Dry me a river: characterising and monitoring how aquatic and terrestrial invertebrates respond to drying and anthropogenic pressures in temporary streams

Kieran J. Gething

School of Science and Technology
Nottingham Trent University
Thesis submitted in partial fulfilment of the
requirements for the degree of Doctor of Philosophy

April 2024

Front matter

Copyright Statement

Abstract

Temporary streams, those which sometimes dry, comprise >50% of the global river network and support communities which include both aquatic and terrestrial species. As such, temporary streams support high biodiversity, including rare and specialist species, but such ecosystems face multiple natural and anthropogenic pressures, such as climate change and agriculture. To inform management strategies that protect temporary streams, we need a better understanding of how these pressures influence their aquatic–terrestrial biodiversity, and how to effectively monitor communities in such dynamic ecosystems. In this thesis, I assess the responses of aquatic invertebrate assemblages to co-occurring drying and agricultural pressures and investigate the role of agricultural ditches in supporting specialist drying-tolerant insects. I also evaluate the role of connectivity in shaping terrestrial assemblages around the channel and test methods for characterising in-channel terrestrial assemblages in relation to environmental variables indicative of human impacts during wet and dry phases. I found that flow permanence was the key driver of both aquatic and terrestrial assemblages, with the balance of connectivity and isolation provided by wet and dry phases maintaining populations that include generalist and specialist invertebrate taxa. Pitfall trapping, hand searching and predictions made from habitat surveys were capable of characterising terrestrial assemblages, suggesting these methods may allow more frequent and widespread monitoring by managers and citizen scientists. Holistically monitoring both aquatic and terrestrial assemblages may provide novel insights as to the ecological impacts of the multiple pressures impacting temporary streams, informing better recognition and protection of these dynamic river ecosystems in a time of unprecedented global change.

Citation

Gething, K. J. (2024) *Dry me a river: characterising and monitoring how aquatic and terrestrial invertebrates respond to drying and anthropogenic pressures in temporary streams*. PhD Thesis. Nottingham Trent University, Nottingham.

Contents

List of Figures

List of Tables

Acknowledgements

Firstly, I would like to express my immense gratitude to Rachel Stubbington and Tim Sykes who have supported me throughout my PhD journey and consistently pushed me to produce the best research I am capable of. Rachel and Tim have offered profound support to both my PhD research and my personal development over the last 4 years for which I am very grateful, and I look forward to continuing to learn from and work alongside both of you. For their countless contributions which have immeasurably improved my PhD research, I would also like to thank the other members of my extended supervisory and development team, past and present: Judy England, Erika Whiteford, Iain Barber, Rob Mortimer, Carl Smith and Andrew Hirst. I would also like to recognise the contributions of all members of the "Temporary Stream Dream Team" for their insights which have shaped my PhD at every stage.

I would like to express my gratitude to Nottingham Trent University, the Environment Agency, Hampshire and Isle of Wight Wildlife Trust and the Vitacress Conservation Trust for funding my PhD research. I would like to thank Maggie Shelton for facilitating landowner introductions and the landowners themselves for granting access to sampling sites. Fieldwork and sample processing would not have been possible without Tim Sykes, Helen Wallis, Jackie Greef, Gareth Williams, Abby Whiley, Sam Poole, Giulio Biondi, Jess Goldring, Maddy Chaborska, Olivia Greenway and Sam Davies, thank you all. For assistance with identifying invertebrates, I thank Chris Terrell-Nield, Craig Macadam, Gloria Tapia and Jon Webb. I thank Andy House and Jon Webb for providing the datasets used in Chapters 3 and 7. I thank Andrew Hirst, Carl Smith, Romain Sarremejane and Tom Aspin for statistical guidance throughout my PhD. Finally, I thank my examiners, Deb Finn and Jaime Martin, for an enjoyable viva and for their suggestions which improved the final version this thesis.

Research dissemination

Publications and reports

Biondi, G., **Gething, K. J.**, Kabir, J., Sykes, T. and Stubbington, R. (2022) The invertebrate biodiversity in the hidden headwater springs and streams of the southern Chalk. *Freshwater Biological Association News*, 85, 8–11. https://irep.ntu.ac.uk/id/eprint/47092

Bunting, G., England, J., **Gething, K. J.**, Sykes, T., Webb, J. and Stubbington, R. (2021) Aquatic and terrestrial invertebrate community responses to drying in chalk streams. *Water and Environment Journal*, 35, 229–241. https://doi.org/10.1111/wej.12621

Gething, K. J. (2023) *Predicting invertebrate richness and rarity in aquatic-terrestrial ecosystems* in The Applied Ecologist. Available at: https://appliedecologistsblog.com/2023/04/03/kieran-gething-predicting-invertebrate-richness-and-rarity-in-aquatic-terrestrial-ecosystems/ (accessed April 2023).

Gething, K. J., Hayes, C., Webb, J., Sykes, T., England, J. and Stubbington, R. (2022) Living on the edge: predicting invertebrate richness and rarity in disturbance-prone aquatic–terrestrial habitats. *Ecological Solutions and Evidence*, 3, e12196. https://doi.org/10.1002/2688-8319.12196

Gething, K. J., Sykes, T., Biondi, G., Macadam, C. and Stubbington, R. (2021) Ditching misconceptions: rare temporary stream specialists in man-made habitats. *Freshwater Biological Association News*, 83, 14–18. https://irep.ntu.ac.uk/id/eprint/44941

Kabir, J., Biondi, G., **Gething, K. J.**, Aspin, T., Sykes, T. and Stubbington, R. (2024) Spring forth diversity: specialist species enhance the conservation value of headwater springs and streams at the landscape scale. *River Research and Applications*, 1–12. https://doi.org/10.1002/rra.4275

Roque, A., **Gething, K. J.** and Stubbington, R. (2021) *The effects of drying on invertebrate communities in the winterbourne headwaters of the River Thames*. Scholarship Projects for Undergraduate Researchers (SPUR) report. Nottingham: Nottingham Trent University and Environment Agency. http://dx.doi.org/10.13140/RG.2.2.24652.90242

Shuker, L., **Gething, K. J.**, Hayes, C. and England, J. (2023) The Modular River Survey and its application in ecological studies. *Freshwater Biological Association News*, 86, 4–8. https://irep.ntu.ac.uk/id/eprint/48422

Stubbington, R., **Gething, K. J.** and Sykes, T. (2022) *Chalk streams: why 'England's rainforests' are so rare and precious* in The Conversation. Available at: https://theconversation.com/chalk-streams-why-englands-rainforests-are-so-rare-and-precious-172827 (accessed January 2022).

Webb, J., **Gething, K. J.**, Kratz, C. C., England, J., Drewitt, A. L. and Stubbington, R. (2022) A standardised multi-method survey to enhance characterisation of riparian invertebrate communities. *Water and Environment Journal*, 36, 425–432. https://doi.org/10.1111/wej.12775

Note: where published work forms part of this thesis the Contributor Roles Taxonomy (CRediT: Brand et al., 2015) is used to highlight author roles at the end of the relevant chapter.

Datasets

The dataset used in Chapter 3 can be requested from Wessex Water Ltd.. The datasets used in Chapters 4–6 will be made publicly available as their corresponding chapter is published. The dataset used in Chapter 7 is available at:

Gething, K. J., Hayes, C., Webb, J., Sykes, T., England, J. and Stubbington, R. (2022), Living on the edge: Predicting invertebrate richness and rarity in disturbance-prone aquatic–terrestrial ecosystems. *Dryad dataset*: https://doi.

org/10.5061/dryad.xwdbrv1hg

Oral presentations

England, J., Charlton, M., Finney, M., Hannah, D., **Gething, K. J.**, Khamis, K., Sarremejane, R., Stubbington, R. and Watts, G. (2023) *Insights from groundwater dominated streams in a changing climate* at the Symposium for European Freshwater Sciences – SEFS13, Newcastle.

England, J., Collier, R., **Gething, K. J.**, Johns, T., Sarremejane, R., Stubbington, R., Sykes, T., Wilkes, M. and White, J. (2023) *Restoration to increase ecological resilience to climate change in groundwater dominated streams* at the Scientific Advances in River Restoration conference – SARR, Liverpool.

England, J., **Gething, K. J.**, Hayes, C., Gurnell, A., Shuker, L., Stubbington, R. and Wharton, G. (2023) *Modular River Physical survey (MoRPh): a high resolution, physical habitat and geomorphological survey for citizen scientists* at the Symposium for European Freshwater Sciences – SEFS13, Newcastle.

Gething, K. J. (2022) *Recognising and protecting dynamic river ecosystems* at the Chalk Stream Headwaters Forum, Winchester.

Gething, K. J. (2023) *Recognising and protecting the aquatic–terrestrial biodiversity of dynamic river ecosystems* at the Centre for Health, Ageing and Understanding Disease (CHAUD) Seminar Series, Nottingham.

Gething, K. J., Bunting, G., England, J., Sykes, T., Webb, J. and Stubbington, R. (2020) *Recognising and protecting dynamic river ecosystems* at the Test and Itchen Catchment Partnership Meeting, Online.

Gething, K. J., Hayes, C., Webb, J., Sykes, T., England, J. and Stubbington, R. (2021) *Predicting invertebrate assemblage characteristics in seasonally inundated terrestrial riverine habitats* at the Symposium for European Freshwater Sciences – SEFS12, Dublin.

Gething, K. J., Sarremejane, R., England, J., Sykes, T. and Stubbington, R. (2023) *Under pressure: macroinvertebrate community responses to agriculture in temporary streams* at the Symposium for European Freshwater Sciences – SEFS13, Newcastle.

Gething, K. J., Sykes, T., England, J. and Stubbington, R. (2021) *Agricultural stressors magnify differences in macroinvertebrate composition between temporary and perennial streams* at the Society for Freshwater Science Annual Meeting, Online.

Gething, K. J., Sykes, T., England, J. and Stubbington, R. (2021) *Aquatic invertebrate community responses to agricultural impacts in chalk streams* at the Temporary Rivers and Streams Meeting, Nottingham.

Gething, K. J., Sykes, T., England, J. and Stubbington, R. (2021) *The role of ditches in supporting a temporary stream specialist, Paraleptophlebia werneri* at the Symposium for European Freshwater Sciences – SEFS12, Dublin.

Gething, K. J., Sykes, T. and Stubbington, R. (2022) *Artificial ditches support populations of rare insects in temporary streams* at the 36th Congress of the International Society for Limnology – SIL, Berlin.

Gething, K. J., Sykes, T. and Stubbington, R. (2022) *Ditching misconceptions: drying specialist species in artificial habitats* at the Joint Aquatic Sciences Meeting – JASM, Grand Rapids, Michigan.

Gething, K. J., Sykes, T. and Stubbington, R. (2022) *Rare temporary river specialist insects: how rare are they really?* at the Temporary Rivers and Streams Meeting, Nottingham.

Gething, K. J., Sykes, T. and Stubbington, R. (2023) *Why did the arthropod cross the river channel - to get to the other side?* at the Temporary Rivers and Streams Meeting, Nottingham.

Gething, K. J., Sykes, T. and Stubbington, R. (2023) *Working 9 to 5: diurnal variability in invertebrate activity does not compromise ecosystem* *health assessments in dry stream channels* at the Symposium for European Freshwater Sciences – SEFS13, Newcastle.

Gething, K. J., Webb, J., Smith, C. and Stubbington, R. (2020) *Identifying sites of high terrestrial invertebrate richness and rarity from simple habitat surveys* at the California Aquatic Bioassessment Workgroup and the California Chapter Society for Freshwater Science Meeting – hosted by the California Environmental Protection Agency, Online.

Kabir, J., Biondi, G., **Gething, K. J.**, Sykes, T., England, J. and Stubbington, R. (2023) *Spring forth diversity! Local-scale actions support regional biodiversity in a project co-created with national stakeholders* at the Strategic Research Themes Conference, Nottingham.

Stubbington, R. Collier, R., **Gething, K. J.**, Hayes, C., England, J., Sarremejane, R. and Sykes, T. (2023) *Towards better biomonitoring of temporary aquatic ecosystems: insights from dry streams in wet places* at the National Research Institute for Agriculture, Food and Environment, Lyon.

Stubbington, R., England, J., **Gething, K. J.**, Hayes, C. and Sykes, T. (2023) *Towards better biomonitoring of wet and dry temporary rivers and streams* at the Symposium for European Freshwater Sciences – SEFS13, Newcastle.

Stubbington, R., Hayes, C., **Gething, K. J.** and Lavictoire, L. (2021) *When rivers run dry: how climate changes biodiversity in 'winterbourne' chalk streams* at the NTU Green Academy Learn Over Lunch Lecture Series, Online.

Poster presentations

Biondi, G., Goldring, J., **Gething, K. J.**, Sykes, T. and Stubbington, R. (2021) *The invertebrate biodiversity of headwater chalk springs* at the Animal, Rural and Environmental Science Research Conference, Nottingham.

Gething, K. J. and Stubbington, R. (2021) *Predicting invertebrate assemblage characteristics in seasonally inundated terrestrial riverine habitats* at the

Science and Technology Annual Research Conference, Nottingham.

Gething, K. J., Sykes, T., Mortimer, R. and Stubbington, R. (2020) *Recognising and protecting the aquatic–terrestrial biodiversity of dynamic river ecosystems* at the UK Environment Agency Knowledge Exchange, Bristol.

Gething, K. J., Sykes, T. and Stubbington, R. (2022) *Ditching misconceptions: rare temporary stream specialists in artificial habitats* at the Environment Agency Knowledge Exchange, Online.

Gething, K. J., Sykes, T. and Stubbington, R. (2021) *The role of ditches in supporting temporary stream specialist species* at the Animal, Rural and Environmental Science Research Conference, Nottingham.

Gething, K. J., Sykes, T. and Stubbington, R. (2023) *Under pressure: macroinvertebrate community responses to agriculture in temporary streams* at the Environment Agency Knowledge Exchange, Online.

Gething, K. J., Sykes, T., Webb, J., England, J. and Stubbington, R. (2020) *Characterising terrestrial beetle responses to standardised physical habitat indicators* at the Temporary Rivers and Streams Meeting, Nottingham.

Roque, A., **Gething, K. J.**, Stubbington, R. (2021) *The effects of drying on invertebrate communities in the temporary headwaters of the River Thames* at the Scholarship Projects for Undergraduate Researchers (SPUR) Celebration Event, Nottingham.

Community engagement

Gething, K. J. (2021) *Aquatic invertebrates from drying streams (seminar)* at the NTU Green Academy COP26 Climate Conference Campaign Event, Nottingham.

Gething, K. J. (2020) Lockdown took a lot away, but what has it added to our PhDs? in the *Environment Agency PhD Network Newsletter*.

Gething, K. J., Collier, R. and Sykes, T. (2023) *Sampling the aquatic and terrestrial invertebrates in your winterbourne* at Hamble Brook, Hambledon.

Gething, K. J., Evingar, S. and Sykes, T. (2021) Candover Brook: A hotspot for aquatic and terrestrial invertebrate diversity… in the *Candovers Parish Magazine*.

Gething, K. J. and Sykes, T. (2021) *What lives in your river and why it is important?* at Hurstbourne Tarrant Primary School, Hurstborune Tarrant.

1 Introduction

Freshwater ecosystems support communities with high aquatic biodiversity (Strayer & Dudgeon, 2010) as well as terrestrial assemblages (e.g. Bartrons et al., 2018; Lafage et al., 2019). However, this aquatic–terrestrial biodiversity is increasingly threatened by interacting pressures such as climate change, pollution, flow modification and habitat loss which are increasing in intensity over space and time (Dudgeon et al., 2006; Dudgeon, 2010; Reid et al., 2019). Although declining biodiversity is a common trend across aquatic and terrestrial domains (e.g. Schuch et al., 2012; Dirzo et al., 2014; Lister & Garcia, 2018), freshwater ecosystems may be particularly affected (Reid et al., 2019). For example, mean population trends summarised by the Living Planet Index decreased by 84% for monitored freshwater vertebrate species between 1970 and 2012, relative to 38% and 36% in terrestrial and marine species, respectively (WWF, 2016; Hildrew & Giller, 2023). Similarly, 35–45% of species from key invertebrate taxa (Ephmeroptera, Odonata, Plecoptera and Trichoptera) are in decline (Sánchez-Bayo & Wyckhuys, 2019; Hildrew & Giller, 2023).

The biodiversity of riverine ecosystems, and its responses to environmental conditions, have been studied for many decades (e.g. Hynes, 1970; Armitage et al., 1983; Extence et al., 2013), largely in perennial reaches, in which flow permanence promotes aquatic biodiversity (Datry et al., 2014a; Soria et al., 2017). However, more than half of the global river network is comprised of temporary reaches (Datry et al., 2014b; Messager et al., 2021), which cease to flow and sometimes dry (Leigh et al., 2016; Datry et al., 2017a). Their flowing and dry phases allow temporary streams to support both aquatic and terrestrial species (Corti & Datry, 2016; Bunting et al., 2021), including specialist aquatic species that are adapted to tolerate drying (Bogan et al., 2015, 2017; Macadam et al., 2021), meaning their overall biodiversity can be higher than that of perennial streams (Korhonen et al., 2010; Stubbington et al., 2017b).

Although research on the aquatic assemblages of such temporary reaches has proliferated in recent decades (Leigh et al., 2016; Stubbington et al., 2017a), we still have limited understanding of how their assemblages respond to the multiple pressures faced by riverine ecosystems. The terrestrial assemblages that colonise dry stream channels have received limited attention (Steward et al., 2022) and thus, we need methods to assess the health of such terrestrial assemblages and their responses to the pressures faced by temporary streams.

Connectivity between biotic communities is key to maintaining biodiversity (Bennett, 1999; Loke & Chisholm, 2023), particularly in temporary stream ecosystems where species may need to recolonise a habitat after being lost due to wetting/drying (Corti & Datry, 2012; Sarremejane et al., 2018; Cañedo-Argüelles et al., 2020), or where isolation by drying may enable the survival of some species (Aspin & House, 2022). Both flowing and dry channels can act as corridors that facilitate movement of aquatic and terrestrial species along river networks (Bogan & Boersma, 2012; Rosado et al., 2015; Sánchez-Montoya et al., 2022). Aquatic assemblages in temporary streams influence the composition of assemblages in other waterbodies in a catchment (e.g. via aerial dispersal away from the channel: Bogan & Boersma, 2012). Equally, adult life stage colonists of aquatic insects from other waterbodies may influence the composition of aquatic assemblages in temporary streams if, for example, they predate upon temporary stream fauna (Pineda-Morante et al., 2022). However, the role of connectivity among waterbodies within a catchment, including between populations of drying-tolerant specialists in a stream and artificial waterbodies such as ditches, in shaping the aquatic assemblages of temporary streams remains unknown.

Flowing streams can be barriers to dispersal for larger terrestrial species (e.g. mammals: Wallace, 1854; Bennett, 1999), but drying may allow cross-channel movements (Sánchez-Montoya et al., 2022). For smaller organisms (e.g. insects), movement of terrestrial and aerial dispersers is discouraged by linear features such as vehicle tracks (Mader, 1984; Lövei et al., 1998; Andersson et al., 2017), railway lines (Mader et al., 1990), hedgerows (Mauremooto et al., 1995) and thus potentially also dry stream channels. However, the role of temporary streams, whose flowing and dry states present a temporally variable barrier to animal movement, in influencing connectivity between cross-channel populations of terrestrial invertebrates has not been studied.

The temporary streams make up a greater proportion of the river network in arid, semi-arid and dry-temperate climates (e.g. north Africa and the Mediterranean: Tooth, 2000; Messager et al., 2021), and thus research has typically focused on such areas. However, temporary streams also occur in areas with wet-temperate climates, such as the UK. Some such temporary streams are groundwater-fed, including chalk streams which typically have temporary, 'winterbourne' headwater and perennial downstream reaches (Sear et al., 1999; Mondon et al., 2021). It is estimated that 85% of chalk streams occur in southern and eastern England (Salter & Singleton-White, 2019; Mondon et al., 2021). As such, chalk streams are globally rare habitats (Mainstone, 1999; Stubbington et al., 2022b) that support unique communities of plant, vertebrate and invertebrate taxa (Westlake et al., 1972; Britton et al., 2017; Bunting et al., 2021), and many are internationally designated (Mainstone, 1999). Chalk streams experience many of the pressures that influence rivers globally (e.g. pollution: Robinson et al., 2023). However, the ecological effects of these pressures have primarily been documented in their perennial reaches, and thus research on the aquatic–terrestrial community responses to such pressures in temporary reaches is required to promote and protect their unique biodiversity.

In this thesis, I assess responses of aquatic assemblages to anthropogenic pressures in chalk streams, and compare responses between better-studied perennial and less-well-studied temporary reaches. I also use the perennial and temporary reaches of chalk streams to test methods for characterising terrestrial assemblages in and around stream channels, and attempt to identify assemblage responses to common environmental drivers (e.g. temperature, moisture).

1.1 Aim and objectives of this thesis

I aimed to assess responses of different biotic groups to environmental conditions in riverine ecosystems that include temporary reaches, and to inform monitoring and management strategies that promote their ecological health. To address this aim, I pursued four objectives:

Objective 1. Characterise and compare the response of biotic communities to different types and intensities of human impacts in temporary streams.

Objective 2. Test the role of connectivity in shaping the biotic communities of temporary streams.

Objective 3. Adapt and evaluate methods to characterise the biotic communities of temporary streams across their flowing and dry states.

Objective 4. Make recommendations for management of temporary streams to maximise biodiversity.

