87	-23.54		-0.01	0.47		4.31
IVS	2009	0.23	0.00	0.00	0.07	0.03	0.00	2.36	0.00
	2014	0.85	0.31			-3.60	-1.34	8.29	
	2016	1.73	-0.71		-21.02	-2.49	-0.96	4.90	4.67
	2017	3.04	-2.43		-22.91	-3.68	-4.16	2.86	2.60
BBS	2009	-1.41	0.12	0.00	0.34	0.36	0.15	0.00	0.87
	2014	2.02	4.13	4.13	1.13	-2.65	-2.15	3.72	-20.88
	2016	0.29	-0.14	3.17	1.06	0.19	-2.06	-20.15	-19.45
	2017	1.04	-0.54	-22.61	-21.84	0.19	-3.65		2.14
RPC	2009	-0.55	0.00	0.00	0.21	0.53	0.50	1.21	0.78
	2014	4.70			-4.25	-4.48	-4.33	2.64	0.56
	2016								
	2017	0.29		-18.28	1.39	0.18	-1.58	-1.08	5.08

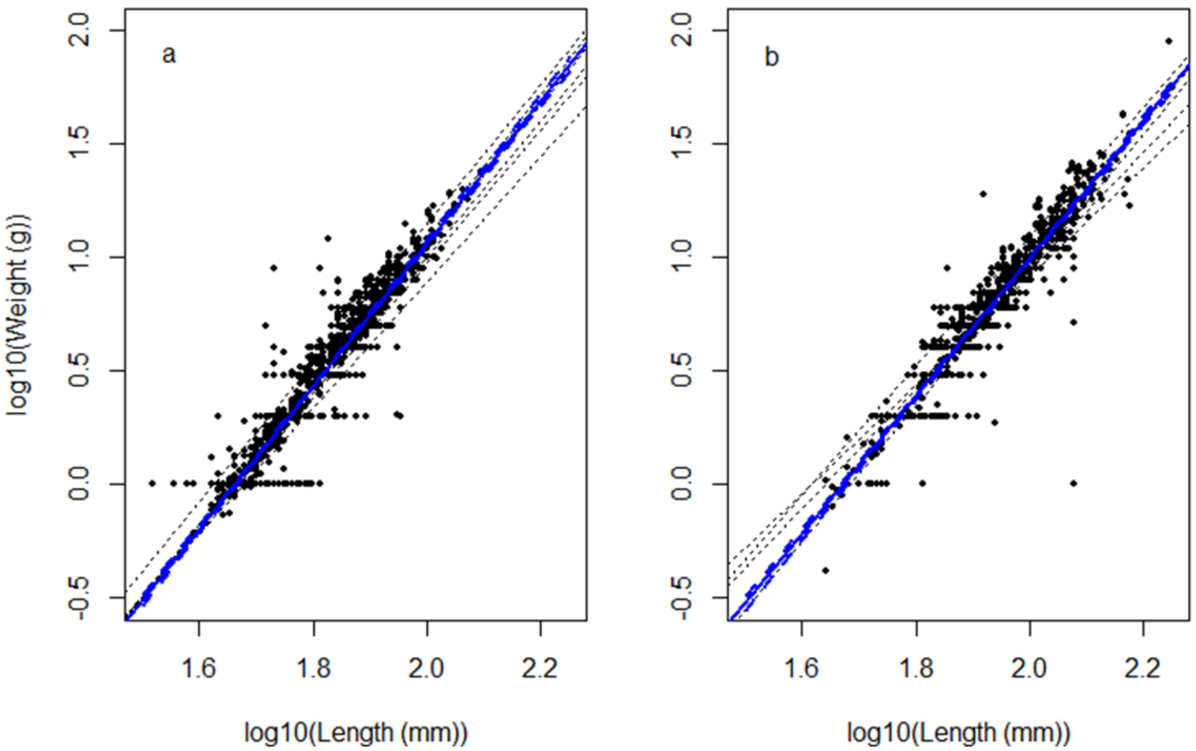

Figure 9.6. Mass~Length regression plots for a) coho salmon and b) Dolly Varden. Blue solid line = all years regression, blue dashed lines = 95% CI, black dashed lines = individual year regression lines.