1.2 Structure of this thesis

This thesis is structured in four main sections (**Figure 1.1**). The first, a literature review, outlines the physical characteristics of temporary streams, the aquatic–terrestrial communities found in temporary streams and their responses to environmental conditions including anthropogenic pressures. The second section details my studies on aquatic assemblage responses to anthropogenic pressure and how such assemblages are shaped by connectivity with other waterbodies in a catchment. Specifically, Chapter 3 reports the differing responses of assemblages in perennial and temporary reaches to an anthropogenic pressure, agriculture (**Objective 1**). Chapter 4 considers the landscape context of temporary streams, and the potential importance of a catchment's ditches in supporting their aquatic assemblages (**Objective 2**). The third section reports upon my studies of the terrestrial assemblages of temporary streams and surrounding habitats. Section three, Chapter 5 assesses the connectivity between assemblages on each side of the channel, and how this connectivity varies over time in perennial and temporary reaches (**Objective 2**). Chapters 6 and 7 adapt and evaluate methods for characterising terrestrial temporary stream assemblages in relation to environmental conditions during their dry and flowing phases, respectively (**Objectives 1** and **3**). The final section integrates insights from the literature review, aquatic and terrestrial assemblage sections to develop our understanding of temporary stream communities, and how we can better monitor and manage them (**Objective 4**).

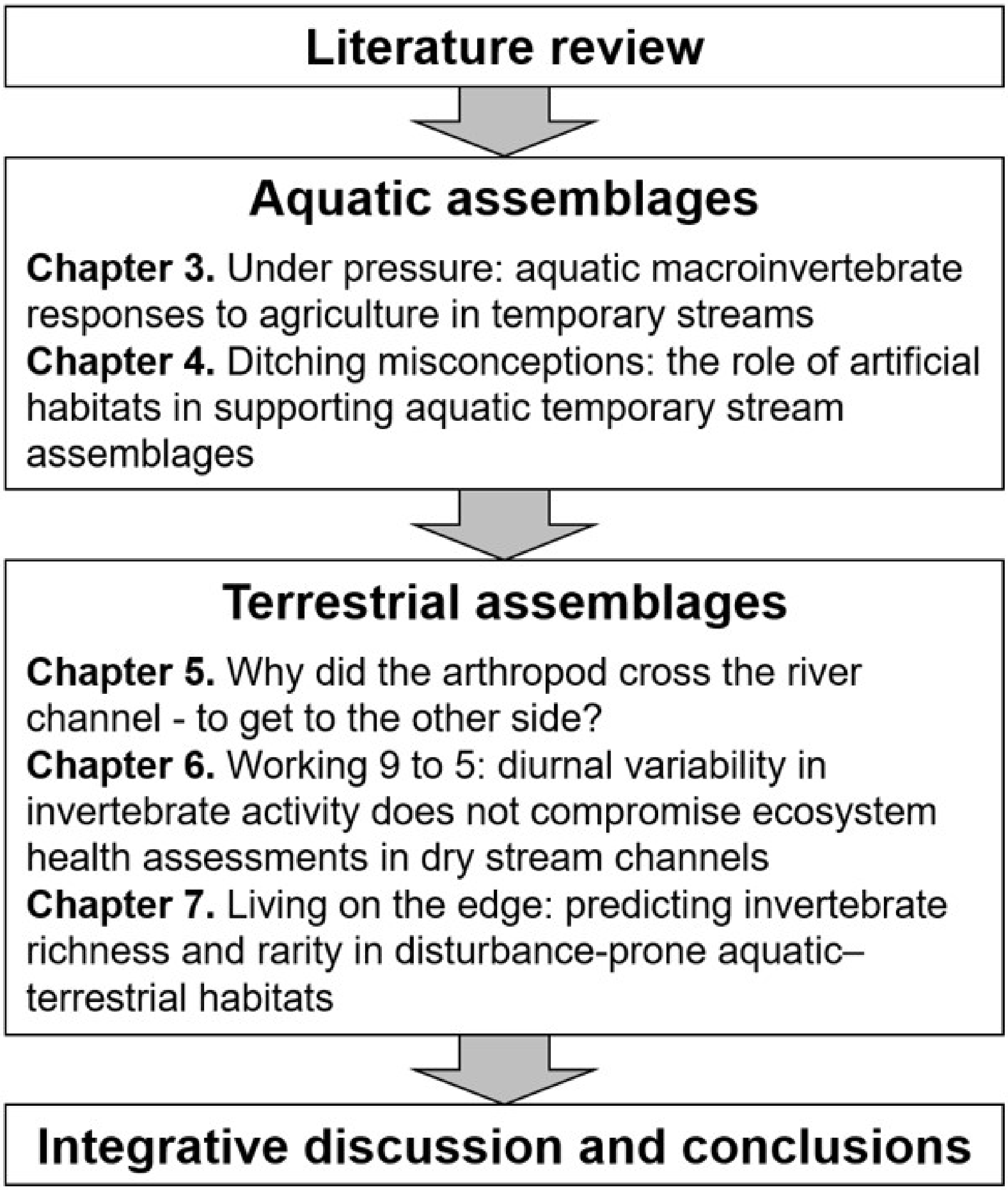


Figure 1.1: The structure of this thesis in four main sections: Literature review, Aquatic assemblages, Terrestrial assemblages and Integrative discussion and conclusions.

2 Literature review: Invertebrate responses to flow permanence and habitat quality

Temporary streams are dynamic ecosystems that transition between flowing, ponded and dry phases (Leigh et al., 2016; Datry et al., 2017a). Such transitions vary in space and time, allowing temporary streams to support diverse communities that comprise lotic, lentic and terrestrial species (Bogan & Lytle, 2007; Stubbington et al., 2017b). Like communities in all riverine ecosystems, temporary stream communities face increasing pressures, such as climate change, land use intensification and exploitation of water resources (Dudgeon et al., 2006; Dudgeon, 2010; Reid et al., 2019). In this chapter I summarise current understanding of temporary streams, their communities and the pressures they face to contextualise the research presented in Chapters 3–7. In section 2.1, I outline the terms used to define, the geographical distribution of, and the physical characteristics of temporary streams and their surrounding riparian habitats. Section 2.2 details the biotic groups characterised in Chapters 3–7, and their responses to environmental conditions in temporary streams and analogous ecosystems. Finally, in section 2.3, I evaluate the methods used to characterise temporary stream communities and their responses to in-channel conditions, and highlight the key impacts on temporary stream ecosystems that effective community characterisations are needed to mitigate.

2.1 Definitions, distribution and physical characteristics of temporary streams

2.1.1 Defining temporary streams

Temporary streams are lotic systems which cease to flow (Williams & Hynes, 1976; Williams, 2006; Leigh et al., 2016), and sometimes partially or completely dry (Stanley et al., 1997; Datry et al., 2014a; Stubbington et al., 2018a). This definition encompasses streams with a range of flow permanence regimes (e.g. flow cessation for one day to drying for many years), and thus the term *temporary* can describe any stream which does not flow perennially (Larned et al., 2010; McDonough et al., 2011; Busch et al., 2020). Some authors also use terms such as *non-perennial* or *intermittent rivers and ephemeral streams* (IRES) as equivalent terms for temporary streams (see Uys & O'Keeffe, 1997; Boulton et al., 2014; Datry et al., 2017a). Additional terms can be used to define specific types of temporary flow permanence regime (Williams, 1996; Datry et al., 2016b; Stubbington et al., 2018a). In particular, precipitation-driven flow events characterise ephemeral streams (Uys & O'Keeffe, 1997; Michaelides et al., 2018). In contrast, intermittent streams flow more predictably, often seasonally (Busch et al., 2020), with wet phases that typically last >6 months and shorter dry phases that occur in summer and autumn (Rosgen, 1985; Svec et al., 2005). The temporary chalk streams that are the focus of this thesis are intermittent streams, locally named 'winterbournes' because increased winter groundwater levels initiate their flowing phases (Berrie, 1992; Sear et al., 1999; Armitage & Bass, 2013).

2.1.2 Distribution of temporary streams

Temporary streams are present on every continent (Datry et al., 2017a), and comprise >50% of the global river network (Datry et al., 2014b; Messager et al., 2021). Temporary streams are particularly prevalent in arid and semi-arid areas (Tooth, 2000; Messager et al., 2021), representing the most common form of flow in Australia, the southern Mediterranean Basin and the south-western United States (Levick et al., 2008; Datry et al., 2014b). In wet-temperate climates (e.g. north-western Europe), temporary streams (or more correctly, temporary reaches) are also widespread (Datry et al., 2014b, 2017a), commonly occurring as low-order, headwater streams (Fritz et al., 2013).

Within catchments, temporary streams can occur upstream of, downstream of or between perennial reaches (e.g. Shivoga, 2001; Storey & Quinn, 2008; White et al., 2018), with this variable spatial arrangement of flow influencing transfers of water, sediment (Gamvroudis et al., 2015), energy (Paredes et al., 2020) and organisms (Shivoga, 2001; Storey & Quinn, 2008) into/out of temporary reaches, thus influencing their ecology. In addition, catchments include other natural and artificial waterbodies such as springs, ponds and ditches (e.g. Williams et al., 2004) which, depending on their connectivity (Shurin et al., 2009), may also influence the ecology of temporary streams (e.g. Pineda-Morante et al., 2022).

2.1.3 Physical characteristics of temporary streams

2.1.3.1 Influences on flow permanence in temporary streams

Localised transitions between flowing, ponded and dry phases are influenced by catchment geology and bed sediments, which influence the direction, volume and speed of water exchange between the aquifer, hyporheic zone and the surface stream (Hendricks & White, 2000; Mojarrad et al., 2019; Pipan & Culver, 2019). Such hydrological exchange is a key determinant of the spatial distribution of surface and subsurface aquatic habitats and the chemical properties of water (Stanford & Ward, 1993; Franken et al., 2001; Malard et al., 2002, 2003), in turn influencing habitat availability and suitability for stream organisms (Boulton, 1993; Boulton et al., 2010; Stubbington et al., 2017a). For example, upwelling may occur where groundwater is under high pressure (Winter, 2007; Francis et al., 2010), transporting inorganic nutrients to the surface (Wondzell, 2011). Conversely, downwelling is likely to occur where the water table or aquifer is lower than the channel bed (Charlton, 2008), changing the distribution of surface water, with the potential to cause alternating temporary and perennial reaches (Datry et al., 2014b; Costigan et al., 2017), and supplying hyporheic habitats with dissolved oxygen and organic matter (Boulton et al., 1998; Franken et al., 2001).

At the catchment scale, the frequency, magnitude, timing, duration and rate of change of flow events (see Richter et al., 1996; Poff et al., 1997; Zeiringer et al., 2018) are key in determining the resource availability and habitat conditions for aquatic (Bond & Cottingham, 2008; Sponseller et al., 2013; Stubbington et al., 2017b) and terrestrial (Levick et al., 2008; Sánchez-Montoya et al., 2016; Bunting et al., 2021) organisms, and thus in determining the composition of temporary stream communities (Larned et al., 2010; Datry et al., 2014a). Over different timescales, both weather and climate control the net amount of water available via inputs of precipitation and temperature-controlled outputs (i.e. evapotranspiration). Although short-term fluctuations in atmospheric conditions (i.e. weather) can initiate flow in some temporary streams (e.g. rainfall in an ephemeral stream: Sefton et al., 2017), climate is the primary driver of flow permanence in seasonally intermittent streams (Hannaford & Buys, 2012; Stubbington et al., 2018b; Sefton et al., 2019).

A catchment's physical characteristics are a key secondary influence on flow permanence (Day, 1983; Larned et al., 2011; Mirus & Loague, 2013) that increase the relative importance of long-term precipitation/evapotransipration trends (i.e. climate). For example, where a catchment's geology comprises shallow permeable strata (e.g. the chalk of southern England), aquifers may store and transport individual molecules of water as groundwater for months to years (Shand et al., 2003; Smedley et al., 2003). Thus, prolonged periods of precipitation, in particular during winter, recharge the aquifer and sustain flows over longer periods (Hisdal et al., 2001; Arnott et al., 2009; Larned et al., 2011), minimising the influence of isolated weather events on flow permanence (Sear et al., 1999). However, antecedent conditions, such as the amount of recharge in the preceding winter, ultimately determine whether the aquifer acts as a source or sink of water (Holman, 2006; Hugman et al., 2012; Salter & Singleton-White, 2019). Surface features (e.g. exposed sediments, vegetation, human-made structures) also influence flow permanence in temporary streams via interactions with water moving toward the channel (Emmett, 1970; Govers et al., 2000; Lintern et al., 2018). For example, stream hydrology can be influenced by the presence of coarse surface sediments (grains typically >1 mm: Nassif & Wilson, 1975; Mazaheri & Mahmoodabadi, 2012) and vegetation (Gabarrón-Galeote et al., 2013; Zhang et al., 2018) which typically slow the rate of overland flow toward the channel.

Humans have profoundly changed lotic ecosystems (Kopf et al., 2015; Dubois et al., 2018; Haidvogl, 2018), and typically impact the hydrology of riverine ecosystems by altering natural processes at local and catchment scales. For example, changes in land uses such as forestry, agriculture and urbanisation modify the dynamics of flow towards and thus within the channel (McGrane, 2016; Lintern et al., 2018). While many natural surface sediments allow infiltration, urbanisation decreases surface permeability and increases runoff speed and volumes (O’Driscoll et al., 2010; Martin et al., 2012; Rosburg et al., 2017). Abstraction (e.g. for agriculture: Biemans et al., 2011; Merchán et al., 2013) reduces flows and may cause some perennial streams to become temporary and existing temporary streams to experience longer dry phases (Fu et al., 2004; Bernard & Moetapele, 2005; Larned et al., 2010). Although the impacts of anthropogenic climate change on flow regimes remain somewhat uncertain (Arnell et al., 2015; Reid et al., 2019), increasing aridity may be increasing the prevalence of, and the dry-phase durations experienced by, temporary streams in some regions (Sauquet et al., 2021; Tramblay et al., 2021; Zipper et al., 2021). Conversely, impoundments, flow augmentation and wastewater releases that support urban areas may cause temporary streams to become perennial (Hassan & Egozi, 2001; Barnett et al., 2008; Skoulikidis et al., 2017).

2.1.3.2 Sediment and channel shape in temporary streams

In all lotic ecosystems, vegetation and sediment cause friction and turbulence within the water, influencing the hydrology of the channel (Clifford et al., 1992; Rodrigues et al., 2006; Charlton, 2008). In temporary streams, sediment deposition is likely to occur during transitions from flowing to ponded states or when flow is slowed upon entering the hyporheic zone (Bond & Cottingham, 2008; Datry et al., 2017b). When flow resumes, sediment may be remobilised, resulting in pulsed transport through the catchment (Levick et al., 2008). This relationship between sediment and flow determines the availability and suitability of instream habitats for aquatic flora and fauna (Palmer et al., 2000; Bunn & Arthington, 2002; Hauer et al., 2018). Channel shape is also a key determinant of surface water distribution, with wide channels, such as those impacted by cattle poaching (River Restoration Centre, 2020), having a larger bed surface area (relative to narrower channels) resulting in reduced flow velocity because of increased friction, increased transmission losses and an increased water surface area for evaporation. In uniform trapezoidal channels, a reduction in flow is likely to dewater the entire cross section at a similar rate, whereas the uneven distribution of sediment in natural channel cross sections is likely to create depressions where water may persist for longer periods or be sustained by hyporheic upwelling (Sear et al., 1999).

2.1.3.3 The riparian zone as a determinant of physical channel characteristics

The riparian zone is a transition zone between terrestrial and aquatic environments characterised by a distinct vegetational assemblage (Donahue et al., 2002; Décamps et al., 2009). The proximity of the riparian zone to the channel means it has physical effects on instream processes and flow permanence (Naiman et al., 2005b; Brooks et al., 2012). Riparian vegetation adds structural heterogeneity to the wider ecosystem, slows overland flow promoting water infiltration and sediment deposition and stabilises marginal sediment deposits (Donahue et al., 2002; Naiman et al., 2005a). Riparian vegetation often has a higher water requirement than other terrestrial vegetation, with high uptake of groundwater influencing the permanence of water within the channel (Burt et al., 2002; Lupon et al., 2018). However, as a reach dries riparian vegetation also shades the channel, limiting evapotranspiration and temperature at the bed, promoting moisture retention in sediment and persistence of surface water pools (Datry et al., 2017b; Scrine et al., 2017). Additionally, leaves shed seasonally or by desiccation-stressed vegetation may accumulate as litter in the dry channel, adding nutrients to and retaining moisture within the system (Pettit et al., 2006; Brintrup et al., 2019).

2.2 The invertebrate fauna of temporary stream ecosystems

Invertebrates are among the most abundant and diverse group of animals on earth, and underpin global biodiversity and ecosystem functioning via pollination activities, by transferring energy up the food chain and across ecosystem boundaries (e.g. between aquatic and terrestrial domains: Eisenhauer & Hines, 2021). Invertebrates have a wide range of environmental preferences and tolerances of anthropogenic activities (Armitage et al., 1983; Extence et al., 1999; Rainio & Niemelä, 2003; Webb et al., 2018). As such, invertebrates are often used to monitor environmental conditions and represent the health of an ecosystem (e.g. Extence et al., 2013; Paisley et al., 2014). Invertebrates also inhabit both aquatic and terrestrial environments, making the group ideal for studying dynamic habitats that transition between such states, such as temporary streams. Therefore, invertebrates are used to test hypotheses relating to biodiversity in temporary streams and the responses of such biodiversity to environmental pressures in Chapters 3–7 of this thesis. Here, I review the responses of aquatic and terrestrial invertebrate groups that are common in temporary streams to a range of environmental conditions to contextualise the research presented in later chapters. Where possible, I have prioritised evidence from studies of invertebrates in chalk winterbournes and comparable groundwater-fed, seasonally intermittent streams in wet-temperate countries. Where information from such systems is limited, I have drawn upon the global temporary stream literature and upon studies from other habitats that also experience fluctuations between wet and dry phases (e.g. exposed riverine sediments, riparian zones).

2.2.1 Aquatic macroinvertebrates

2.2.1.1 Aquatic habitat provision in temporary streams

The spatiotemporal occurrence of aquatic macroinvertebrates often reflects species-specific environmental preferences and dispersal abilities, and biotic interactions (Heino, 2013). Flow regimes strongly influence aquatic habitat availability and suitability for macroinvertebrates, especially in temporary streams where flowing and ponded phases support different aquatic assemblages (Hynes, 1958; Hill & Milner, 2018; Buffagni, 2020). Additionally, macroinvertebrate distributions are affected by physicochemical parameters, such as dissolved oxygen and nutrient concentrations (Vannote et al., 1980; Giller & Malmqvist, 1998; Yuan, 2010; Ocon et al., 2013), water temperature (Jacobsen et al., 1997; Burgmer et al., 2007; Scrine et al., 2017) and sediment composition (Wood & Armitage, 1997; Ciutti et al., 2004; Extence et al., 2013), but the influence of these variables is often moderated by the flow regime (Gómez et al., 2017; Jaeger et al., 2017; von Schiller et al., 2017). Such hydrological and physicochemical conditions vary over time, meaning species may be lost as conditions exceed their tolerances. The ability of those species to subsequently recolonise a habitat then depends upon their dispersal ability, the ability of the species to survive in nearby habitats that experience less-harsh conditions (i.e. refuges) and the connectivity of source and sink habitats (Shurin et al., 2009).

2.2.1.2 Environmental determinants of aquatic temporary stream assemblages

The duration of flowing phases and surface water availability are key determinants of temporary stream aquatic assemblage composition (Bonada et al., 2007; Leigh & Datry, 2017; Aspin et al., 2019). Longer flowing phases provide more time for aquatic macroinvertebrates to colonise from dry-phase refuges (Datry et al., 2017b) and thus, aquatic richness increases from flow onset and typically peaks around the end of the flowing phase (Boulton & Lake, 1992; Larned et al., 2010; Godoy et al., 2016), but see Verdonschot et al. (2015). Despite this increasing richness, the more limited time in which colonisation can occur (relative to perennial streams) means temporary streams rarely support taxonomic richness as high as comparable perennial streams when a single site/flow state is considered (Meyer et al., 2003; Datry et al., 2014a). In streams where flow velocity and surface water extent decrease gradually, richness may persist but diversity often declines after flow cessation because competitive generalists begin to dominate the assemblage (Stubbington et al., 2011). In addition to duration, the characteristics of flow play a role in structuring macroinvertebrate assemblages. For example, flow velocity regulates water temperature and dissolved oxygen concentrations (O’Connor, 1967; Boulton & Lake, 1992; Sprague, 2005), the amount of food transported from upstream reaches (Vannote et al., 1980; Gomi et al., 2002) and connectivity among reaches for migration and breeding (Williams & Hynes, 1977; Shama et al., 2011).

Temperature: Influences on aquatic macroinvertebrates

In perennial streams, water temperatures typically increase with distance downstream (Caissie, 2006), with surface water and groundwater temperature being similar at the source (Benson, 1953). Headwater temperatures are often more variable than in large lowland rivers (Caissie, 2006), because less energy is required to heat smaller water bodies. During flowing phases, temporary stream water temperatures respond similarly to perennial streams with similar physical characteristics, such as width, depth and shading, because they experience similar environmental controls (e.g. spatial, seasonal and diurnal variations in heating duration and intensity). After flow cessation, water temperatures typically rise (Gómez et al., 2017), but are more heavily influenced by diurnal and seasonal factors than during flowing phases. Temperature shifts caused by transitions from flowing to dry phases can influence macroinvertebrate assemblage composition, with most mayflies and stoneflies (order: Ephemeroptera and Plecoptera, respectively) only tolerating cooler temperatures typical of flowing reaches (<28˚C) relative to taxa such as beetles (<45˚C: Quinn et al., 1994; US Environmental Protection Agency, 2006; Stewart et al., 2013), which can often withstand higher temperatures in isolated pools. Water temperature also has indirect effects on aquatic invertebrates through interactions with other physicochemical variables (e.g. dissolved oxygen).

Dissolved oxygen: Influences on aquatic macroinvertebrates

Dissolved oxygen concentrations are influenced by flow characteristics (e.g. velocity and turbulence) and water temperature (Rounds et al., 2013). Fast-flowing water, particularly in steep headwater reaches with coarse substrates, is often turbulent which increases dissolved oxygen concentrations by physical aeration (Nakamura & Stefan, 1994; Hondzo, 1998). Additionally, water temperature is a key control on dissolved oxygen concentrations, because oxygen dissolves more readily at lower temperatures (Rounds et al., 2013). Thus, sensitive mayflies, stoneflies and caddisflies (order: Trichoptera), many species of which require low water temperatures and typically have large gills to maximise oxygen uptake (Campbell, 1990), are common in small, groundwater-fed, seasonally intermittent streams (e.g. Storey & Quinn, 2008; White et al., 2018). As flow ceases, less turbulence and higher water temperatures reduce dissolved oxygen concentrations (Gómez et al., 2017; Hayes et al., 2017), eventually excluding mayflies, stoneflies and caddisflies (Hille et al., 2014; Verdonschot et al., 2015). Such conditions favour species with higher thermal tolerances such as the fly larvae *Chironomus*, who store oxygen in haemoglobin (Armitage et al., 1995), or beetles who breathe atmospheric oxygen (Madsen, 2012).

Nutrients and sediment: Influences on aquatic macroinvertebrates

Transitions between dry, ponded and flowing phases influence nutrient and sediment dynamics in temporary streams, which in turn affect their macroinvertebrate assemblages. Dry phases slow transport through the catchment, leading to a build-up of material on surrounding slopes and in the channel (Obermann et al., 2007; Ramos et al., 2015), with the relative length and timing of flowing and non-flowing phases determining the nature and volume of the build-up (Datry et al., 2017b). In ephemeral streams with rapid flow resumption and high responsiveness to heavy rainfall events, accumulated sediment and nutrients are mostly transported downstream by the high-magnitude (relative to baseflow) initial flows (Ramos et al., 2015), with concentrations declining exponentially between the initial peak and the end of the flowing phase (Lillebø et al., 2007; von Schiller et al., 2011). In groundwater-fed temporary streams, such as winterbournes, flow resumption is typically more gradual, which may reduce the proportion of sediment and nutrient transport by first flows. In such streams, seasonal patterns in biological activity (e.g. macrophyte growth in spring and summer), cause variability in sediment transport and nutrient availability within years (Bowes et al., 2005), while the chemical environment is typically stable over multi-year timescales, promoting invertebrate biodiversity (Berrie, 1992). Thus, the variable lengths of ponded/dry phases within and between years and the differing character of flow resumption (i.e. fast or slow) among streams means nutrient and sediment accumulation and transport is typically more variable in temporary than perennial streams (Skoulikidis & Amaxidis, 2009; Bernal et al., 2013; Shumilova et al., 2019).

Upon flow resumption, the rate of biochemical processing in organic matter accumulations (e.g. leaf litter) increases, releasing carbon, nitrogen and phosphorus-based nutrients (von Schiller et al., 2011; Datry et al., 2018), with organic matter typically releasing greater amounts of nutrients (particularly nitrates and phosphates) than sediments (Shumilova et al., 2019). Nutrients have indirect influences on macroinvertebrate assemblage structure, because they are key determinants of vegetation abundance, distribution and composition (Barko & Smart, 1986; Sand-Jensen et al., 2000; O'Hare et al., 2018). Excess nutrients from natural or anthropogenic sources can fuel the growth of algae, which respire rapidly to produce hypoxic conditions, reducing dissolved oxygen concentrations below the tolerance thresholds of many macroinvertebrates (Giller & Malmqvist, 1998; Cook et al., 2018). Oxygen reductions are particularly pronounced in temporary stream pools, where nutrient concentrations often increase after flow cessation (Ramos et al., 2015; Gómez et al., 2017).

Substrate characteristics including the sediment grain size distribution, amount of interstitial space and capacity to promote vegetation growth all influence habitat suitability for macroinvertebrates. For example, an abundance of fine sediment can reduce survival of mayfly, stonefly and caddisfly species with a high oxygen demand (because their large gill surfaces become coated: Kaller et al., 2001; Corbin & Goonan, 2010; Extence et al., 2013), and filter-feeding species (e.g. mussels: Aldridge et al., 1987). Additionally, fine sediment can impede vertical movements by blocking interstitial pathways (Vadher et al., 2015, 2022; Korbel et al., 2019), thus controlling the size of organisms that can move into hyporheic habitats as surface water is lost.

2.2.2 Terrestrial invertebrates

2.2.2.1 Terrestrial habitat provision in temporary streams

The spatiotemporal extent of surface water is the key determinant of terrestrial habitat availability in temporary streams (Levick et al., 2008; Sánchez-Montoya et al., 2016). Dynamic mosaics of flowing, ponded, terrestrial and transitional in-channel habitats also create a varied spatiotemporal distribution of resources (Larned et al., 2010), with drying and newly dry in-channel habitats containing stranded aquatic prey, a low density of terrestrial organisms (Boulton & Lake, 1992; Ballinger & Lake, 2006) and nutrient-rich substrates (Larned et al., 2010; McDonough et al., 2011). This resource variability, connectivity between favourable habitat patches and the proximity of source populations are key controls on terrestrial colonisation during and after drying (see **Colonisation of temporary stream habitats**: Stetler et al., 1997; Datry et al., 2017b) and, therefore, the overall biodiversity of temporary streams (Bogan & Lytle, 2007; Stubbington et al., 2017b).

2.2.2.2 Environmental determinants of terrestrial temporary stream assemblages

Although factors including food and competitor-free space may attract organisms to a drying channel, the suitability of newly available in-channel habitats for terrestrial fauna is determined by habitat conditions, with sediment characteristics, vegetation, light intensity, temperature, moisture and connectivity with the riparian zone all influencing assemblage composition

(Rainio & Niemelä, 2003; Cole et al., 2008; Lambeets et al., 2009). These environmental variables filter organisms entering the channel from the riparian zone and wider catchment, resulting in distinct in-channel assemblages (Steward et al., 2011). These in-channel assemblages can be diverse, and often include numerous ant, beetle and spider species (Steward et al., 2011; Bunting et al., 2021; Hayes, 2022).

Beetles (order: Coleoptera) are a diverse order that includes species with specific habitat preferences (Adis & Junk, 2002; Lambeets et al., 2008; Ghannem et al., 2018), thus allowing them to be used as biomonitors of habitats including river channels. Beetles are also among the most common in-channel fauna encountered in regions with wet-temperate climates (e.g. Corti & Datry, 2016; Bunting et al., 2021; Hayes, 2022). Therefore, the research presented in Chapters 5–7 of this thesis focus on beetles as indicators of dry-phase habitat conditions. A few studies have characterised the terrestrial beetle fauna of temporary streams (e.g. Robinson, 2019; Bunting et al., 2021; Hayes, 2022), and exposed riverine sediment (ERS - in-channel gravel, sand and silt shoals: Sadler et al., 2004; Bates et al., 2007) assemblages are somewhat comparable to terrestrial temporary stream assemblages (Stubbington et al., 2017b), in that they are disturbed by inundation (Bates et al., 2006). Thus, I also use ERS research to inform discussion of temporary stream beetle assemblages.

Hydrology and moisture: Influences on terrestrial invertebrates

Water is a key variable affecting species' distributions, particularly in habitats experiencing water level fluctuations, such as temporary streams. Many beetle taxa can survive inundation (Hoback et al., 1998; Adis & Junk, 2002), for durations that vary among species, life stages and seasons (Kolesnikov et al., 2012). Beetle taxonomic richness can be similar in perennial, intermittent and ephemeral channels, but high taxonomic turnover between reaches suggests beetles respond (either directly or indirectly) to gradients of flow permanence (Moody & Sabo, 2017). This turnover is likely driven by the value of moisture/water as a resource and tolerance to disturbance by inundation.

In habitats ranging from temperate ERS to arid coastal wetlands, distance from surface water bodies and sediment moisture influence beetle assemblage composition (Blake et al., 2003; Bates et al., 2007; Pardo et al., 2008; Tsafack et al., 2019), because water and moisture drive the distribution of other key resources (e.g. vegetation and prey: Wallin & Ekbom, 1994; Blake et al., 2003). Thus, beetles with differing life cycles, body morphologies, and hunting and breeding strategies become sorted along moisture gradients (e.g. perennial to ephemeral flow: Frouz et al., 2004; Williams et al., 2014a; Moody & Sabo, 2017) as they identify the optimal habitat structure (e.g. vegetation assemblage and associated microclimate) and prey assemblage and density for their species-specific preferences (Eyre et al., 2001a, 2001b; Liere et al., 2019; Magura & Lövei, 2019). For example, moisture influences survival and motility of sediment-dwelling beetle larvae (Krogerus, 1948), and thus taxonomic richness typically increases with moisture availability (Williams et al., 2014b). Additionally, many riparian beetles rely on aquatic environments for food (Paetzold et al., 2005), with species that occur closer to the water's edge typically having specialist aquatic hunting strategies (Bates et al., 2007; Lambeets et al., 2008) that allow emerging aquatic invertebrates to dominate their diet (Hering & Plachter, 1997; Paetzold et al., 2005; Ramey & Richardson, 2017).

Inundation of dry in-channel habitats represents a significant risk to terrestrial beetles, who may be drowned or injured by flow and entrained debris (Corti & Datry, 2012). As such, water's edge assemblages are strongly associated with inundation-tolerant predators (e.g. the ground beetles *Bembidion decorum* and *B. punctulatum*: Paetzold et al., 2005; Bates et al., 2007; Lambeets et al., 2008; O'Callaghan et al., 2013a), and may include species (e.g. the tiger beetle *Oxycheila polita*) that actively drift in flowing water (Cummins, 1992). This tolerance suggests that, at least for some species, the risks posed by inundation are outweighed by the benefits of in-channel resources (e.g. aquatic prey: Ramey & Richardson, 2017), and predator avoidance. Thus, inundation tolerance may be a key trait that allows new or recently disturbed habitats to be colonised (see **Colonisation of temporary stream habitats**: Bonn et al., 2002; Corti & Datry, 2012).

Sediment and vegetation characteristics: Influences on terrestrial invertebrates

Sediment grain size distribution and stability influence terrestrial beetle assemblage composition (Thiele, 1977a; Eyre et al., 2001b; Dennis et al., 2002; Fenster et al., 2006). For example, sediments composed of larger grains have larger interstices, which promote the survival of sediment-dwelling species (Paetzold et al., 2008; Langhans & Tockner, 2014). Taxonomically rich assemblages occur on both coarse and fine sediments (Sadler et al., 2004; Baiocchi et al., 2012). Thus, variable flow and drying patterns may result in sediment heterogeneity among habitat patches, and thus spatiotemporally diverse beetle assemblages. Sediment characteristics such as grain size can also influence moisture availability and temperatures at the sediment surface and thus, because many beetles have species-specific moisture and thermal tolerances (Sadler & Bell, 2002; Bates et al., 2006; Birkett et al., 2018), species distributions (Henshall et al., 2011).

Vegetation characteristics: Influences on terrestrial invertebrates

Vegetation may affect beetles that preferentially move by walking because dense vegetation such as grass reduces their mobility via increased resistance (Heydemann, 1957; Thomas et al., 2006; Allema et al., 2019). Dense vegetation may also impede beetle flight by restricting wing movement (Thiele, 1977b), reducing their ability to pursue prey or escape predation. Many beetle species are predatory (Luff, 2007) and thus, vegetation is rarely a feeding resource. However, vegetation may affect the in-channel distribution of predators, such as the snail-hunting ground beetle *Cychrus caraboides*, by influencing prey distributions (Wallin & Ekbom, 1994; Bartholomew et al., 2000). Thus, heterogeneous vegetation assemblages, which have variable structural complexity and plant densities, and support more prey species and microhabitats, often support greater beetle diversity (Ramey & Richardson, 2017; Hayes, 2022). Dry stream channels also support persisting, drying-tolerant aquatic vegetation, further increasing overall habitat heterogeneity and shading at the channel bed (Hayes, 2022), likely promoting in-channel beetle diversity.

Moisture, sediment and vegetation interactions: Influences on terrestrial invertebrates

Beetle assemblages are shaped by species' responses to both individual and interacting environmental variables. Because spatiotemporal patterns of drying (and associated influence on sediment deposition and vegetation assemblages) in temporary streams are variable (Datry et al., 2017b), flow permanence is a key driver of in-channel beetle distributions. During flowing phases, the margins of temporary streams which dry from upstream to downstream, such as groundwater-dominated chalk streams (Berrie, 1992; White et al., 2018), are likely to support similar beetle assemblage distributions to ERS adjacent to perennial streams, with inundation-tolerant species being present at the water's edge (Paetzold et al., 2005; Bates et al., 2006). When the stream dries, depending on the extent of remaining surface and subsurface water, the vegetation in a reach becomes increasingly similar to that in surrounding habitats, promoting similarity in terrestrial invertebrate assemblages between in-channel and surrounding habitats (Hayes, 2022).

Fine sediments often retain moisture and promote vegetational development more readily than coarse, well-drained sediments (Baniya et al., 2020), resulting in covariation of sediment size, moisture and vegetation cover, with associated effects on microhabitat heterogeneity, shading and temperature (Sadler & Bell, 2002; Bates et al., 2006). In riverine settings, sediment characteristics, moisture retention, vegetation heterogeneity and nutrient availability also vary longitudinally (Petts et al., 2000; Hadwen et al., 2010) and laterally (Paetzold et al., 2005; Bates et al., 2006). Such spatial variation in environmental conditions results in high species turnover between headwater and lowland reaches (Eyre et al., 2001a, 2001b), and between water's edge and more distant assemblages (Paetzold et al., 2005; Bates et al., 2006). Longitudinally, natural headwater habitats are typically characterised by coarse substrates, low sediment moisture and riparian shading which limits in-channel light and thus vegetation (Eyre et al., 2001a), and support more generalist species, with some specialist aquatic hunters (e.g. *Bembidion*: Eyre et al., 2001b). Lowland sites often have more fine sediment, increased substrate moisture and more extensive vegetative cover than headwater sites, which promotes a richer assemblage that includes fewer generalists and some ERS specialists (e.g. *Bembidion tetracolum*: Eyre et al., 2001b). Laterally, inundation-tolerant aquatic hunters (e.g. *Bembidion decorum* and *Bembidion punctulatum*) show a greater affinity to water's edge habitats, than areas further from the channel (Bates et al., 2006).

2.2.3 Colonisation of temporary stream habitats

2.2.3.1 Key concepts

For the aquatic and terrestrial assemblages that inhabit temporary streams, wetting and drying respectively represent opportunities to exploit an increased habitat area which potentially has fewer competitors and predators, and an abundance of novel resources (e.g. Steward et al., 2022). To exploit these time-limited opportunities in temporary streams, individuals use a combination of resistance (i.e. tolerate disturbance in-situ: Lake, 2013), and/or resilience strategies (i.e. some capacity to recover from disturbance: Lake, 2013) to colonise during and after drying/wetting (Fournier et al., 2023).

Resistance is key in shaping temporary stream assemblages (Vander Vorste et al., 2016), and is dependent upon species-specific traits and life histories

(Strachan et al., 2015; Datry et al., 2017d). For example, the stonefly *Nemoura lacustris* and the mayfly *Paraleptophlebia werneri* lay drying-tolerant eggs in winterbourne chalk streams (Tapia et al., 2018; Macadam et al., 2021). These drying-tolerant eggs allow the species to survive dry phases in-situ and exploit the opportunities presented by flow resumption (Tapia et al., 2018), without needing to recolonise from nearby habitats.

An assemblage's resilience is determined by rates of dispersal into the stream channel from surrounding habitats (e.g. perennial reaches, the riparian zone), with populations linked by such dispersal being termed 'metapopulations' (Gilpin & Hanski, 1991; Leibold et al., 2004). As discussed below, the formation/maintenance of a metapopulation spanning temporary streams and their surrounding habitats is typically controlled by the spatiotemporal distribution of populations (representing potential temporary stream colonists), the dispersal ability of organisms in those populations and the effects of environmental conditions on dispersal.

Spatiotemporal distribution of potential colonists

Temporary stream assemblages contain species that also occur in surrounding habitats (Steward et al., 2011; Bogan & Boersma, 2012), with such habitats being key sources of aquatic and terrestrial colonists during transitions between wet and dry phases. The spatial arrangement of such source habitats relative to a temporary stream is key in influencing assemblage composition, with differences in assemblage composition typically increasing with distance (Heino et al., 2015; Sarremejane et al., 2017a). However, the effects of distance can be mitigated, for example by upstream perennial reaches that allow aquatic fauna to passively drift into a newly wetted reach (Vander Vorste et al., 2016; Gill et al., 2022; Fournier et al., 2023). The timing of wet/dry phases can also be key in driving the composition of in-channel assemblages. For example, ground beetles (family: Carabidae) are most active in the UK between May and June (Luff, 2007). If a channel is dry between May and June, it is likely to support a diverse ground beetle assemblage (e.g. Bunting et al., 2021), whereas a channel that dries at other times of year may support fewer ground beetle species, not necessarily because the in-channel habitat is not suitable for ground beetles, but because surrounding habitats do not contain potential colonists at these time of year.

Dispersal ability of potential colonists

Assemblage recovery rates are also determined by the ability of an individual to disperse between the source and recipient habitat. For example, the adults of some aquatic invertebrates such as dragonflies and damselflies are strong aerial dispersers (Corbet, 1999; Nagy et al., 2019) that can colonise isolated waterbodies >1 km away (Purse et al., 2003; Jaeschke et al., 2013; Pineda-Morante et al., 2022). In contrast, some mayflies and stoneflies are relatively weak dispersers, with most adults flying <150 m (Jackson & Resh, 1989; Petersen et al., 1999). Such dispersal abilities are also dependent upon life stage, with many adult beetles being capable of flight, making them highly mobile, whereas larvae are restricted to crawling short distances (Lindroth, 1992; Luff, 2007).

Environmental controls on dispersal

Environmental conditions also influence colonisation of temporary reaches. For example, hedges can impede the movement of ground beetles (Mauremooto et al., 1995), meaning patches of vegetation may isolate some ground beetle populations from temporary streams. In aquatic environments such as winterbourne chalk streams, the rheophile *Gammarus pulex* is restricted to temporary sites which it can swim to from perennial refuges between dry phases (Punchard & House, 2009; Aspin & House, 2022). Colonisation by *G. pulex* has knock-on effects for temporary stream assemblages via interspecific interactions. *Gammarus pulex* is a highly competitive and predatory species (MacNeil et al., 1997; Kelly et al., 2002; Dick et al., 2013), and thus it can limit the abundance of of less competitive species including specialist drying-tolerant species (Aspin & House, 2022). In contrast, at sites where *G. pulex* is excluded by drying, drying-tolerant specialists can be more abundant (Aspin & House, 2022).

2.2.3.2 Colonisation by aquatic invertebrates

Aquatic macroinvertebrates can colonise temporary streams during their juvenile, aquatic life stages and during their adult life stages, which may be aquatic or terrestrial. As terrestrial adults, flying is a key mode of colonisation for many true flies (order: Diptera), mayflies (Ephemeroptera), stoneflies (Plecoptera) and caddisflies (Trichoptera), among others, but the propensity and ability for aerial dispersal varies among species (Sarremejane et al., 2020). Aquatic colonisation can occur by passive dispersal modes, such as drift where individuals are transported downstream by flowing water, or actively with individuals swimming or crawling up- or downstream to colonise new habitats (Giller & Malmqvist, 1998; Baumgartner & Robinson, 2017; Hildrew & Giller, 2023). Benthic habitats may also be colonised by individuals that have persisted in subsurface sediments during dry phases (Vander Vorste et al., 2016).

Assemblage development is strongly influenced by the spatial distribution of more permanent habitats relative to the temporary stream (Datry et al., 2016c; White et al., 2018). Newly available aquatic habitats are often colonised quickly (e.g. within 4 months: Hill et al., 2019). However, because some taxa, such as gastropods (Cañedo-Argüelles et al., 2015), have weak dispersal abilities, it can take >2 years for some temporary streams to develop assemblages comparable to those in perennial reaches and >10 years for some individual taxa to return (Westwood et al., 2017; Sarremejane et al., 2019).

2.2.3.3 Colonisation by terrestrial invertebrates

Due to abundant resources, dry temporary streams attract predators and scavengers, such as ground and rove beetles (Williams & Hynes, 1976; Maamri et al., 1997; Corti et al., 2013). These predators often migrate from the riparian zone – a nearby source of dry-channel colonists (Corti & Datry, 2016; Stubbington et al., 2017b). Ground beetles have been shown to colonise new in-channel habitats, such as those created by river restoration (Januschke & Verdonschot, 2016) and other habitats which are only available periodically, often seasonally, such as arable fields (French et al., 2001; Allema et al., 2019). Thus, beetles may often colonise temporary habitats, and this is also likely true of chalk winterbournes and other seasonally intermittent streams (Bunting et al., 2021; Hayes, 2022), due to their somewhat predictable annual cycles of terrestrial habitat availability.