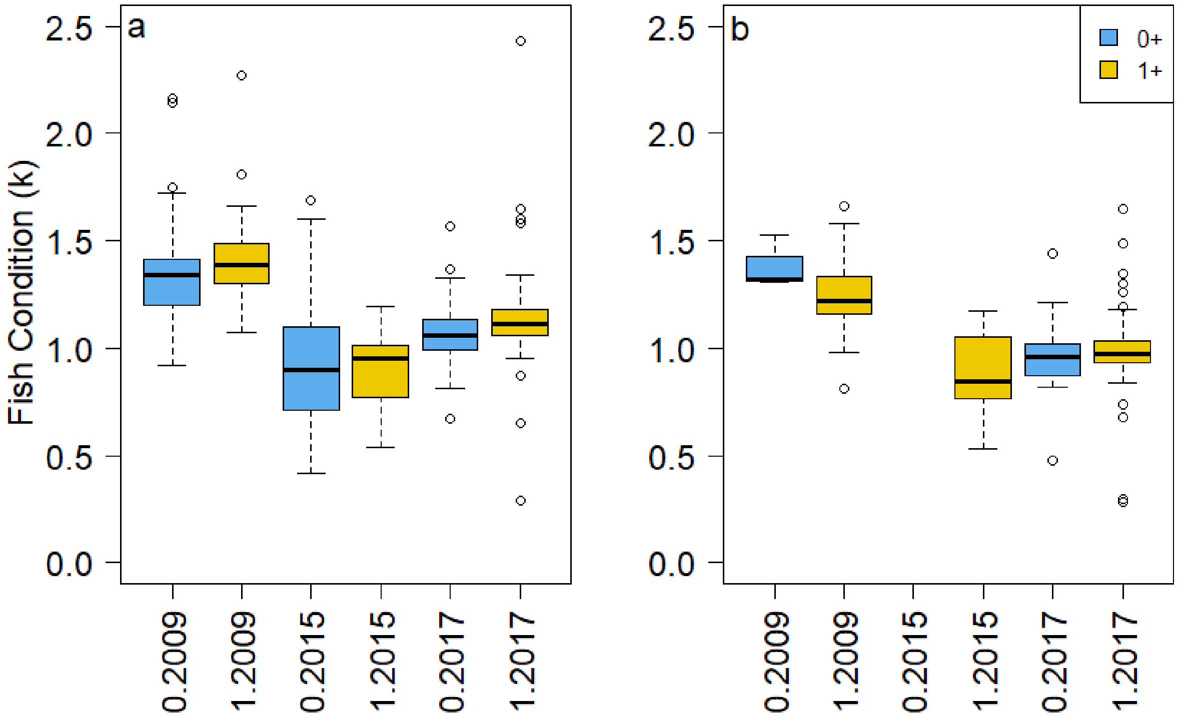

Figure 9.7. Juvenile salmon condition for 0+ and 1+ cohorts of a) coho salmon and b) Dolly Varden.

Table 9.10. Mass Abundance regression model coefficients

		2009	**2013**	**2014**	**2015**	**2016**	**2017**
WPC	**α**	-0.90 (-1.60, -0.20)	-0.77 (-0.91, -0.62)	-0.38 (-1.65, 0.88)		-0.76 (-1.53, 0.01)	0.41 (-0.98, 1.80)
	β	0.72 (0.03, 1.41)	0.34 (0.20, 0.49)	0.21 (-1.04, 1.46)		-0.06 (-0.85, 0.73)	-0.08 (-1.45, 1.30)
IVS	**α**	-1.99 (-3.26, -0.72)	-1.52 (-2.03, -1.00)	1.00 (0.52, 1.49)	0.16 (-0.48, 0.79)	0.53 (0.30, 0.76)	-0.15 (-0.79, 0.50)
	β	1.57 (0.31, 2.82)	1.07 (0.56, 1.58)	-0.86 (-1.34, -0.37)	-0.76 (-1.53, 0.01)	-0.46 (-0.69, -0.23)	-0.08 (-0.72, 0.56)
BBS	**α**	-0.62 (-1.38, 0.14)	-1.23 (-2.57, 0.12)	0.29 (-1.02, 1.60)	0.62 (-0.05, 1.29)	1.15 (0.10, 2.19)	0.13 (-0.72, 0.97)
	β	0.35 (-0.57, 1.28)	1.05 (-0.28, 2.38)	0.89 (-0.41, 2.18)	-0.88 (-1.69, -0.07)	-1.03 (-2.06, -0.00)	-0.15 (0.98, 0.68)
RPC	**α**	-0.36 (-2.05, 1.33)	-1.15 (-2.46, 0.17)	0.79 (-0.32, 1.90)	0.67 (0.27, 1.07)	0.44 (-0.09, 0.98)	0.12 (-1.17, 1.41)
	β	0.04 (-1.63, 1.72)	0.78 (-0.81, 2.37)	0.22 (-0.88, 1.32)	-0.76 (-1.16, -0.37)	-0.22 (-0.75, 0.31)	0.10 (1.17, 1.38)

Table 9.11 Information theoretic approach regression model results. The top five models are reported in the main text and repeated here for completeness.

Time Since Flood	**Slow flow habitat availability**	**Total freshwater prey density**	**k**	**AICc**	**Weight**	**Evidence ratio**
+X*		+X*	5	7.76	0.5406	1.0
+X*			3	8.85	0.3136	1.7
+X*	-X		5	11.2	0.0946	5.7
+X*	-X	+X	7	12.8	0.0445	12.1
		+X*	3	16.8	0.0057	94.2
	-X	+X*	5	21.2	0.0007	820.9
			1	23.9	0.0001	3125.5
	-X		3	26.3	0.0000	10421.1

9.4 Chapter 7

Table 9.12. P values for permutation tests of ellipsoid components and null model ellipsoids. P values in bold are significant at p < 0.05

Semi axis length	**1**	**2**	**3**	**4**	**5**
Pre-2005	**< 0.001**	**0.008**	**0.034**	**0.002**	**0.002**
Post-2005	**0.004**	0.809	**0.002**	**0.006**	**0.003**
Pre-2014	**0.012**	0.677	**0.026**	0.086	**0.004**
Post-2014	0.074	0.206	0.104	**0.002**	**0.016**
Relative semi axis length		**2**	**3**	**4**	**5**
Pre-2005		**0.002**	**0.004**	**0.002**	**0.002**
Post-2005		0.088	**0.002**	**0.004**	**0.004**
Pre-2014		0.096	**0.020**	**0.046**	**0.002**
Post-2014		0.591	0.068	**0.002**	**0.014**
			Volume		
Pre-2005				**0.002**	
Post-2005				**0.004**	
Pre-2014				**0.002**	
Post-2014				**0.008**	