Adult ground beetles preferentially disperse over short distances by walking (Thiele, 1977b; Erwin et al., 1979; Jopp & Reuter, 2005), and some species can also fly for longer distances (>5 km: Heydemann, 1967; Desender, 2000), allowing them to rapidly colonise new habitats (Lambeets et al., 2008). The in-channel occurrence of species not found in the riparian zone indicates that both ground and aerial dispersal modes may contribute to the colonisation of temporary streams (Steward et al., 2011), but the origin of colonists and drivers of colonisation from distant habitats are poorly characterised. Some ground and rove beetle species breed at the edge of shrinking water bodies (e.g. temporary riparian ponds) in spring or autumn (Lott, 2001), and overwinter in the riparian zone (Andersen, 1968, 2011). However, a few larger species breed by water then travel distances >1 km to hibernate away from the channel during winter (Krogerus, 1948; Luff, 1998). Thus, although some species travel greater distances, the occurrence of most species is likely controlled by the spatial distribution of suitable feeding, breeding and hibernating habitats.

In temporary streams with rapid flow onset, beetles can disperse downstream by ‘rafting’ on coarse organic matter (Corti & Datry, 2012; Rosado et al., 2015), allowing colonisation along riparian corridors (Bonn et al., 2002). Although more vulnerable to damage by entrained debris, beetles can survive inundation (i.e. without rafting), identify riverbanks while submerged and swim toward them (Jenkins, 1960; Lehmann, 1965). In temporary streams with perennial headwaters, downstream transport of organisms may also contribute to the colonisation of dry habitats by terrestrial species. However, colonisation of dry channels and the potential barriers to channel colonisation by terrestrial invertebrates are rarely studied.

2.3 The impact of humans on temporary stream communities and how to biomonitor them

2.3.1 Human impacts on temporary stream communities

Due to their global prevalence, temporary streams, like all freshwater ecosystems, are impacted by physical channel modification, water resource use, land use practices and climate change (Dudgeon et al., 2006; Reid et al., 2019). At varying spatial scales, these four factors already influence flow characteristics (i.e. the frequency, magnitude, timing, duration and rate of change in flow) in river systems that include temporary streams, such as England's chalk stream networks (Stubbington et al., 2022a; Robinson et al., 2023). In turn, changes to the flow regime may be detrimental to temporary stream biodiversity (Paetzold et al., 2008; Leigh & Datry, 2017) and ecosystem functioning (Arroita et al., 2017), because assemblages are often adapted to site-specific flow characteristics (Stubbington et al., 2016, 2017b). With limited legal protection (Acuña et al., 2014), the impacts of channel modification, water resource use, land use practices and climate change on the flow regime and communities supported by temporary streams are predicted to intensify (Reid et al., 2019).

2.3.1.1 Channel modification

Physical modification of the channel is a common impact facing river ecosystems (Dudgeon et al., 2006), with many temporary streams being channelised and straightened to make way for transport infrastructure such as roads and dredged to reduce flood risk (Lake et al., 2017). Physical modification can influence flow permanence by blocking exchanges of water between the channel, the riparian zone and the hyporheic zone (Hancock, 2002; Sprößig et al., 2020). Modification also homogenises microhabitats (e.g. by altering in-channel flow and sediment dynamics: Paetzold et al., 2008), resulting in lower in-channel biodiversity (Horsák et al., 2009; Buffagni et al., 2016). Riparian habitats within both relatively natural and anthropogenic (i.e. agricultural) land uses can support high taxonomic and functional diversity (Vanbergen et al., 2005; Sprößig et al., 2020), but connectivity between in-channel and riparian habitats is also key for maintaining biodiversity. For example, where physical modification such as bank reinforcement decouples the river from surrounding riparian habitats, the riparian zone becomes drier (Sprößig et al., 2020) and supports lower terrestrial beetle richness relative to more natural riparian habitats (Paetzold et al., 2008), influencing the pool of potential channel colonists.

2.3.1.2 Exploitation of water resources

Human exploitation of water resources, such as surface and ground water abstraction, can cause perennial rivers to become temporary (e.g. Fu et al., 2004; Mukherjee et al., 2018) and temporary streams to experience longer dry phases (Wessex Water Ltd, 2008; Van Loon et al., 2016), although climate change also plays a role in shifting flow permanence (see **Section 2.3.1.4 Climate change**: Datry et al., 2022). Conversely, temporary streams may be perennialised by wastewater discharge (Garcia & Pargament, 2015), and simultaneously experience reductions in water quality (Karaouzas et al., 2018; Menció & Boix, 2018). Changing flow characteristics influence the composition of temporary stream communities (Bunn & Arthington, 2002; Bestgen et al., 2019), in particular where assemblages are adapted to site-specific conditions (Stubbington et al., 2016, 2017b). For example, drying-tolerant specialist insects typically develop from eggs to adults within 3 months (Tapia et al., 2018). Abstractions that shorten flowing phases may prevent this development, whereas discharges that lengthen flowing phases may allow more competitive generalist species to colonise and outcompete the specialists (Punchard & House, 2009; Aspin & House, 2022).

2.3.1.3 Land use

Anthropogenic land uses lead to physical modification (see **Section 2.3.1.1 Channel modification**) and also influence the flow characteristics, chemical condition and biological communities of temporary streams (Chiu et al., 2017). Among land use types, agriculture has wide ranging impacts because chemical and nutrient pollution, fine sediment and effluent discharge interact with temporary flow permanence regimes to alter water and physical habitat quality (Food and Agriculture Organization of the United Nations, 2017; Whelan et al., 2022). For example, flow cessation results in the deposition of nutrients, fine sediment and other pollutants (Bond & Cottingham, 2008; Gómez et al., 2017), which can be rapidly remobilised and transported downstream after flow resumption (Levick et al., 2008). Agricultural land uses encroach into riparian habitats, where vegetation is often cleared and in turn influences interception of pollutants from the wider catchment (Spooner et al., 2002; Feld et al., 2018), the quality and quantity of organic nutrients that enter the stream (Nakano & Murakami, 2001) and the amount of shading provided to in-channel habitats (Bowler et al., 2012).

Many aquatic invertebrates are sensitive to agricultural pollutants, subsequent changes in chemical water quality variables (e.g. pH, conductivity, dissolved oxygen concentrations: Jones et al., 2023) and differing levels of fine sediment (Wood & Armitage, 1997; Hawkes, 1998; Paisley et al., 2014), with richness and diversity being negatively correlated with the extent and intensity of agricultural land use in a catchment (Genito et al., 2002; Hepp et al., 2010). In temporary streams, aquatic organisms may be exposed to pulses of nutrients, fine sediment and other pollutants which are mobilised after flow resumption (Levick et al., 2008), although such pulses are often short-lived, with concentrations decreasing exponentially between first flows and the end of the flowing phase (Lillebø et al., 2007; von Schiller et al., 2011). Aquatic assemblages in temporary streams experience increasing nutrient concentrations and fine sediment deposition, and decreasing dissolved oxygen concentrations after flow cessation (Stubbington et al., 2011; Gómez et al., 2017; von Schiller et al., 2017), and thus may have some tolerance of agriculture where the effects of such land use manifests via comparable stressors (*sensu* Vinebrooke et al., 2004).

In riparian zones, where habitats with naturally high beetle taxonomic and functional richness are fragmented by areas of anthropogenic land use, taxonomic and functional richness decline (Shepherd, 2013). For example, habitat fragmentation caused by arable and pastoral land uses can reduce riparian beetle abundance, taxonomic and functional richness relative to reaches with more contiguous forest habitats (Gómez-Cifuentes et al., 2017; Cajaiba et al., 2018), again influencing the pool of potential dry-phase colonists. At smaller spatial scales, dense riparian vegetation may buffer in-channel communities against agricultural impacts (e.g. by intercepting pollutants: Spooner et al., 2002; Feld et al., 2018). Despite such potential impacts, agricultural environments can still support diverse terrestrial beetle assemblages, with some taxa that are common in agricultural environments (e.g. *Poecilus*, *Pterostichus*: Clark et al., 1997) also occurring in dry stream channels (e.g. Bunting et al., 2021).

2.3.1.4 Climate change

Under climate change, stream drying is increasing in space and time in many global regions (Döll & Schmied, 2012; Ficklin et al., 2018; Zipper et al., 2021). Although total precipitation volumes may not change, inputs are predicted to become more intense but occur less often (O'Gorman, 2015; Watts et al., 2015; Masson-Delmotte et al., 2021; Kendon et al., 2023). Less frequent precipitation may increase dry phase length and reduce the quality and quantity of dry-phase refuges (Snelder et al., 2013; Tramblay et al., 2021; Stubbington et al., 2022a), such as pools. The high intensity of precipitation events that do occur may interrupt dry phases and alter physical habitat structure via high flows (Verdonschot et al., 2010). Additionally, predicted increases in the frequency, magnitude or duration of extreme events, such as droughts and heatwaves (Sutanto et al., 2020), may increase both water temperatures in the channel and air temperatures in dry channels and the riparian zone. These changing in-channel and riparian zone characteristics will likely influence vegetative communities, moisture retention, the thermal regime and sediment size and stability (Ramos et al., 2015; Sánchez-Montoya et al., 2016; Gómez et al., 2017; Baniya et al., 2020).

The timing of flowing and dry phases is key for many temporary stream invertebrates that time their life cycles to coincide with semi-predictable flowing phases (see drying-tolerant specialist insects in **Section 2.3.1.2 Exploitation of water resources**: Tapia et al., 2018; Macadam et al., 2021). For desiccation-sensitive organisms, a decline in refuge quality and quantity may limit in-situ persistence and thus community recovery (Hill & Milner, 2018; Gill et al., 2022; Viza et al., 2023). Local recovery may be limited if high flows after flow resumption wash organisms out of refuges to downstream habitats (Fournier et al., 2023). For terrestrial species, rapid flow resumption may limit opportunities to escape inundation (e.g. Corti & Datry, 2012) resulting in passive dispersal (e.g. rafting: Corti & Datry, 2012) or injury/death and incorporation into aquatic food webs (e.g. Ramey & Richardson, 2017). Finally, changing vegetative, moisture, thermal and sediment characteristics will also influence the composition of aquatic and terrestrial invertebrate assemblages (see **The invertebrate fauna of temporary stream ecosystems**: Stewart et al., 2013; Langhans & Tockner, 2014; Ramey & Richardson, 2017; Cook et al., 2018).

2.3.1.5 Legal status

Despite increasing recognition of their prevalence and potential to support biodiversity (Datry et al., 2014b, 2016b, 2017c; Leigh et al., 2016), temporary streams receive limited legal protection worldwide (Acuña et al., 2014). For example, under the European Union's Water Framework Directive 2000/60/EC (WFD), which requires waterbodies to achieve good ecological status, temporary streams are recognised in one category (R-M5) which is only found in the Mediterranean region (European Commission, 2000). Thus, in non-Mediterranean regions that apply the WFD, temporary streams do not receive the monitoring or protection afforded by the WFD. In the US, the definition of "Waters of the United States" (WOTUS) is debated (US Environmental Protection Agency, 2023), thus the protection of temporary streams depends upon an irregular patchwork of state and local regulations. Similarly, in the UK, temporary streams are not widely protected, although site-specific designations reflect biodiversity and geological features (e.g. Natural England, 2023). Here, winterbournes are increasingly recognised as an integral part of the chalk stream networks of southern and eastern England (House of Lords Library, 2021; Rangeley-Wilson, 2021; Stubbington et al., 2022b), Thus, to promote their protection, further evidence of the biodiversity supported by temporary streams and methods that can be used to assess their ecological status are required.

2.3.2 Biomonitoring temporary stream communities

Biomonitoring uses the occurrence of taxa to indicate the state of the environment (Hildrew & Giller, 2023), including both natural and anthropogenic disturbances. Aquatic and terrestrial invertebrates are widespread, easily sampled and identified to a sufficient taxonomic level, and their assemblages comprise a variety of species with differing tolerances (Paisley et al., 2014), enabling them to indicate differences in environmental conditions within and between habitats in space and time. As such, aquatic macroinvertebrate assemblages are routinely used to detect the effects of general anthropogenic degradation (Paisley et al., 2014) and changing habitat availability associated with drought (Chadd et al., 2017), as well as individual stressors including flow velocity (Extence et al., 1999), fine sediment (Extence et al., 2013; Turley et al., 2015), salinisation (Pickwell et al., 2022), organic pollution (Armitage et al., 1983; Hawkes, 1998) and pesticides (Liess & Ohe, 2005; Beketov et al., 2009). Although few indices characterise terrestrial invertebrate assemblage responses to specific environmental drivers (but see Fowles et al., 1999; Webb et al., 2018), they can be used to monitor change in environmental conditions as a result of habitat restoration (Borges et al., 2021) and are responsive to factors including inundation (Joy, 1910; Andersen, 1968; Kolesnikov et al., 2012), temperature (Tuf et al., 2012; Saska et al., 2013), tillage (Müller et al., 2022) and urbanisation (Magura & Lövei, 2021).

Biomonitoring assemblages in habitats that transition between aquatic and terrestrial domains can be challenging (e.g. Stubbington et al., 2019; Crabot et al., 2021; Munné et al., 2021). For example, in temporary streams, aquatic assemblages can only be sampled during flowing or lentic phases, and during these phases their responses to a range of environmental conditions (e.g. organic pollution, land use) are often moderated by drying (Soria et al., 2020; Stubbington et al., 2022c). A compounding issue is the perception of temporary streams as solely aquatic ecosystems, even during their dry phases when aquatic assemblages cannot be sampled. Thus, temporary stream biomonitoring to date has largely used aquatic rather than terrestrial organisms (Stubbington et al., 2018a). One index, the Monitoring Intermittent Streams (MIS) index, takes steps to incorporate river-associated terrestrial invertebrates in assessments of community responses to drying by adapting the kick sampling method that is routinely used to sample aquatic invertebrates (England et al., 2019). However, considering terrestrial assemblages as supplementary extensions of the more frequently sampled aquatic assemblages underestimates their biodiversity (Steward et al., 2011; Bunting et al., 2021), their contributions to ecosystem function (Ramey & Richardson, 2017) and potential as biomonitors (Steward et al., 2018; Robinson, 2019; Hayes, 2022). One reason why terrestrial invertebrate assemblages are rarely sampled is the lack of a consistent sampling method (e.g. Webb et al., 2022), with studies to date using variants of pitfall trap and hand search methods that are commonly used to sample riparian and terrestrial assemblages (e.g. Steward et al., 2011; Robinson, 2019; Hayes, 2022). Thus, a more holistic approach that allows managers to infer the state of the environment regardless of in-channel conditions by redressing the bias against biomonitoring using terrestrial assemblages should be developed.

A challenge in monitoring all riverine ecosystems is the limited time and resources available to sample them. Citizen science, the collection or processing of data by members of the public (Haklay et al., 2021), can generate large, high-quality biological and environmental datasets (e.g. Kosmala et al., 2016; Ratnieks et al., 2016; Shuker et al., 2017; Brooks et al., 2019). For example, biological data is collected by the Angler's Riverfly Monitoring Initiative (Partnership, 2021), which covers hundreds of freshwater sites across the UK, including some temporary streams. Across Europe, temporary stream citizen science has focused on environmental observations (e.g. CrowdWater, DRYRivERS: CrowdWater App, 2023; DRYRivERS App, 2023; Truchy et al., 2023). However, few citizen science projects involve the sampling of biotic communities from temporary streams (but see Hampshire and Isle of Wight Wildlife Trust, 2023), and none have characterised their terrestrial assemblages because no simple, but robust, sampling method has been defined.

2.4 Research gaps

This literature review has identified multiple knowledge gaps concerning the status of aquatic assemblages in agricultural areas, and the assembly and subsequent monitoring of terrestrial assemblages in temporary streams. In particular, the research presented in the following chapters will:

Chapter 3. Compare the responses of aquatic assemblages to human impacts, in particular those associated with agricultural land use, in perennial and temporary streams (*Objective 1*).

Chapter 4. Assess the potential importance of catchment-wide networks of artificial and natural watercourses, in particular ditches, in supporting the persistence of aquatic assemblages in temporary streams (*Objective 2*).

Chapter 5. Test the local-scale connectivity between communities that surround perennial and temporary stream channels (*Objective 2*).

Chapter 6. Assess the utility of standard methods (i.e. hand searching and pitfall trapping) for characterising terrestrial in-channel assemblages, and which may enable monitoring by citizen scientists (*Objectives 1* and *3*).

Chapter 7. Evaluate the utility of a citizen science habitat survey for characterising terrestrial in-channel assemblages, in particular during wet phases when they cannot be directly sampled (*Objectives 1* and *3*).

Chapter 8. Discuss how the findings of Chapters 2–7 can be applied to better monitor and manage the aquatic–terrestrial communities supported by temporary streams in a time of unprecedented global change (*Objective 4*).

2.5 The study area

The research presented in this thesis focuses on the communities supported by the winterbourne chalk streams of southern England. Winterbournes, and chalk streams more broadly, are globally rare ecosystems, with up to 80%

occurring in southern and eastern England (Mondon et al., 2021). Their flow regimes and water chemistry allow them to support high aquatic biodiversity (Berrie, 1992) and, as such, they are of regulatory interest, are a focus for temporary stream biomonitoring and are highly valued by the wider public, receiving frequent attention from print, broadcast and social media (e.g. Anthony, 2018; Stubbington et al., 2022b).

Southern England has a wet temperate climate (Kottek et al., 2006), with a mean annual air temperature of 10.5°C which typically peaks with a mean monthly air temperature of 22.3°C in July, and is lowest at 1.7°C in January (Met Office, 2016). Air temperature extremes range between -18.2°C and 38.5°C (Met Office, 2016). Across southern England, mean annual precipitation ranges from 550–950 mm (Met Office, 2016). October to January is typically the wettest period with up to 45 wet days (i.e. days with >1 mm of precipitation) and June to August being the driest with 25 days wet days (Met Office, 2016). Large parts of southern and eastern England are underlain by chalk ($CaCO_3$: British Geological Survey, 2021), which absorbs precipitation and acts as an aquifer (Sear et al., 1999). Above this chalk aquifer, like in most of England, agriculture occupies >50% of the total land area, with urban areas covering <10% (Department for Levelling Up, Housing & Communities, UK Government, 2022).

Groundwater levels in the aquifer control flow permanence of any given reach and thus, most winterbournes are in the headwaters of catchments with perennial reaches occurring downstream (Berrie, 1992; Sear et al., 1999). Seasonal changes in groundwater levels mean winterbournes are seasonally intermittent (Berrie, 1992). High winter precipitation promotes aquifer recharge, initially forming pools in lower parts of the channel cross section. As groundwater levels rise, flow resumption often occurs slowly, over days–months within any given reach as pools become connected (Berrie, 1992; Sear et al., 1999). After resumption, flowing phases typically last for >6 months between winter and spring. During flowing phases, like all chalk streams, winterbournes are often characterised by clear water, which has a relatively stable temperature close to that of the underlying groundwater (approx. 11°C: Crisp et al., 1982) and is high in nutrients that promote macrophyte growth (Berrie, 1992). However, water from chalk aquifers can also contain legacy pollutants, such as plant protection products (Stuart et al., 2011; Robinson et al., 2023). Between late spring and autumn, declining groundwater levels cause flow cessation and drying from upstream to downstream, although some reaches may retain in-channel pools.

Winterbournes are typically small, <1 m deep and <5 m wide, and when flowing through rural areas are often not managed by physical structures (e.g. concrete banks, weirs) which prevent the channel from interacting with the floodplain (e.g. **Figure 15.2**, **Figure 15.3**). Many winterbournes have been straightened and rerouted to follow the course of field boundaries and roadsides, where they often resemble trapezoidal drainage ditches (Gething et al., 2021; Rangeley-Wilson, 2021). When dry, the channels are linear hollows with similar vegetation to surrounding habitats (typically pasture or scrubland: Hayes, 2022). This historic, unsympathetic management combined with the potential for winterbournes to support biodiversity has sparked recent interest from regulators and non-governmental organisations who seek to more holistically biomonitor and restore habitats that support their aquatic–terrestrial communities (e.g. Rangeley-Wilson, 2021; Hampshire and Isle of Wight Wildlife Trust, 2023).

3 Under pressure: aquatic macroinvertebrate responses to agriculture in temporary streams

3.1 Introduction

Agriculture is essential to supporting Earth's growing population, but threatens the integrity of riverine ecosystems globally (Mateo-Sagasta et al., 2017; Reid et al., 2019). Agricultural pressure influences aquatic assemblages via stressors such as elevated fine sediment and nutrient levels and decreased dissolved oxygen concentrations, which have effects ranging from the loss of sensitive species to wholesale shifts in ecosystem structure and function (Wood & Armitage, 1997; Dodds, 2007; Sánchez-Bayo et al., 2016). Agriculture may be particularly damaging in reaches exposed to other pressures, which have compounding effects on their communities. For example, temporary streams comprise more than half of the global river network (Datry et al., 2014b; Messager et al., 2021), and contain communities shaped by the occurrence of dry phases. Temporary streams are widespread in cool, wet temperate climates (Stubbington et al., 2017b), and often occur in agricultural areas (Armitage & Bass, 2013; Karaouzas et al., 2018; White et al., 2018), imposing both agricultural and drying pressure upon their communities. However, temporary streams are under-represented in studies of agriculture in riverine ecosystems (Gerth et al., 2017).

Aquatic macroinvertebrates are a diverse group that are often used to monitor ecological responses to agricultural pressure (e.g. when agricultural pressure manifests as sediment and nutrient stressors: Extence et al., 2013; Paisley et al., 2014). The limited available evidence suggests that, as in perennial streams (e.g. Genito et al., 2002), taxonomic and trait composition differs between macroinvertebrate assemblages in agricultural and non-agricultural temporary streams (Botwe et al., 2015; Gerth et al., 2017). In contrast to perennial streams however, temporary stream assemblages are prefiltered by drying pressure (Matthaei et al., 2010; Leigh & Datry, 2017) and may thus be adapted to comparable pressures (*sensu* Vinebrooke et al., 2004). For example, drying pressure manifests as multiple stressors including: decreasing aquatic habitat provision, increasing fine sediment and dissolved nutrient concentrations, and decreasing dissolved oxygen concentrations as water temperature and the density of respiring aquatic organisms increases (Stubbington et al., 2011; Gómez et al., 2017; von Schiller et al., 2017). These stressors are comparable to those exerted by agricultural pressure, which can decrease aquatic habitat provision via abstraction for irrigation (Fu et al., 2004; Hao et al., 2008), increase water temperatures via a loss of riparian shading and increase fine sediment and nutrient concentrations via runoff, collectively decreasing dissolved oxygen concentrations (Allan, 2004; Withers et al., 2014; dos Reis Oliveira et al., 2019). Such a combination of stressors typically result in homogeneous, stress-tolerant assemblages (Díaz et al., 2008; Wang et al., 2019; Edegbene et al., 2020), like those in temporary (Datry et al., 2014a; Gutiérrez-Cánovas et al., 2015) and agricultural (Delong & Brusven, 1998; Gething, 2021) streams. Thus, temporary stream macroinvertebrate assemblages may have some tolerance of agricultural pressure (which manifests as similar stressors: Storey, 2016), experiencing smaller differences in composition than between agricultural and non-agricultural perennial streams.

Temporary streams support rare, specialist macroinvertebrate species that can tolerate drying (Stubbington et al., 2017b; Macadam et al., 2021). These species include mayflies and stoneflies from families that are generally sensitive to low dissolved oxygen concentrations and fine sediment (Armitage et al., 1983; Extence et al., 2013), common agricultural stressors. However, the occurrence of the temporary stream specialist mayfly *Paraleptophlebia werneri* and stonefly *Nemoura lacustris* in drainage ditches and streams in agricultural landscapes (Chalkley, 2006; Gething et al., 2021) indicates they may be co-tolerant of drying and agricultural pressure, unlike their co-sensitive congeners (Chadd et al., 2017). Thus, like temporary stream assemblages more broadly (Storey, 2016), the temporary stream specialist species may be unaffected by agricultural land uses, which they experience as an intensification of the drying-related stressors to which they are adapted.

I assessed the effects of agricultural land use on macroinvertebrate taxonomic and trait variability in temporary and perennial streams. I hypothesised that (H1) assemblage variability between areas with higher and lower agricultural land use is lower in temporary than perennial reaches (**Figure 3.1B**), because assemblages in temporary streams are prefiltered by drying which promotes co-tolerance of agriculture; (H2) assemblage variability between temporary and perennial reaches is lower in areas with higher agricultural land use (**Figure 3.1B**), because their assemblages are filtered to tolerant taxa/traits; and (H3) the occurrence of temporary stream specialists is unaffected by agricultural land use, because they are adapted for co-tolerance of agriculture by comparable drying-related stressors.

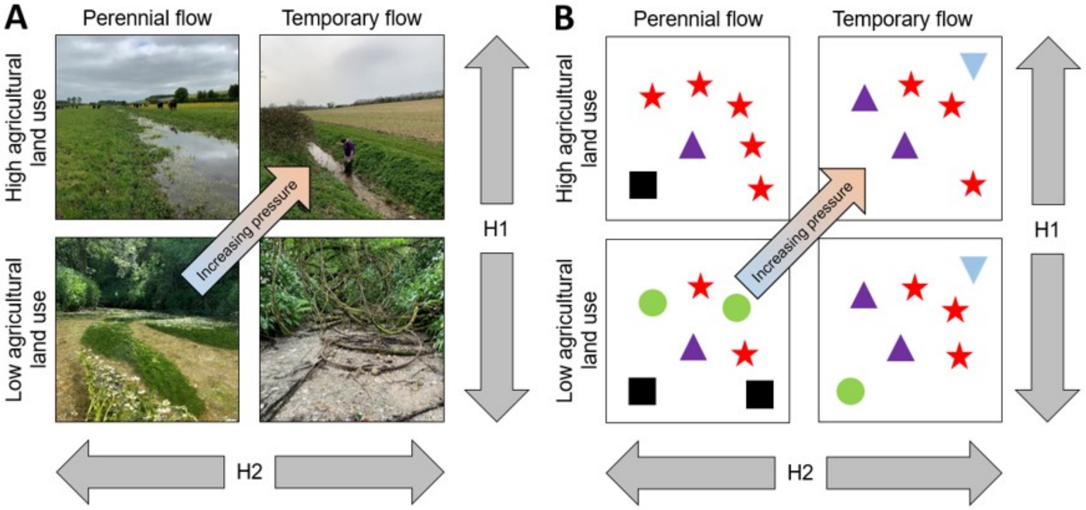


Figure 3.1: The (A) habitats and (B) hypothesised assemblage shifts with differing combinations of temporary and perennial flow and high and low agricultural land use. Grey arrows show the habitats compared by hypotheses (H) 1 and 2; symbols represent different taxa or traits.

3.2 Methods

3.2.1 Data collection

Study area

Data were collected by Wessex Water (a water company operating in southern England) on seven tributary streams of the Hampshire Avon, southern England (**Table 3.1**, see **Figure 1.5** in Allen et al., 2019). The region has a temperate oceanic climate (Cfb: Kottek et al., 2006), with mean (± SD) annual minimum and maximum air temperatures of 6.1 ± 3.9°C and 15.0 ± 5.7°C, respectively and a mean annual rainfall of 754 mm (Met Office, 2022). The Hampshire Avon catchment has primary land uses of pastoral (42%) and arable agriculture (39%: National River Flow Archive, 2021). The area is underlain by a chalk aquifer that experiences seasonal fluctuations in water levels (Sear et al., 1999), resulting in reaches with both temporary and perennial flow, including in all 7 tributary streams. Flow in such groundwater-fed systems is typically stable over long timescales (i.e. months–years), being mostly unaffected by short-term hydroclimatic events (e.g. rainfall: Sear et al., 1999).

Table 3.1: Number of sites and samples collected from temporary (T) and perennial (P) reaches of 7 streams in southern England.

	Sites	T sites	P sites	Samples	T samples	P samples
Chitterne Brook	4	3	1	5	3	2
Fonthill Brook	3	2	1	8	4	4
Nine Mile River	4	4	0	8	8	0
R. Bourne	7	5	2	14	6	8
R. Ebble	7	5	2	25	13	12
R. Till	8	4	4	23	12	11
R. Wylye	4	2	2	15	3	12
Total	**37**	**25**	**12**	**98**	**49**	**49**

The 37 sites were selected by Wessex Water to monitor aquatic communities in their area using guidance from Murray-Bligh (1999; updated as Murray-Bligh & Griffiths, 2022). Briefly, sites were 5–20 m in length depending upon the width of the channel. Sites were selected to be representative of the entire reach (i.e. to include the range of habitats and thus fauna present). In the three years prior to macroinvertebrate sampling, sites were visited once per month and the presence/absence of water recorded. To allow comparisons between temporary and perennial reaches, sites were assigned to a flow category (FlowCat: temporary or perennial). Temporary reaches were those that had been recorded as dry in at least one of the 36 months prior to macroinvertebrate sampling. During this period, mean (± SE) discharge was 0.50 ± 0.02 $m^3 s^{-1}$ (range: 0–2.23 $m^3 s^{-1}$) in temporary reaches and 0.84 ± 0.02 $m^3 s^{-1}$ (0.14–6.70 $m^3 s^{-1}$) in perennial reaches. Temporary reaches had flowed for 14.9 ± 9.7 months and been dry for 21.1 ± 9.7 months on average, with flow resuming 2–34 months prior to macroinvertebrate sampling.

Aquatic macroinvertebrates

Aquatic macroinvertebrate samples were collected by Wessex Water from temporary (n = 49 samples: **Table 3.1**) and perennial (n = 49 samples) reaches in spring, summer and autumn 2006 and 2007 using a standard three-minute kick sampling methodology supplemented by a one-minute hand search (Murray-Bligh & Griffiths, 2022). In the laboratory, macroinvertebrates were identified predominantly to species level, except Diptera which were identified to the lowest practical level between species and family (mostly genus). Some individual Arhynchobdellida, Coleoptera, Ephemeroptera, Gastropoda, Lepidoptera and Trichoptera were identified to the lowest possible taxonomic resolution and at least to family level. All taxa were recorded as present/absent.

Physicochemical characteristics and land use

Land use buffers with a radius of 100 m around each macroinvertebrate sampling site were extracted from the UK Centre for Ecology & Hydrology LCM2007: Land Cover Map (Morton et al., 2014) using Quantum GIS v.3.16 (QGIS Development Team, 2021). I selected this radius because land uses 60–200 m from a sampling location influence the distribution of common agricultural pollutants (e.g. fine sediment) and are a key driver of macroinvertebrate assemblage composition (Sponseller et al., 2001; Feld, 2013). Specifically, I selected 100 m as an intermediate value that also prevented overlap of land use characterisations among sites.

To characterise stressors indicative of agricultural land use, substrate samples were collected by Wessex Water at each macroinvertebrate sampling site in spring 2006 and 2007. A hole saw (10 × 5 cm) was twisted into the sediment at 6–8 representative locations and the extracted substrate aggregated into a 2.5-L composite sample. Substrate samples were returned to the laboratory, air dried, and sieved to determine the relative proportions of silt (<0.06 mm), sand (0.06–2 mm), gravel (2–64 mm) and cobble (>64 mm). Total phosphorus (mg kg^{-1}) and total oxidised nitrogen (mg kg^{-1}) were determined for each sediment sample.

3.2.2 Data analysis

Data preparation

To minimise the influence of macroinvertebrate identification to multiple taxonomic levels on my analyses, I assigned taxa to a most likely taxon (Cuffney et al., 2007). For example, where a sample contained 20 *Agapetus fuscipes*, 10 *Agapetus*, one Glossosomatidae and no other members of the same family, the sample was adjusted to contain 31 *Agapetus fuscipes*. Where a sample contained 10 *Drusus annulatus*, 10 *Limnephilus lunatus* and 10 Limnephilidae, the sample was adjusted to contain 15 *Drusus annulatus* and 15 *Limnephilus lunatus*. The final dataset included 85%, 11% and 4% of taxa assigned to species, genus and family, respectively.

To characterise functional composition, I used three biological traits (maximum size, respiration and locomotion) with 20 modalities and two ecological 'traits' (i.e. environmental preferences: trophic and temperature preference) with 6 modalities that respond to both drying and agricultural stressors (**Table 3.2**: Tachet et al., 2010; Schmidt-Kloiber & Hering, 2015). I weighted the affinity of each taxon to multiple modalities within a trait using a fuzzy coding approach, to represent intra-taxon trait variability (Chevenet et al., 1994). I represented taxa identified to species with their species trait profile or, where species-level information was not available, with the highest resolution profile available (mostly genus). I represented taxa identified to genus/family with the average trait profile of all species in that taxon (Demars et al., 2012). The trait modalities I assigned to each taxon ranged from zero (no affinity) to three or five (high affinity: Tachet et al., 2010). Due to differing numbers of modalities within traits, I standardised modalities within traits so that each trait summed to one, thus representing the relative abundance of each modality per taxon and ensuring equal weighting of the five traits (Demars et al., 2012; England et al., 2021). I multiplied the resulting taxa-by-trait matrix by the taxa-by-sample matrix to obtain a trait-by-sample matrix for analysis.

Table 3.2: Trait modality associations with flow permenance and agricultural land use, where supporting literature refers to Aspin et al., 2019[1]; Bonada et al., 2007[2]; Datry et al., 2017a[3]; Díaz et al., 2008[4]; Edegbene et al., 2020[5]; Sarremejane et al., 2017[6] and Wang et al., 2019[7]

Trait	Justification	Literature
Maximum body size	Temporary flow and higher agricultural land use favour small bodied organisms that can more easily access interstitial refuges during drying events or when substrates are clogged with fine particulates, relative to intermediate and large bodied organisms that can access unclogged sediments in perennial/low agriculture reaches.	1,2,4,5,6,7
Respiration mode	Temporary flow and higher agricultural land use decrease dissolved oxygen concentrations, favouring air breathing taxa, whereas the higher dissolved oxygen concentrations typical of perennial/low agriculture reaches favour aquatic respiration (e.g. gills).	1,2,4,5,6
Locomotion mode	Burrowing taxa can survive fine sediment deposition and thus characterise temporary/high agriculture reaches whereas perennial/low agriculture reaches promote larger sediment sizes and macrophyte growth, favouring crawling and attached taxa.	1,2,4,5,7
Trophic preference	Temporary flow and higher agricultural land use promote higher nutrient concentrations, and thus favour taxa with eutrophic preferences / tolerances relative to perennial/low agriculture reaches.	3,7
Temperature preference	Variable temperatures in temporary reaches favour taxa with eurythermic preferences/tolerances, whereas perennial flow and lower agriculture land use favour taxa with psychrophilic preferences/tolerances. Higher temperatures in high agriculture reaches favour taxa with thermophilic preferences/tolerances.	1,7

I generated a categorical variable (AgriCat) to characterise the broad effects of agriculture on macroinvertebrate assemblages variability. First, I applied indicator species analysis (IndVal: Dufrêne & Legendre, 1997) to a Euclidean distance matrix containing 4 abiotic variables: Total phosphorus, total oxidised nitrogen, silt and sand (i.e. common agricultural pollutants). I repeated IndVal 98 times, in which the boundary for "high" and "low" agriculture was sequentially increased from 1 to 99% of total land use. For each iteration, I calculated the root-mean-square (RMS) of IndVal scores for the four abiotic variables. Iterations with a low RMS value signified that the abiotic variables had a low specificity and a fidelity to each category (i.e. approximately half of the material recorded for each abiotic variable was above and below the threshold). The lowest RMS values occurred at 80% agricultural land use, and thus I used this threshold to assign samples to high (n = 62) and low AgriCat (n = 36) categories. After assigning samples to an AgriCat using this threshold approach, I used site observations to verify that samples had been assigned to the appropriate AgriCat. To ensure that samples close to the threshold were not disproportionately influencing my conclusions, I repeated all analyses while excluding 12 samples (four and eight from the low and high AgriCats, respectively) for which 70–90% (i.e. ± 10% of the 80% threshold) of total land use was agriculture. Analyses including and excluding these 12 samples produced comparable results, and thus I present analyses that include all samples.

The 80% threshold resulted in high AgriCat samples with (mean ± SD) 96.3 ± 5.2% (min: 81.6%, max: 98.5%) agricultural land use, compared to 49.8 ± 19.5% (min: 0.0%, max: 74.2%) in low AgriCat samples. Temporary and perennial reaches were comparably represented in high (31 temporary and 31 perennial samples) and low (18 and 18) AgriCats.

Flow permanence and agriculture as drivers of macroinvertebrate assemblages

To characterise assemblages for testing of H1 and H2, I first calculated Sørensen pairwise distances from the taxa-by-sample matrix and Bray-Curtis pairwise distances from the trait-by-sample matrix to represent taxonomic and functional composition, respectively. I then summarised variability in taxonomic and functional composition by calculating the distance between each sample and the centroid of each FlowCat and AgriCat (i.e. multivariate dispersion: Warwick & Clarke, 1993; Benkwitt et al., 2019) using permutational analyses of multivariate dispersions (PERMDISP2: Anderson, 2006). I used the distance of samples from (i.e. variability around) FlowCat (H1) and AgriCat (H2) centroids as response variables in linear models. During preliminary analyses, I identified significant differences in composition among seasons and years, which I controlled by nesting season within year (hereafter, Season) and including Season as a random intercept in all models.

To assess taxonomic and trait variability within temporary and perennial reaches in relation to agricultural land use (H1), I tested whether the distance of samples from each FlowCat centroid differed between the interaction of FlowCat with AgriCat (**Table 3.3**). Acceptance of H1 required variability among temporary FlowCat samples to be unaffected by AgriCat *and* to be lower than among perennial FlowCat samples.

Table 3.3: Model structures testing hypotheses 1–3, where variables to the left of × are response variables, to the right of × are fixed effects and variables in brackets are random effects.

Hypothesis	Structure
1	Distance to FlowCat centroid × FlowCat * AgriCat + (1 | Season)
2	Distance to AgriCat centroid × AgriCat * FlowCat + (1 | Season)
3	Species occurrence × AgriCat + (1 | Season)

To assess taxonomic and trait variability between high and low AgriCat reaches with different flow permanence regimes (H2), I replicated the H1 linear modelling approach, but switched the order of FlowCat and AgriCat as predictors testing whether the distance of samples from each AgriCat centroid differed between the interaction of AgriCat with FlowCat (**Table 3.3**). Acceptance of H2 requires variability among high AgriCat samples to be unaffected by FlowCat *and* to be lower than among low AgriCat samples.

Where differences in variability between FlowCats and between AgriCats were detected, I identified the contribution of each taxon/trait modality to differences using similarity percentage analysis (SIMPER: Clarke, 1993) over 9,999 permutations. I considered a taxon as driving differences if SIMPER P <0.05 and contributions to overall differences were ≥5%.

To contextualise my testing of differences in variability (i.e. H1 and H2), I also tested for differences in composition between FlowCats and AgriCats (see **Supplementary material – Under pressure: aquatic macroinvertebrate responses to agriculture in temporary streams**).

Agriculture as a driver of the occurrence of temporary stream specialists

Based on Armitage & Bass (2013) and Macadam et al. (2021), I identified two temporary stream specialists in the dataset: the mayfly *Paraleptophlebia werneri* and blackfly *Simulium latipes*. Additionally, since sample collection (2006–07) the temporary stream specialist stonefly *Nemoura lacustris* has been widely recorded in the study area (Hammett, 2012; Gething et al., 2021). The aquatic juveniles of *N. lacustris* are morphologically similar to those of

Nemoura cinerea (Armitage & Bass, 2013; Tapia et al., 2018) and records of this species are likely to represent a combination of *N. cinerea* and *N. lacustris* (Aspin & House, 2022). I therefore analysed *N. cinerea* alongside the two other temporary stream specialists.

Paraleptophlebia werneri was exclusive to temporary reaches (in 12 of the 49 samples). *Simulium latipes* and *N. cinerea* occurred mostly in temporary reaches (in 17 and 22 samples, respectively), but were also recorded from perennial reaches (1 and 2 samples). Because the inclusion of perennial reaches may have masked my capacity to detect any effect of agriculture I used temporary reach samples to test H3. I used occurrences of the three specialist species as response variables and AgriCat as a fixed effect in binomial generalised linear mixed-effect models (**Table 3.3**). Acceptance of H3 requires the occurrence of specialist to be unaffected by AgriCat.

To enable the absence of a temporary stream specialist responses to agriculture to be accepted as evidence supporting H3 (rather than a false negative), I re-ran the H3 linear model for all taxa which had >90% of their occurrences in one FlowCat. I used the >90% threshold to ensure selected taxa were similarly affiliated to a FlowCat, providing valid comparisons with temporary stream specialists which had 92–100% of occurrences in temporary reaches. I then discounted taxa with ≤10 occurrences in their testing FlowCat, because ≤10 occurrences were insufficient to assess the influence of AgriCat. Thus, I applied the H3 linear model to the four and 21 taxa using temporary and perennial reach samples, respectively.

I conducted all analyses in R v.4.0.3 (R Core Team, 2020), using the packages biomonitoR (Laini et al., 2022), DHARMa (Hartig, 2020), indicspecies (De Caceres & Legendre, 2009), lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2017) and vegan (Oksanen et al., 2019). For all models, where singular fit warnings were encountered (i.e. a warning indicating that the random intercept, Season, was not explaining and variance), I removed Season to improve model parsimony. I quantified variance attributable to the fixed and random effects using marginal R^2 (R^2M) and conditional R^2 (R^2C). For H1 and H2, I visualised variability in taxonomic (i.e. Sørensen) and functional (Bray-Curtis) distance matrices using 2-dimensional non-metric multidimensional scaling (NMDS) ordinations, run over 500 iterations. While validating ordinations, I noted high stress (>0.2) values for taxonomic composition in temporary reaches. I replotted this NMDS using 3 dimensions to ensure its validity, presenting all combinations of the 3 dimensions in **Figures 3.2B** and **11.1A** and **B**.

3.3 Results

Macroinvertebrate assemblages comprised 237 taxa from 86 families. The non-biting midge family Chironomidae occurred in all samples. The other most frequently occurring taxa overall were the worm *Eiseniella tetraedra* (in 98% of samples) the mayfly *Baetis rhodani* (90%) and the blackfly *Simulium ornatum* (80%). Perennial reaches supported 189 taxa (79.7% of total) and 42.6 ± 12.1 (mean ± SD) taxa per sample, whereas temporary reaches supported 167 taxa (70.5%) and 23.1 ± 9.9 taxa per sample. In temporary reaches, *E. tetraedra* (100%) and *B. rhodani* (86%) occurred most frequently, whereas in perennial reaches *E. tetraedra*, the amphipod *Gammarus pulex*, and the riffle beetle *Elmis aenea* were most frequent (98–100%). High AgriCat reaches supported 209 taxa (88% of total), whereas low AgriCat reaches supported 178 taxa (75%). High and low AgriCat reaches supported 31.4 ± 13.5 (mean ± SD) and 35.4 ± 16.4 taxa per sample, respectively. *Eiseniella tetraedra* (98 and 100% of samples) and *B. rhodani* (89 and 92%) were the most frequently occurring taxa in both high and low AgriCats. When splitting FlowCats by AgriCats, perennial reaches supported 39.3 ± 12.4 (mean ± SD) and 48.2 ± 9.3 taxa per sample at high and low AgriCat, respectively. Temporary reaches supported 23.4 ± 9.3 (taxa per sample) at high and 22.7 ± 11.0 at low AgriCat.

Functional assemblages comprised 25 of the 26 trait modalities considered, with the hydrostatic vesicle respiration mode being absent from all samples. The occurrence of trait modalities was comparable across FlowCats, with temporary and perennial reaches both supporting all 25 modalities. Low AgriCat reaches supported 24 modalities, missing maximum size: >8 cm. All 25 modalities were present in high AgriCat reaches with >8cm leeches *Trocheta subviridis* (Erpobdellidae) and Hirudinidae occurring in 3 samples.

3.3.1 H1. Assemblage responses to agriculture in temporary and perennial reaches

AgriCat did not influence taxonomic variability in temporary reaches (estimate ± SE = -0.04 ± 0.02, P = 0.101, R^2M = 0.321, **Figures 3.2A** and **11.1**). In perennial reaches, high AgriCat reaches were more taxonomically variable than low AgriCat reaches (estimate ± SE = 0.05 ± 0.02, P = 0.033, **Figure 3.2B**), supporting H1. No individual taxon drove differences between AgriCats in perennial reaches (all SIMPER: <5% and/or P >0.05). Functional variability was unaffected by AgriCat in temporary (estimate ± SE <0.01 ± 0.01, P = 0.884, R^2M = 0.317, **Figure 3.2C**) and perennial (estimate ± SE = 0.01 ± 0.01, P = 0.299, **Figure 3.2D**) reaches, supporting H1.

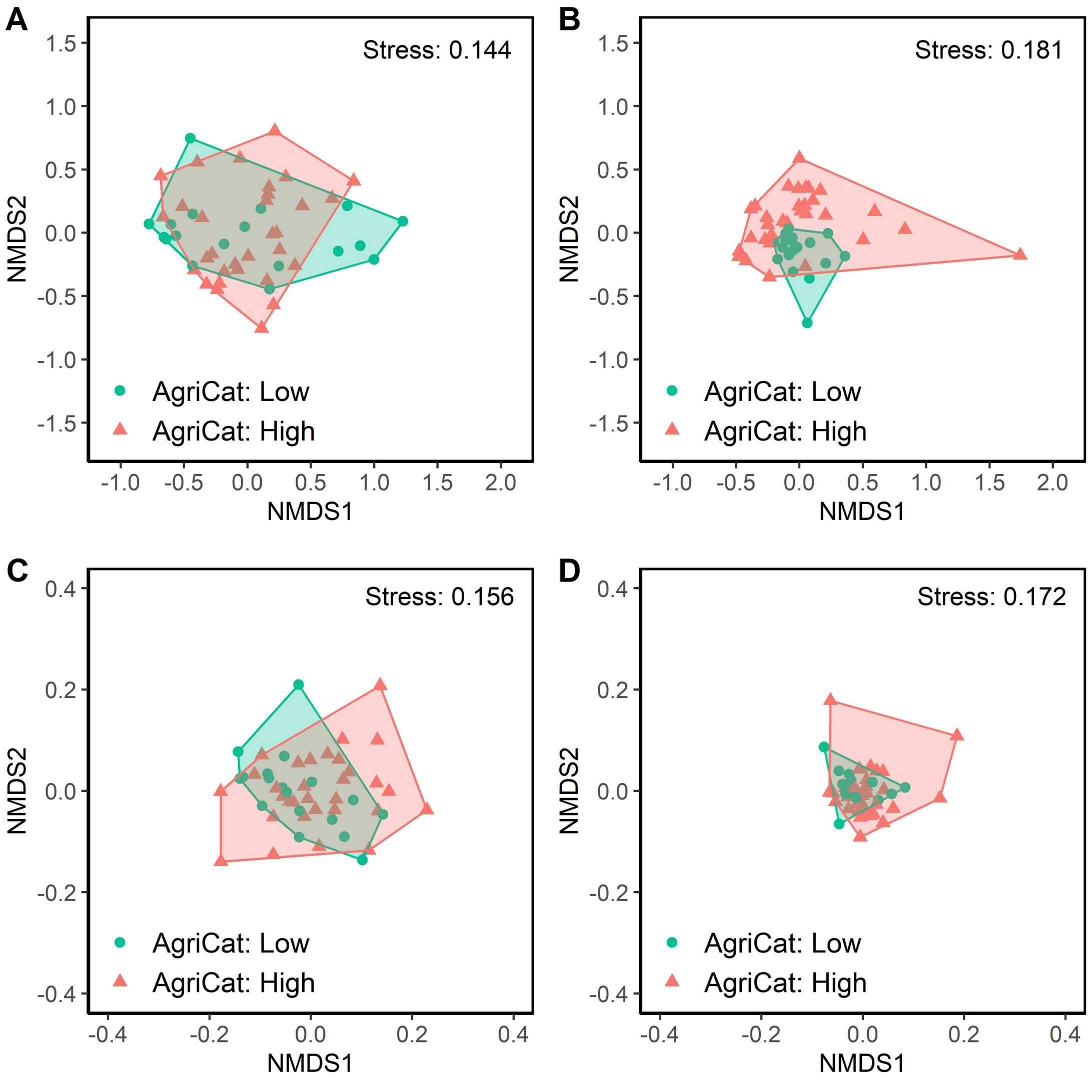


Figure 3.2: Non-metric multidimensional scaling of taxonomic (A and B) and functional (C and D) variability in relation to agricultural land use categories (AgriCat) in temporary (A and C) and perennial (B and D) reaches. Note: A represents NMDS1 and NMDS2 of a three-dimensional ordination, see supplementary information for plots of NMDS3 against NMDS1 and NMDS2.

3.3.2 H2. Agriculture as a driver of assemblage differences between temporary and perennial reaches

Temporary reaches were more taxonomically variable than perennial reaches at high ($P < 0.001$, $R^2M = 0.471$, $R^2C = 0.561$, **Figure 3.3A**) and low ($P < 0.001$, **Figure 3.3B**) AgriCat, contrary to H2. However, differences in variability were smaller in high (estimate ± SE: 0.08 ± 0.02) than low (0.20 ± 0.02) AgriCat reaches, *sensu* H2. Samples from temporary reaches were more functionally variable than those collected in perennial reaches at high ($P < 0.001$, $R^2M = 0.293$, $R^2C = 0.319$, **Figure 3.3C**) and low ($P < 0.001$, **Figure 3.3D**) AgriCat, contrary to H2. Differences in functional variability between FlowCats were comparable in size (both estimate ± SE: 0.04 ± 0.01) across AgriCats. No individual taxon or trait drove differences between FlowCats (all SIMPER: <5% and/or $P > 0.05$).

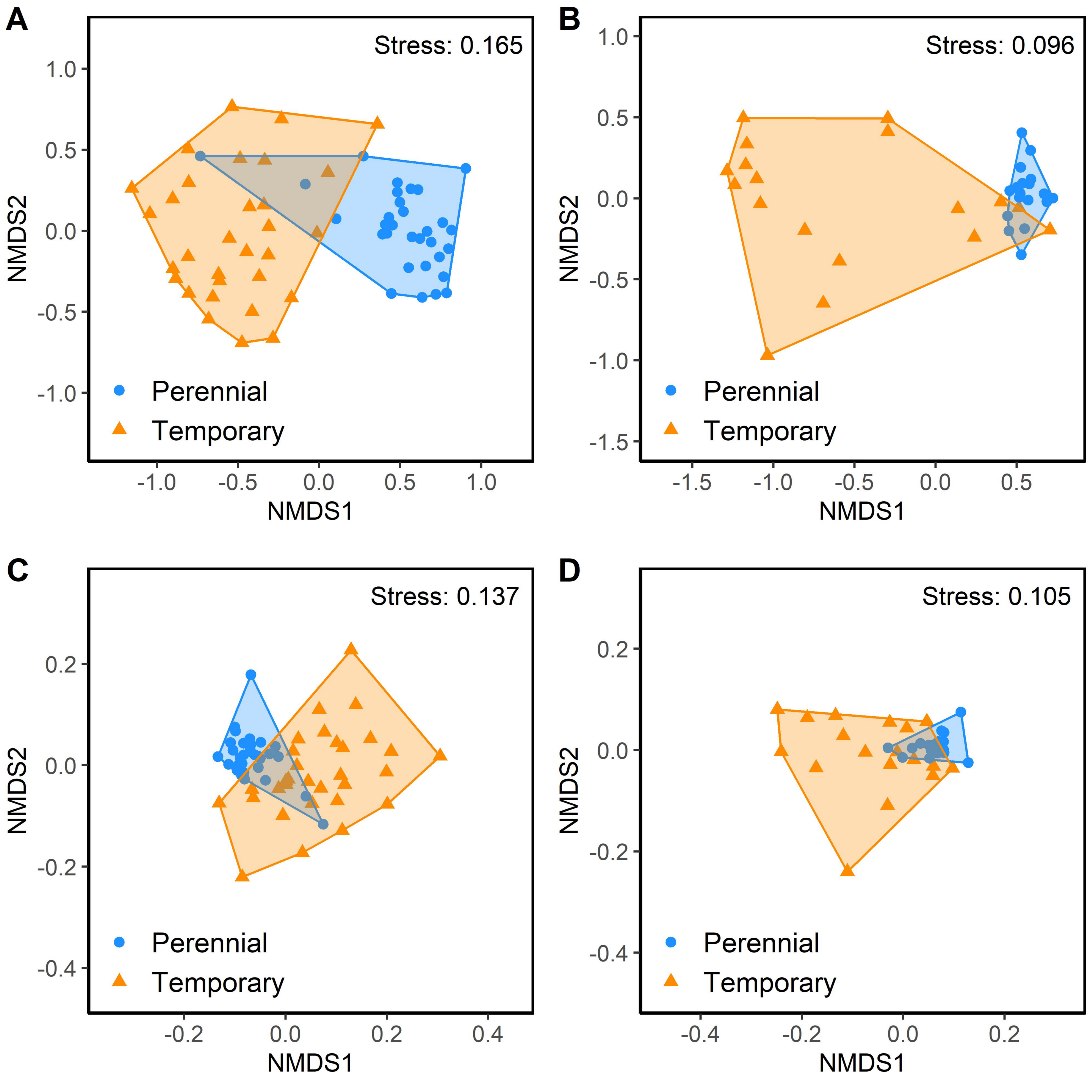


Figure 3.3: Non-metric multidimensional scaling of taxonomic (A and B) and functional (C and D) variability in relation to flow permanence regime in high (A and C) and low (B and D) agricultural land use category (AgriCat) reaches.

3.3.3 H3. Agriculture as a driver of the occurrence of temporary stream specialists

Paraleptophlebia werneri, *S. latipes* and *N. cinerea* occurred more often at high AgriCat (number of occurrences in low:high AgriCat samples: 3:9, 8:9 and 6:16, respectively), but AgriCat did not significantly influence the occurrence of any specialists (P = 0.205–0.337, R^2M = 0.023–0.040, R^2C = 0.184–0.679: **Figure 3.4**), supporting H3. Of the 4 other taxa analysed from temporary reach samples, all occurred more frequently at high AgriCat and the bivalve *Pisidium personatum* (P = 0.031, R^2M = 0.079, R^2C = 0.630) and the blackfly *Simulium aureum* (group, including *Simulium angustipes*, *Simulium aureum*, *Simulium petricolum* and *Simulium velutinum*, which are morphologically indistinguishable as larvae: Davies, 1966; Day et al., 2010) (P <0.001, R^2M = 0.063, R^2C = 0.579) were significantly associated with high AgriCat reaches (**Figure 3.4**). Five of the 21 taxa analysed from perennial reaches were affected by AgriCat. The mayfly *Baetis muticus* (P = 0.042, R^2M = 0.264, R^2C = 0.276) was the only taxon associated with high AgriCat, with the mayflies *Ecdyonurus dispar* (P = 0.016, R^2M = 0.148) and *Caenis rivulorum* (P = 0.028, R^2M = 0.141, R^2C = 0.445), the caddisfly *Mystacides azurea* (P = 0.002, R^2M = 0.294, R^2C = 0.325) and the gastropod *Physa fontinalis* (P = 0.009, R^2M = 0.226) being associated with low AgriCat (**Figure 3.4**). The remaining 3 and 16 taxa from temporary and perennial streams were not associated with either AgriCat (all P >0.05).

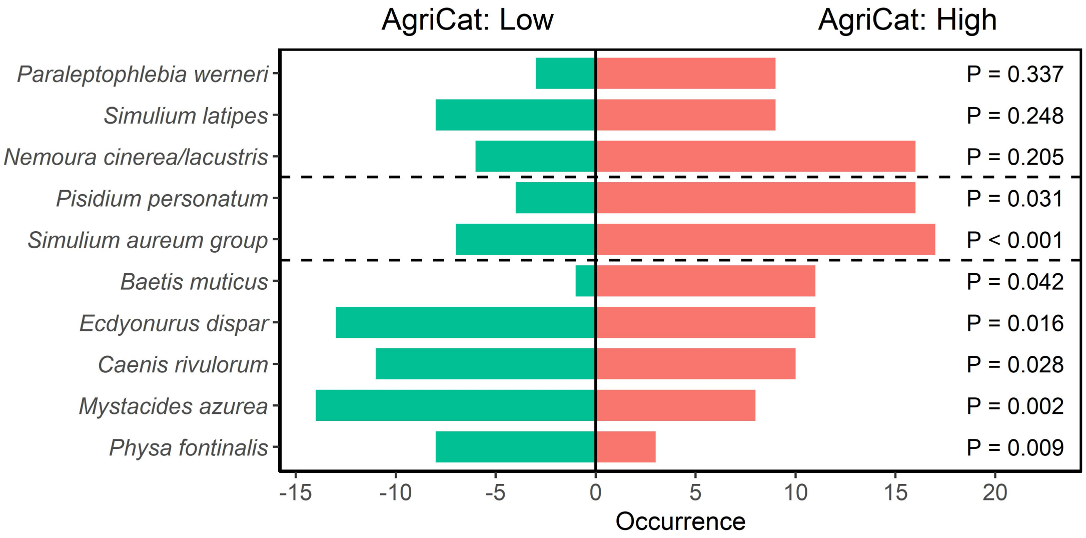


Figure 3.4: The occurrence of temporary stream specialists (top), and species with a similar affinity to temporary (middle) and perennial (bottom) reaches in the low (blue) and high (orange) agricultural land use categories (AgriCat). P values denote the significance of associations between each species and either AgriCat.

3.4 Discussion

Agriculture poses significant threats to freshwater ecosystems (Mateo-Sagasta et al., 2017), but its effects are poorly known in the globe's dominant lotic ecosystem type, temporary streams (Datry et al., 2014b; Messager et al., 2021). I assessed the effect of co-occurring stream drying and agricultural pressure on macroinvertebrate assemblage variability. I detected no effect of agriculture on taxonomic and functional variability among temporary reaches, whereas variability in perennial reaches was higher at high AgriCat, supporting H1 and suggesting that adaptations to drying among temporary stream assemblages may promote co-tolerance of agriculture (Storey, 2016; Loskotová et al., 2023). Taxonomic and functional variability were higher in temporary reaches relative to perennial reaches regardless of agriculture, contrary to H2. The consistently higher variability among temporary stream assemblages suggests that drying may be a bigger influence over aquatic assemblages than agriculture (Matthaei et al., 2010; Leigh & Datry, 2017). The occurrence of temporary stream specialist species was unaffected by agriculture, supporting H3 and highlighting that, beyond one core requirement, such specialists may actually be generalists (Errochdi et al., 2014) capable of surviving in a wide range of natural to impacted habitats (e.g. Chalkley, 2006; Salmela, 2013; Tapia et al., 2018).

3.4.1 H1. Assemblage responses to agriculture in temporary and perennial reaches

Temporary reach assemblages were comparably variable regardless of agriculture, supporting H1 and possibly reflecting the hypothesised adaptations to drying that promote survival of other pressures (e.g. agriculture: Storey, 2016; Loskotová et al., 2023). For example, both drying and agriculture can result in low dissolved oxygen concentrations (Gómez et al., 2017; dos Reis Oliveira et al., 2019), and thus taxa that tolerate low dissolved oxygen (e.g. *Simulium aureum* group: Lock et al., 2014) survive in temporary streams (Armitage & Bass, 2013; Straka et al., 2019), streams impacted by agricultural pollution (e.g. nutrient enrichment: Kazanci & Başören, 2010; Basoren & Kazanci, 2012) and streams exposed to both pressures (e.g. Başören & Kazanci, 2016). In contrast to temporary reaches, perennial reach assemblages were less tolerant of agriculture, with high AgriCat reaches typically being filtered to fewer taxa (*sensu* Durance & Ormerod, 2007) that tolerate site-specific agricultural impacts. Thus, assemblages at each site were likely filtered to the specific set of agricultural stressors they were exposed to, with each site having a different combination of stressors, resulting in higher inter-site variability among high than low AgriCat perennial reaches (Genito et al., 2002).

Like taxonomic variability, functional variability in temporary reaches was comparable regardless of agriculture. This functional co-tolerance of drying and agriculture may arise because the semi-predictable seasonal flow patterns of the study streams (see Berrie, 1992) promote functional redundancy (Boersma et al., 2014; Vander Vorste et al., 2016) and because drying likely promotes co-tolerance of agriculture (Storey, 2016). Thus, despite experiencing drying pressure, temporary stream assemblages may draw on redundant co-tolerances to maintain a comparable state of variability when additional pressures (e.g. agriculture) are applied.

Functional composition in perennial reaches was comparable between AgriCats suggesting that, like temporary reaches, perennial reaches also have functionally redundancies. However, the relatively higher taxonomic variability among assemblages at high than low AgriCat perennial reaches suggests they tolerate less agricultural pressure, potentially because, unlike temporary reach assemblages, they are not exposed to an overarching pressure that promotes co-tolerance. These streams experience multiple pressures, some of which are intensifying (e.g. abstraction, wastewater discharge, climate change: Palmer-Felgate et al., 2008; Watts et al., 2015; White et al., 2018). The cumulative effect of these intensifying pressures may result in increased taxonomic variability and a loss of functions from perennial sites, with potential consequences throughout the river network. Although currently taxonomically and functionally stable, temporary reach assemblages may rely on nearby perennial reaches for colonists (Datry et al., 2014a). Thus, a change in the number and identity of colonists from perennial reaches may influence both the composition and compositional variability of temporary reaches.

3.4.2 H2. Agriculture as a driver of assemblage differences between temporary and perennial reaches

Temporary reaches were more taxonomically and functionally variable than perennial reaches regardless of agriculture, contrary to H2. The consistently higher variability among temporary reaches possibly reflects that different drying durations (i.e. 2–34 months) and likely differing drying intensities filtered communities to site-specific assemblages that can tolerate site-specific hydrological conditions (Wilding et al., 2018; Sarremejane et al., 2019; Arias-Real et al., 2022). This filtering resulted in lower richness but higher inter-site variability in temporary than perennial reaches. Although more variable than perennial reaches, potentially because of site-specific drying/flow conditions, temporary reach assemblages all shared a co-tolerance of agriculture (see H1). Thus, the effects of drying were observed regardless of agriculture, suggesting that drying is a core driver of assemblages variability (Matthaei et al., 2010; Leigh & Datry, 2017). Despite drying likely being the main driver of the assemblage, perennial reaches were more variable at high relative to low AgriCat (see H1), and thus differences in variability between temporary and perennial reaches were less pronounced at high AgriCat, similar to the influence of high AgriCat hypothesised in H2. Again, this likely reflects the lower richness of high AgriCat relative to low AgriCat perennial reaches (Genito et al., 2002; Hepp et al., 2010), with site-specific agricultural impacts filtering assemblages to site-specific assemblages and thus increasing inter-site variability at high AgriCat. Differences in functional variability between temporary and perennial reaches were comparable regardless of AgriCat, further supporting that agricultural pressure is secondary relative to drying effects.

3.4.3 H3. Agriculture as a driver of the occurrence of temporary stream specialists

Paraleptophlebia werneri, *Simulium latipes* and *Nemoura cinerea* occurred more often in high AgriCat reaches, suggesting that their adaptations to drying may allow them to tolerate agriculture, similar to responses by the wider temporary stream assemblage (Storey, 2016; Loskotová et al., 2023). This potential co-tolerance is further supported by the other four taxa that were almost exclusive to temporary streams, all of which occurred more frequently in high AgriCat reaches, two of which (*P. personatum* and *S. aureum* group) were significantly associated with high AgriCat. However, agriculture was not a significant driver of the occurrence of temporary stream specialists, supporting H3. Temporary stream specialists such as *N. lacustris* and *P. werneri* occur in habitats ranging from springs (Biondi et al., 2022) to temporary streams (Tapia et al., 2018; Bunting et al., 2021), perennial ponds (Salmela, 2013) and agricultural ditches (Chalkley, 2006). Thus, beyond their core requirement of drying, temporary stream specialists may be generalists (Errochdi et al., 2014), that tolerate a broad spectrum of physicochemical conditions (similar to Baetidae, which can survive in a wide range of habitats if their hydrological requirements are met: Sarremejane et al., 2019).

For aquatic macroinvertebrates, drying equates to increasingly harsh physicochemical conditions, increased competition for space and resources and increased risk of predation (Stubbington et al., 2011; Gómez et al., 2017; von Schiller et al., 2017). Thus, drying can leave many kilometres of a river network uninhabitable for species that cannot tolerate such conditions. This exclusion of drying-sensitive species may promote the survival of temporary stream specialists by isolating them from competition (House & Tapia, 2014; Aspin & House, 2022). By this mechanism, temporary stream specialists may prefer minimally impacted (e.g. remote temporary chalk springs: Biondi et al., 2022) or even perennial (Prenda & Gallardo-Mayenco, 1999) streams, but are excluded from such reaches by competition. Thus, despite potential exclusion from their preferred habitats by competitors, adaptations to drying may make temporary stream specialists co-tolerant of other pressures, promoting their survival in numerous aquatic habitats (e.g. Chalkley, 2006; Salmela, 2013; Tapia et al., 2018) with a range of temperature, sediment and nutrient conditions (e.g. Prenda & Gallardo-Mayenco, 1999; Errochdi et al., 2014; Vilenica et al., 2021).

3.4.4 Implications for monitoring and further study

Pressures influencing an ecosystem are often hierarchical, with a dominant pressure overriding most or all of the influence of a subordinate pressure (*sensu* Côté et al., 2016). For example, stream size and physicochemical condition are often dominant, dampening the effects of climate change (Durance & Ormerod, 2007), anthropogenic land uses (Villeneuve et al., 2018), physical restoration and management (Greenwood et al., 2012; Omoniyi et al., 2022). My results suggest drying ranks higher than (i.e. is dominant over) agriculture in this pressure hierarchy, and may limit the effectiveness of temporary stream monitoring (e.g. using BMWP-style indices: Buffagni et al., 2009; Wilding et al., 2018; Stubbington et al., 2022c) and management (Acuña et al., 2017) when using techniques developed for perennial streams. Conceptually, complex multi-level hierarchies may govern assemblage dynamics throughout the river network, and thus the effectiveness of monitoring and management that aims to detect and mitigate the effects of all subordinate pressures. Therefore, characterisation of the hierarchy of pressures influencing aquatic assemblages may enable more effective monitoring and management throughout the river network.

Higher-level pressures that are dominant (Côté et al., 2016) may promote tolerance of subordinate pressures, with assemblages adapted to drying potenitally being better equipped to tolerate agriculture (Storey, 2016; Loskotová et al., 2023). However, the assemblage's capacity for co-tolerance in the face of novel and intensifying pressures (e.g. climate change: Sarremejane et al., 2021) remains unclear. A greater understanding of how emerging pressures will alter the pressure hierarchy and thus influence aquatic assemblages is required to secure the future of river network ecosystems in a period of unprecedented environmental change (Stubbington et al., 2022c).

Recent research has highlighted that temporary stream specialists are widespread, both geographically and in terms of the habitats they exploit (e.g.

Bogan et al., 2017; Gething et al., 2021). Here, the co-tolerance of agriculture by species including *N. lacustris* and *P. werneri* challenges their grouping with congeners (i.e. within Nemouridae and Leptophlebiidae) that have higher dissolved oxygen requirements, and which are less tolerant of agriculture and other human pressures. These findings highlight how little is known about the distribution and habitat preferences of temporary stream specialists, and further research is needed to determine whether the theory that they are generalists holds water… or dries like a temporary stream.

4 Ditching misconceptions: the role of artificial habitats in supporting aquatic temporary stream assemblages

4.1 Introduction

Temporary streams, those which dry, are the globe's dominant lotic ecosystems (Datry et al., 2014b; Messager et al., 2021). Flowing phase assemblages in temporary streams often contain fewer species than those in perennial streams (Datry et al., 2014a; Soria et al., 2017), but can include specialist drying-tolerant insects of conservation interest (e.g. the Nationally Scarce mayfly, *Paraleptophlebia werneri*: Macadam et al., 2021). Adaptation to conditions in temporary streams, such as a tolerance of low dissolved oxygen, may promote co-tolerance of human pressures (e.g. agriculture) among species in temporary stream assemblages, in particular drying-tolerant specialists (see **Under pressure: aquatic macroinvertebrate responses to agriculture in temporary streams**). However, competition for resources with and predation by common generalist species may be more influential than adaptations to temporary flow permanence regimes in driving the distribution of drying-tolerant specialists (Aspin & House, 2022). Thus, the availability of, and the amount of competition in temporary habitats may be key determinants of temporary stream assemblage composition and the survival of their specialist species.

Temporary streams often occur in catchments dominated by agricultural land uses (e.g. Gerth et al., 2017; White et al., 2018), which threaten the health of all riverine ecosystems (Mateo-Sagasta et al., 2017; Reid et al., 2019), including temporary streams (Botwe et al., 2015; Gerth et al., 2017). Nonetheless, agricultural catchments can support aquatic assemblages by also providing habitats in artificial waterbodies (Davies et al., 2008a). For example, ditches are linear artificial channels designed for irrigation or land drainage, can have perennial or temporary flow (Williams et al., 2004; Shaw et al., 2015), and often form extensive networks in agricultural catchments (Langheinrich et al., 2004; Davies et al., 2008a; Hill et al., 2016), considerably extending the habitat area available for aquatic assemblages (Herzon & Helenius, 2008).

Ditches increase the environmental diversity of waterbodies in a catchment (Armitage et al., 2003), often promoting differences in assemblage composition between ditches and other freshwater ecosystems (e.g. nearby streams), increasing biodiversity at catchment-to-landscape scales (Williams et al., 2004; Gething, 2021). Ditch assemblages are diverse, often containing a comparable number of taxa to rivers and streams (Verdonschot, 1990; Kavanagh & Harrison, 2014; Gething & Little, 2020). In addition, these assemblages may also include unique, rare or specialist species (Painter, 1999; Watson & Ormerod, 2004; Williams et al., 2004; Rolke et al., 2018), such as *P. werneri* (Chalkley, 2006), allowing ditches to contribute disproportionately to landscape-scale biodiversity. Thus, the habitat area and environmental diversity in agricultural catchments may increase resilience (i.e. capacity for recovery: Gladstone-Gallagher et al., 2019) to disturbance, such as drying or pollution (e.g. Robinson et al., 2023), by increasing the number and proximity of potential colonists (Pelletier et al., 2020). As such, ditches and other artificial waterbodies may promote resilience of assemblages in catchments with naturally low drainage densities (e.g. the chalk downland of southern England: Berrie, 1992), where they may act as 'stepping stones' which maintain metapopulations (i.e. populations linked by dispersal: Gilpin & Hanski, 1991; Leibold et al., 2004) in the landscape.

I assessed the role of ditches in supporting the biodiversity of catchments with perennial and temporary streams, in particular their specialist, drying-tolerant species. I hypothesised that ditches with temporary and perennial flow permanence regimes make distinct contributions to landscape-scale biodiversity (H1). Because ditches typically support populations of rare, specialist species (Painter, 1999; Watson & Ormerod, 2004; Williams et al., 2004; Rolke et al., 2018), I also hypothesised that the abundance of drying-tolerant specialists in a catchment's ditches positively correlates with the abundance of such specialists in the catchment's stream (H2). Finally, because networks of streams and ditches with different flow permanence regimes may contain differing habitat conditions (Armitage et al., 2003) which in turn influence their assemblages (Gething, 2021), I hypothesised that the level of competition and predation negatively correlates with the abundance of drying-tolerant specialists (H3).

4.2 Methods

4.2.1 Data collection

Study area and sampling sites

This study was conducted in the catchments of the Rivers Ems, Itchen, Lavant and Test, in Hampshire and West Sussex, southern England between March and June 2021. The region has a temperate oceanic climate (Cfb: Kottek et al., 2006), with a mean annual rainfall of 754 mm (Met Office, 2022) and mean (± SD) annual minimum and maximum air temperatures of 6.1 ± 3.9°C and 15.0 ± 5.7°C, respectively. The 4 catchments all had primary land uses of arable agriculture (37–50%) and grassland (mostly pastoral agriculture: 26–32%), with few urban areas (2–4%: National River Flow Archive, 2023a, 2023b, 2023c, 2023d). The study area is underlain by a chalk aquifer which experiences seasonal fluctuations in water levels, resulting in surface streams with both temporary and perennial flow (Sear et al., 1999). Stream flow in these groundwater-fed systems is relatively stable, being mostly unaffected by short-term precipitation inputs (Sear et al., 1999).

I identified 10 sub-catchments within the study area in consultation with local environmental managers. For this study, I defined streams as the longest watercourse on a natural flowpath within a sub-catchment, as opposed to ditches, which were channels engineered for surface water drainage along non-natural flowpaths. Following Murray-Bligh & Griffiths (2022), I defined sites as a 10 m length of a channel which represented the range of habitats present in the wider reach. I manually searched aerial images (Google, 2021) of the sub-catchments for candidate sampling sites where streams and ditches were publicly accessible (i.e. next to roads or other public rights of way), because logistic constraints prevented consideration of sites on private land. To ensure a degree of hydromorphological comparability, upon visiting each candidate sampling site I only included streams and ditches that were <4 m wide, <1 m deep and flowing during March 2021. My hypotheses focus on ditches and, therefore, I maximised the number of ditches sampled and, because there are fewer streams than ditches in the study area, selected multiple sites on streams in an attempt to balance their sample sizes for later analyses. In total, I sampled 21 sites on 9 streams and 22 sites on 22 ditches (**Table 4.1**).

Table 4.1: The number of sites and samples collected from streams and ditches per catchment.

Sub-catchment	Stream sites	Stream samples	Ditch sites	Ditch samples
Bourne Rivulet	6	16	2	5
Candover Brook	5	14	0	0
Pillhill Brook	1	3	1	1
River Anton	1	3	1	1
River Arle	1	3	3	7
River Dever	1	3	2	4
River Ems	2	5	2	3
Lower Itchen	0	0	4	8
River Lavant	2	4	3	4
Wallop Brook	2	6	4	10
Total	21	57	22	43

Streams were predominantly groundwater-fed with gravel substrates, and ranged in form from heavily modified to semi-natural (**Figure 12.1**). Ditches received a mixture of groundwater and surface runoff, and ranged in morphology from trapezoidal roadside channels with silty substrates to wider, gravel-filled channels that resembled the study's semi-natural streams (**Figure 12.2**). All except two sub-catchments contained both channel types (**Table 4.1**). Having located no ditches from aerial images of the Candover Brook sub-catchment, I conducted further searches by asking landowners and local people, and by driving the length of the sub-catchment, but found no ditches. Ditches were sampled in the Lower Itchen sub-catchment, but the River Itchen is >10 m wide and thus was not sampled. Based on observations by environmental managers, citizen scientists and landowners, 32 (streams: 17, ditches: 15) sampling sites had temporary flow permanence regimes, with 8 (streams: 3, ditches: 5) being perennial and 3 (streams: 1, ditches: 2) being unknown. Of the 22 ditches sampled, 18 were connected to the catchment's stream by surface water.

Study design and sampling methods

To incorporate seasonal variability in assemblage composition and ensure the capture of identifiable, late-instar drying-tolerant specialist insects, I visited all 43 sampling sites on 3 occasions (i.e. 28th–31st March, 4th–6th May and 1st–4th June). During the first sampling visit at each site, and during the second and third visits where surface water remained, I recorded three physicochemical variables: pH, conductivity (μS/cm) and water temperature (°C). I collected 100 macroinvertebrate samples (March: 43, May: 29, June: 28), with fewer samples being collected during later visits because sites were dry. In total, temporary, perennial and unknown flow permanence regimes were represented by 68, 20 and 11 samples (**Table 4.1**), respectively. Macroinvertebrates were sampled using a one-minute kick methodology (adapted from Murray-Bligh & Griffiths, 2022), with one minute being sufficient to characterise assemblages in small streams (Rutt et al., 1990; Upland Waters Monitoring Network, 2023). In the laboratory, I identified all aquatic macroinvertebrate taxa, predominantly to species or species aggregate level, except true flies (Diptera) and worms (Oligochaeta) which were not further identified, and were not included in the following analyses.

4.2.2 Data preparation and analysis

Data preparation

To minimise the influence of macroinvertebrate identification to multiple taxonomic levels (e.g. to *Agapetus fuscipes*, *Agapetus* and Glossosomatidae) on analyses, I assigned taxa to a most likely taxon (Cuffney et al., 2007), with 96%, 1%, 3% and <1% of individuals assigned to species, genus, family and order, respectively. During data exploration, I excluded a temporary ditch sample from the Pillhill Brook sub-catchment which contained a single beetle (Coleoptera) specimen, because it had a disproportionately large influence on the results.

H1. The contribution of ditches to landscape-scale biodiversity

To assess the contributions of ditches with temporary and perennial flow permanence regimes to landscape-scale biodiversity (H1) I considered 3 elements: (1) the number of taxa with an affinity for; (2) the number of taxa present in; and (3) local contributions to beta diversity (LCBD, i.e. the relative uniqueness of a sampled assemblage: Legendre & De Cáceres, 2013) by ditches with a temporary or perennial flow permanence regime.

To identify taxa with an affinity for ditches with temporary or perennial flow permanence regimes, I used the R package labdsv (Roberts, 2019) to run indicator species analysis (IndVal: Dufrêne & Legendre, 1997) over 999 permutations. IndVal considers each taxon’s specificity (i.e. the proportion of samples within a particular grouping that contain the taxon) and fidelity (i.e. the proportion of a taxon's total abundance which occurs in a particular grouping) to calculate an indicator value representing a taxon's affinity with a grouping (e.g. perennial ditches), where an indicator value of 0 indicates no affinity and 1 indicates that every sample of a grouping contains the taxon, and the taxon does not occur in any other grouping (Dufrêne & Legendre, 1997).

To determine whether the number of taxa present differed among streams and ditches with temporary and perennial flow permanence regimes, I used a linear mixed-effect model (LMM) built using the lme4 package (Bates et al., 2015). I calculated taxa richness (the number of taxa per sample, n = 99 samples) using the vegan package (Oksanen et al., 2019). To meet the LMM assumption of residual normality, I used log+1 transformed richness as the response variable. I used waterbody type (categorical: stream or ditch), flow permanence regime (categorical: temporary, perennial or unknown) and their interaction as predictors of taxa richness. During preliminary analysis, I accounted for the non-independence of repeat samples collected during March, May and June by using sampling visit (categorical: first, second or third) as a random intercept. However, this inclusion resulted in a singular fit warning (indicating that the random intercept was not explaining any variance), so I removed the random intercept to improve model parsimony for the final analysis. To determine the variance in richness explained by waterbody type, flow permanence regime and their interaction, I partitioned the R^2 to quantify the variance explained by each predictor using variancePartition (Hoffman & Schadt, 2016).

To assess LCBD by ditches with temporary and perennial flow permanence regimes, I used a taxa-by-sample matrix to generate a Sørensen distance matrix from which I calculated LCBD per sample using the adespatial package (Dray et al., 2023). I then replicated the LMM outlined above for taxa richness, but used LCBD as the response variable. To interpret whether a lack of differences in LCBD between waterbody types and flow permanence regimes reflected a comparable composition, or a different composition with comparable contributions to LCBD, I tested for differences in composition (represented by the Sørensen distance matrix) between waterbody type, flow permanence regime and their interaction using permutational analysis of variance (PERMANOVA: Anderson, 2017). Each PERMANOVA was run over 999 permutations with a permutation scheme restricted by sampling visit. To identify taxa that contributed to differences in composition among waterbody types and flow permanence regimes, I used similarity percentage analysis (SIMPER: Clarke, 1993) over 9,999 permutations. I considered a taxon as driving differences if SIMPER P <0.05 and contributions to overall differences were ≥5%. To visualise assemblage composition, I used three-dimensional non-metric multidimensional scaling (NMDS) ordinations based on Sørensen distance matrices over 500 iterations.

To support my interpretation of H1, I used pH, conductivity and water temperature data to generate a Euclidean distance matrix summarising physicochemical conditions during sample collection. I tested for differences in physicochemical composition (represented by the Euclidean distance matrix) between waterbody type, flow permanence regime and their interaction using permutational analysis of variance (PERMANOVA: Anderson, 2017). Each PERMANOVA was run over 999 permutations with a permutation scheme restricted by sampling visit.

H2. The role of ditches in supporting drying-tolerant specialists in streams

To test whether the abundance of drying-tolerant specialists in a sub-catchment's ditches positively correlates with the abundance of such specialists in the sub-catchment's stream (H2), I used LMMs. I identified two drying-tolerant specialists in the dataset, the Nationally Scarce mayfly *P. werneri* (in 17 samples, 1,007 individuals) and the Nationally Rare stonefly *Nemoura lacustris* (in 23 samples, 1,861 individuals: Macadam et al., 2021). During preliminary analyses, models attempting to correlate abundance of drying-tolerant specialists in streams and ditches failed assumptions of residual normality and homogeneity of variance. Therefore, I tested whether the abundance of drying-tolerant specialists in streams is higher in sub-catchments where drying-tolerant specialists also occur in ditches. During preliminary analyses for my abundances vs occurrence model, LMMs using common methods, such as a log+1 transformed response variable or a Poisson error distribution (e.g. Garrido et al., 2019; Alvarado-Montero et al., 2021) were overdispersed (i.e. a model assumption was violated). Therefore, I used negative binomial generalised LMMs (NB-GLMMs), which can model overdispersed count data (Hilbe, 2011). To build NB-GLMMs, I first extracted stream samples from the dataset (n = 57) and used the abundance of one of the two drying-tolerant specialists from those samples as the response variable. For each stream sample, I then determined whether *N. lacustris* or *P. werneri* also occurred in a ditch sample from the same sub-catchment and sampling visit, and used this occurrence as a predictor of specialist abundance in streams.

H3. The role of competitors and predators in driving the abundance of drying-tolerant specialists

Nemoura lacustris and *P. werneri* eat detritus and dead plant material ≤1 mm, and living microphytes (Tachet et al., 2010; Schmidt-Kloiber & Hering, 2015). I considered taxa that eat living macroinvertebrates as potential predators of *N. lacustris* and *P. werneri*. Food preferences are mostly classified to genus (Tachet et al., 2010; Schmidt-Kloiber & Hering, 2015) and thus, to identify taxa that may be predators of or competitors for food with *N. lacustris* and *P. werneri*, I used the genus-level food preferences for all taxa identified to genus or species. For taxa identified to family, I used the averaged food preferences for all members of the family. I used the biomonitoR package (Laini et al., 2022) to extract taxa that (1) may be predators/competitors of *N. lacustris* and *P. werneri* and (2) occurred in ≥25 samples, 25 being the minimum number of occurrences needed to define a relationship (Jenkins & Quintana-Ascencio, 2020). In total, 12 taxa that occurred in ≥25 samples and had food preferences that overlapped with those of or may have allowed predation of *N. lacustris* and *P. werneri* (see **Table 12.1**).

To summarise the overall level of competition and predation pressure potentially felt by *N. lacustris* or *P. werneri*, I first multiplied the abundance of each of the 12 taxa by their affinity for each food source. I summed values for all taxa per food source, representing an estimation of the potential competition for detritus, dead plant material, living microphytes and living macroinvertebrates per sample. Because competition with *N. lacustris* and *P. werneri* may have occurred across 3 food sources, I summed values for detritus, dead plant material and living microphytes into an overall potential competition score. Theoretically, predation and competition scores range between 0 and 34,749, with the maximum being equal to the abundance of the 12 identified taxa. For example, if all 12 taxa (represented by 34,749 individuals) fed exclusively on living macroinvertebrates (i.e. an affinity of 1), the overall predation score = 34,749 × 1 = 34,749. The theoretical maximum of the overall competition score is also 34,749 because, although there are 3 contributing food sources, a taxon's affinity for any combination of those 3 food sources cannot exceed 1.

To assess whether the potential level of competition and predation negatively correlates with the abundance of drying-tolerant specialists (H3), I used NB-GLMMs with the abundance of *N. lacustris* or *P. werneri* in all samples (n = 99) as a response, the overall amount of potential competition and predation as predictors and sampling visit as a random intercept. To quantify variability in the influence of individual competitor/predator taxa on *N. lacustris* and *P. werneri* abundance, I attempted to model the abundance-weighted affinities for competition and predation per taxon, but these models failed assumptions of residual normality, homogeneity of variance and absence of outliers. Therefore, I used the occurrence of the 12 taxa as predictors of *N.*

lacustris and *P. werneri* abundance, with sampling visit as a random intercept.

To aid interpretation of H3, I tested whether streams and ditches with perennial and temporary flow permanence regimes contained a comparable abundance of potential competitors/predators. I replicated the LMM testing for differences in richness between waterbody types and flow permanence regime used in H1, but used the overall competition and predation scored for *N. lacustris* and *P. werneri* as response variables.

I conducted all analyses in R v.4.0.3 (R Core Team, 2020). All LMM assumptions were verified using the DHARMa package (Hartig, 2020).

4.3 Results

I recorded 122 taxa represented by 45,194 individuals, with the most common taxa being the amphipod *Gammarus fossarum/pulex* (20,886 individuals in 63 samples), the mayfly *Serratella ignita* (4,409 individuals, 45 samples) and the gastropod *Gyralus laevis* (1,941 individuals, 59 samples). Streams supported 90 taxa (74% of taxa, 36,408 individuals), of which 19,045 individuals (35 samples) were *G. fossarum/pulex*, 3,543 individuals (33 samples) were *S. ignita* and 1,699 individuals (23 samples) were *Nemoura lacustris*. In ditches, *Gammarus fossarum/pulex* (1,841 individuals, 28 samples), the amphipod *Niphargus* (1,056 individuals, 19 samples) and *S. ignita* (866 individuals, 12 samples) were the most common taxa, with ditches supporting 95 taxa (78%, 8,786 individuals).

Sites with perennial flow supported 91 taxa (75% of taxa, 15,358 individuals), whereas temporary sites supported 61 taxa (50%, 26,469 individuals) and sites with unknown flow permanence regimes supported 51 taxa (42%, 3,367 individuals). The most common taxa at perennial sites were *G. fossarum/pulex* (6,517 individuals, 20 samples), *S. ignita* (2,954 individuals, 14 samples) and the caddisfly *Agapetus fuscipes* (1,390 individuals, 12 samples). At temporary sites, the most common taxa were *G. fossarum/pulex* (13,918 individuals, 32 samples), *N. lacustris* (1,848 individuals, 28 samples) and *G. laevis* (1,618 individuals, 43 samples).

Perennial streams (n = 9 samples) supported 63 taxa (11,787 individuals total, mean ± SD: 1,310 ± 790 individuals per sample), temporary streams (n = 45 samples) supported 53 taxa (23,595 individuals total, 525 ± 710 individuals per sample), perennial ditches (n = 11 samples) supported 68 taxa (3,571 individuals total, 325 ± 238 individuals per sample) and temporary ditches (n = 22 samples) supported 38 taxa (2,873 individuals total, 131 ± 117 individuals per sample). *Gammarus fossarum/pulex* was the most common taxon in perennial streams (9 of 9 samples, 5,543 individuals), temporary streams (30 of 45 samples, 13,476 individuals) and perennial ditches (11 of 11samples, 974 individuals), with *Niphargus* (14 of 22 samples, 996 individuals) being the most common taxon in temporary ditches. *Serratella ignita* (9 of 9 samples, 2,484 individuals), *N. lacustris* (22 of 45, 1,692), the mayfly *Caenis pusilla/rivulorum* (4 of 11, 474) and *G. fossarum/pulex* (8 of 22, 442) were the second most common taxa in perennial streams, temporary streams, perennial ditches and temporary ditches, respectively.

4.3.1 H1. The contribution of ditches to landscape-scale biodiversity

Taxa affinity to streams and ditches with perennial or temporary flow permanence regimes

Ditches supported 32 taxa (26% of all recorded) that were not found in streams (**Table 12.2**) although these taxa occurred in few samples (mean ± SD: 1.8 ± 1.5 samples), and at low abundance (6.2 ± 11.3 individuals total). Beetles were the most diverse group, being represented by 11 taxa including the Nationally Scarce *Hydraena rufipes* (Foster, 2010). Odonates were exclusive to ditches (4 taxa, 59 individuals in 8 samples from 4 sites), including the IUCN Near Threatened southern damselfly, *Coenagrion mercuriale* (Boudot, 2020).

Five taxa were unique to ditches with temporary flow, whereas 19 taxa were exclusive to perennial ditches (**Table 12.2**).

IndVal identified 9 taxa with an affinity for ditches with a perennial flow permanence regime: the damselflies *Calopteryx splendens* (IndVal = 0.636, P = 0.001) and *C. mercuriale* (IndVal = 0.364, P = 0.002), the Nationally Rare caddisfly *Synagapetus dubitans* (IndVal = 0.241, P = 0.046: Wallace, 2016), the caddisflies *Limnephilus lunatus*, *Potamophylax latipennis* and *Sericostoma personatum* (IndVal = 0.375–416, P = 0.010–0.046), the mayfly *Ephemera danica* (IndVal = 0.625, P = 0.002), the alderfly *Sialis lutaria* (IndVal = 0.546, P = 0.005) and the snail *Physa fontinalis* (IndVal = 0.507, P = 0.006). One taxon, the amphipod *Niphargus* (IndVal = 0.491, P = 0.025) had an affinity for temporary ditches. One taxon had an affinity for temporary streams (*N. lacustris*, IndVal = 0.385, P = 0.033), with 17 taxa having an affinity for perennial streams (**Table 12.3**).

The richness and local contributions to beta diversity of stream and ditch assemblage

Richness did not differ between streams (mean ± SD: 11.9 ± 6.6 taxa per sample) and ditches (10.7 ± 7.1 taxa per sample, P = 0.173, model R^2 = 0.481, partitioned R^2 = 0.034, **Figure 4.1A**). Relative to sites with perennial flow permanence regimes (20.7 ± 6.4 taxa), richness was lower at sites with temporary (8.3 ± 3.7 taxa, Estimate ± SE = -1.077 ± 0.155 , P <0.001, model R^2 = 0.481, partitioned R^2 = 0.423) and unknown flow permanence regimes (12.8 ± 6.4 taxa, Estimate ± SE = -0.390 ± 0.188, P = 0.041, model R^2 = 0.481, partitioned R^2 = 0.423, **Figure 4.1A**). Richness was unaffected by interactions between waterbody type and flow permanence regime (P = 0.385–0.525, model R^2 = 0.481, partitioned R^2 = 0.024, **Figure 4.1A**), with perennial streams supporting 23.7 ± 6.8 taxa, perennial ditches supporting 18.2 ± 5.1 taxa, temporary streams supporting 9.5 ± 3.5 taxa and temporary ditches supporting 5.9 ± 3.1 taxa. LCBD did not differ between waterbody types, flow permanence regimes or their interaction ($P = 0.072$–0.833, $R^2 = 0.222$, **Figure 4.1B**).

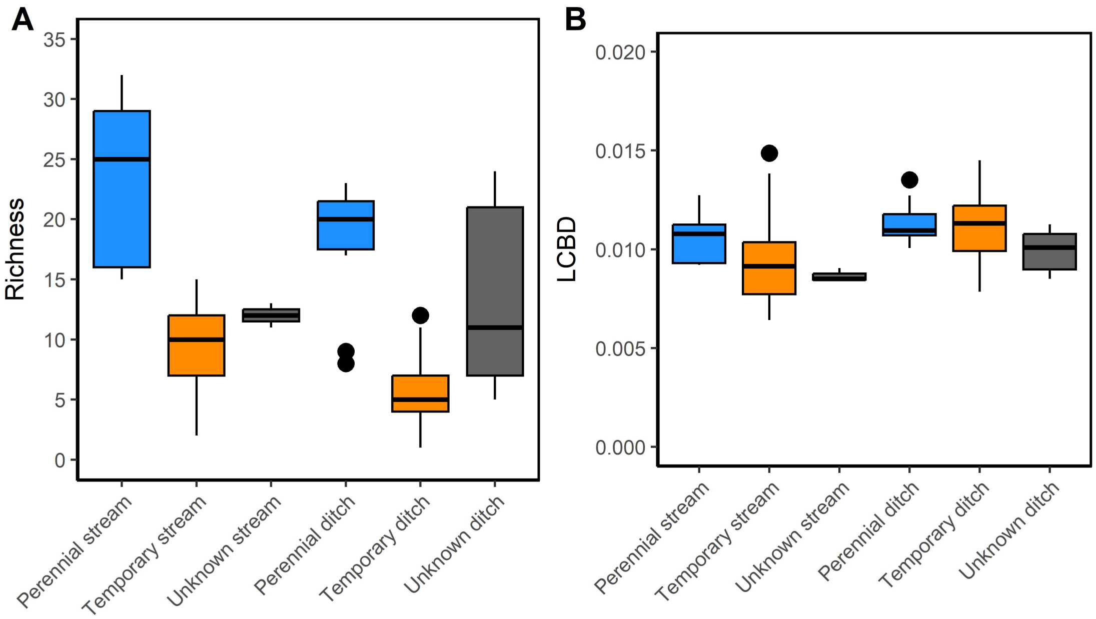


Figure 4.1: The richness (A) and local contributions to beta diversity (LCBD: B) of samples collected in streams and ditches and at sites with perennial, temporary and unknown flow permanence regimes. The centre line represents the median, boxes represent the interquartile range, whiskers represent the minimum/maximum values which are within 1.5× the interquartile range of the first and third quartiles and filled circles represent outliers.

Macroinvertebrate assemblages composition differed between streams and ditches (PERMANOVA: F(1) = 3.615, P = 0.001, R^2 = 0.030), among flow permanence regimes (F(2) = 9.411, P = 0.001, R^2 = 0.156) and between an interaction of waterbody type and flow permanence regime (F(2) = 2.536, P = 0.001, R^2 = 0.042, **Figure 4.2**). Composition differed between streams and ditches when considering only sites with temporary flow permanence regimes (F(1) = 2.823, P = 0.009, R^2 = 0.042) and only sites with perennial flow permanence regimes (F(1) = 4.975, P = 0.002, R^2 = 0.217), but the variance in composition explained by waterbody type (i.e. the R^2) was 5× higher in perennial than temporary sites. *Niphargus* drove differences in composition between temporary ditches and temporary streams (SIMPER: 11.3%, P = 0.008), and was more abundant in ditches (996 individuals, 14 of 22 samples) than streams (288 individuals, 29 of 45 samples). No other individual taxon drove differences in composition between any other combination of waterbody type and flow permanence regime (all SIMPER: <5% and/or P >0.05).

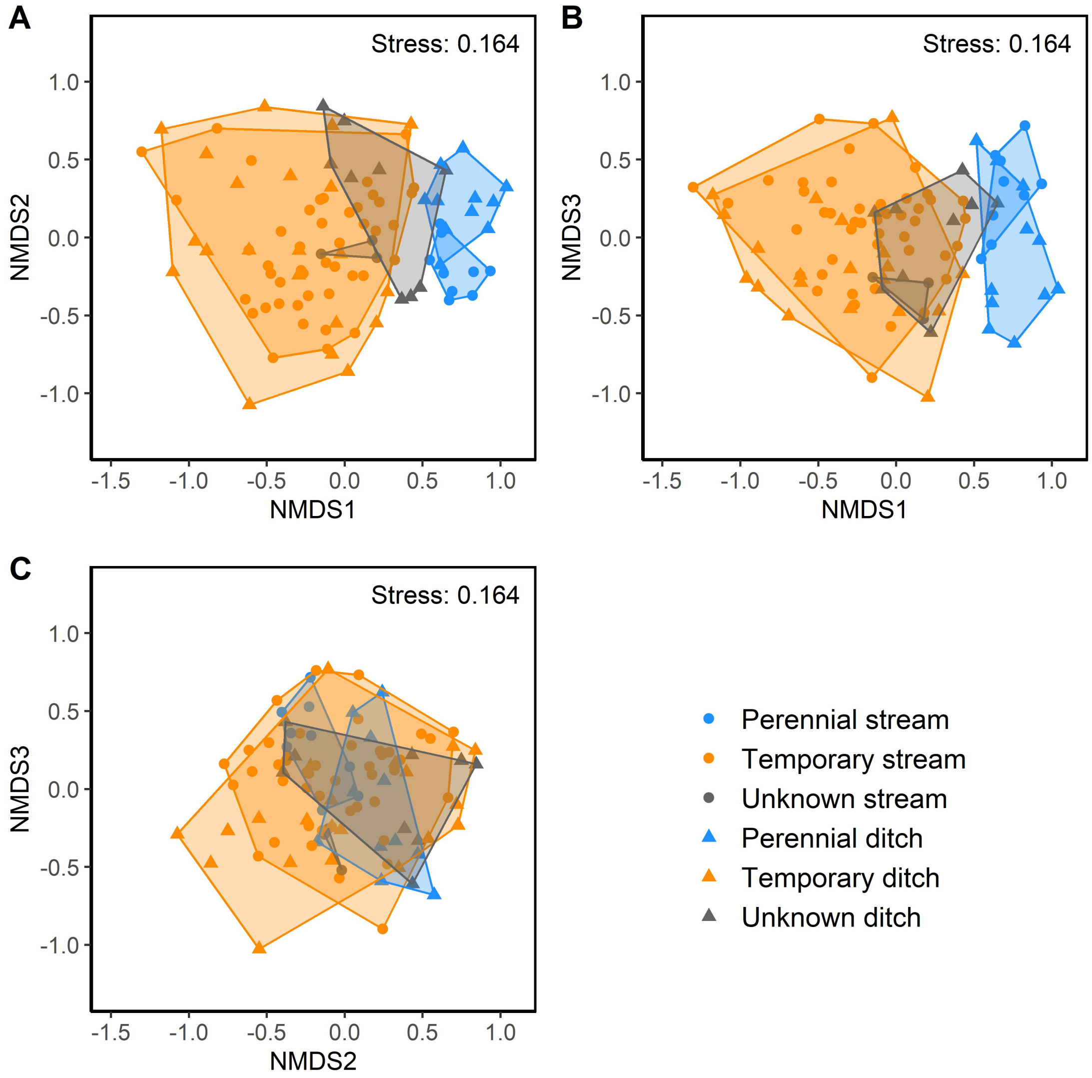


Figure 4.2: Non-metric multidimensional scaling axes 1 and 2 (A), 1 and 3 (B) and 2 and 3 (C) of macroinvertebrate assemblages in streams and ditches with perennial, temporary and unknown flow permanence regimes.

Physicochemical conditions (i.e. pH, conductivity and water temperature) did not vary between streams and ditches (PERMANOVA: F(1) = 0.352, P = 0.784, R^2 = 0.004), among flow permanence regimes (F(2) = 1.978, P = 0.123, R^2 = 0.040) or between an interaction of waterbody type and flow permanence regime (F(2) = 1.140, P = 0.271, R^2 = 0.023).

4.3.2 H2. The role of ditches in supporting drying-tolerant specialists in streams

Nemoura lacustris and *P. werneri* occurred in 23 and 17 of the 57 stream samples, respectively. The 57 stream samples had 16 and 19 corresponding ditch samples (i.e. ditch samples collected in the same sub-catchment and on the same sampling visit) that contained *N. lacustris* and *P. werneri*, respectively. In 1 sub-catchment (Wallop Brook, during the 1st and 2nd sampling visits), *N. lacustris* occurred in ditch samples, but not in stream samples. *Nemoura lacustris* abundance at stream sites where ditches in the same sub-catchment and sampling visit also supported *N. lacustris* was 50.7 ± 68.9 (mean ± SD) individuals, relative to 21.7 ± 72.3 individuals when *N. lacustris* was absent from ditches (**Figure 4.3A** and **C**). However, *N. lacustris* abundance in streams was not affected by the occurrence of *N. lacustris* in ditches (Estimate ± SE = 2.986 ± 1.766, P = 0.091, R^2M = 0.151, R^2C = 0.428), contrary to H2, in part reflecting the variability in *N. lacustris* abundance in both waterbody types (**Figure 4.3A**). *Paraleptophlebia werneri* abundance in streams was higher when ditch populations of *P. werneri* were present (Estimate ± SE = 3.907 ± 0.997, P <0.001, R^2M = 0.305, R^2C = 0.363, **Figure 4.3B**), with streams supporting 40.4 ± 46.2 individuals when ditch populations were present and 1.2 ± 6.7 individuals when ditch populations were absent (**Figure 4.3D**), supporting H2.

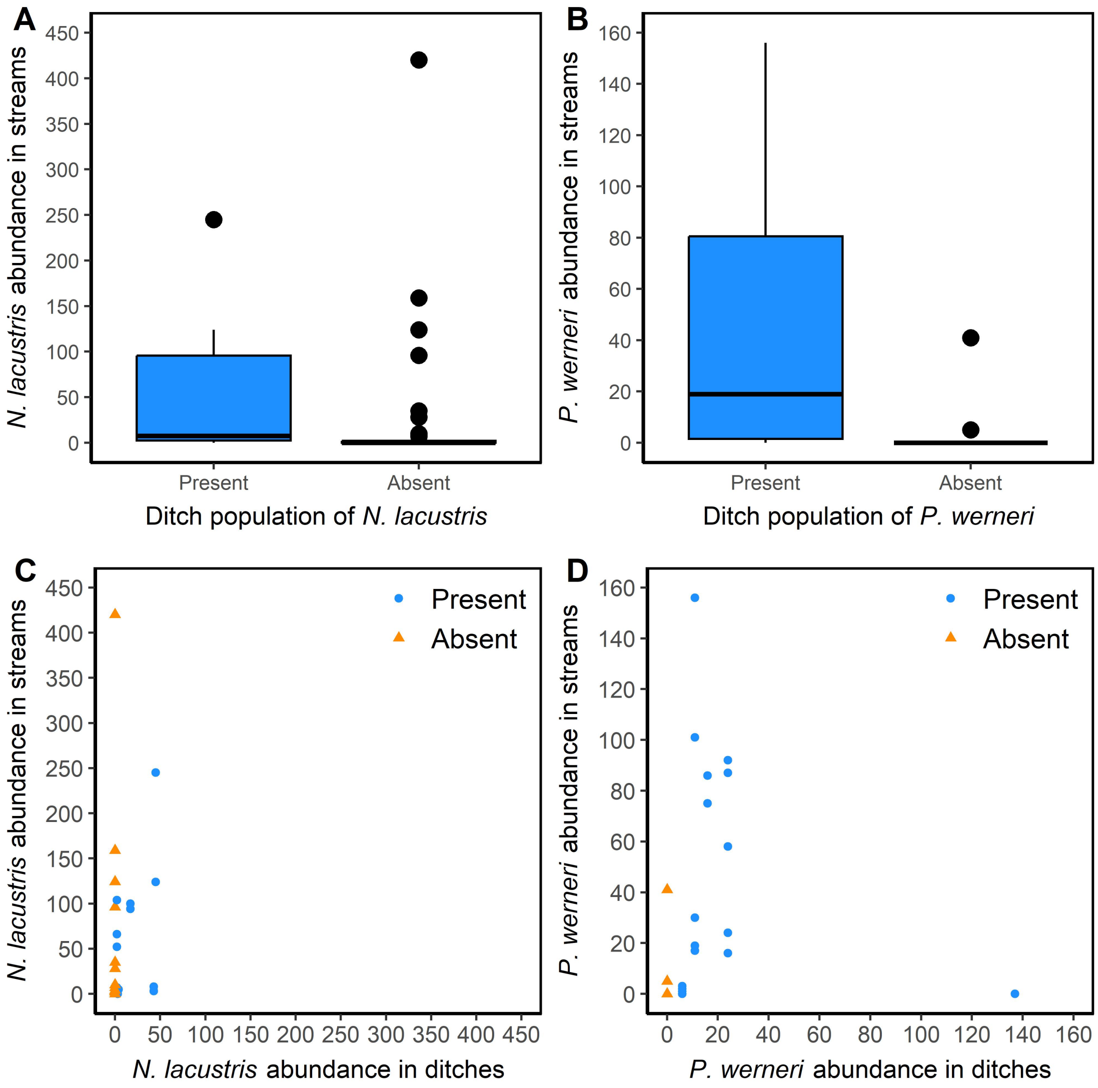


Figure 4.3: The abundance of *Nemoura lacustris* (A, C) and *Paraleptophlebia werneri* (B, D) in streams when a population of the same species is present/absent in ditches (A, B) and relative to the abundance of the same species in a sub-catchment's ditches (C, D).

4.3.3 H3. The role of competitors and predators in driving the abundance of drying-tolerant specialists

Nemoura lacustris occurred in 39 samples and *P. werneri* occurred in 36 samples, with the species co-occurred in 14 samples. *Nemoura lacustris* was typically represented by 18.8 ± 56.5 (mean ± SD) individuals per sample (range = 0–420 individuals), and *P. werneri* by 10.2 ± 28.7 individuals per sample (range = 0–156). Their 12 competitors/predators resulted in comparable overall levels of potential competition (*N. lacustris*: mean ± SD = 215 ± 350, range = 1–2,120, *P. werneri*: mean ± SD = 215 ± 340, range = 1–2,125) and predation (*N. lacustris*: mean ± SD = 20 ± 40, range = 0–240; *P. werneri*: mean ± SD = 25 ± 40, range = 0–240, **Figure 4.4**). *Nemoura lacustris* abundance only exceeded 50 individuals when abundance-weighted levels of competition and predation were <310 and <40, respectively, and was consistently absent when abundance-weighted levels of competition was >350 and predation was >41. However, *N. lacustris* abundance was not influenced by the potential level of competition (Estimate ± SE = <0.001 ± <0.001, P = 0.910: **Figure 4.4A**) or predation (Estimate ± SE = -0.038 ± 0.043, P = 0.367, R^2M = 0.103, R^2C = 0.313: **Figure 4.4B**). *Paraleptophlebia werneri* abundance only exceeded 50 individuals per sample when abundance-weighted competition was <200 and abundance-weighted predation was <30. *Paraleptophlebia werneri* was absent when competition and predation were >355 and >50, respectively. Abundance of *P. werneri* was not significantly affected by the level of competition (Estimate ± SE = -0.009 ± 0.007, P = 0.217: **Figure 4.4C**), or the level of predation (Estimate ± SE = 0.027 ± 0.061, P = 0.656, R^2M = 0.208, R^2C = 0.335: **Figure 4.4D**).

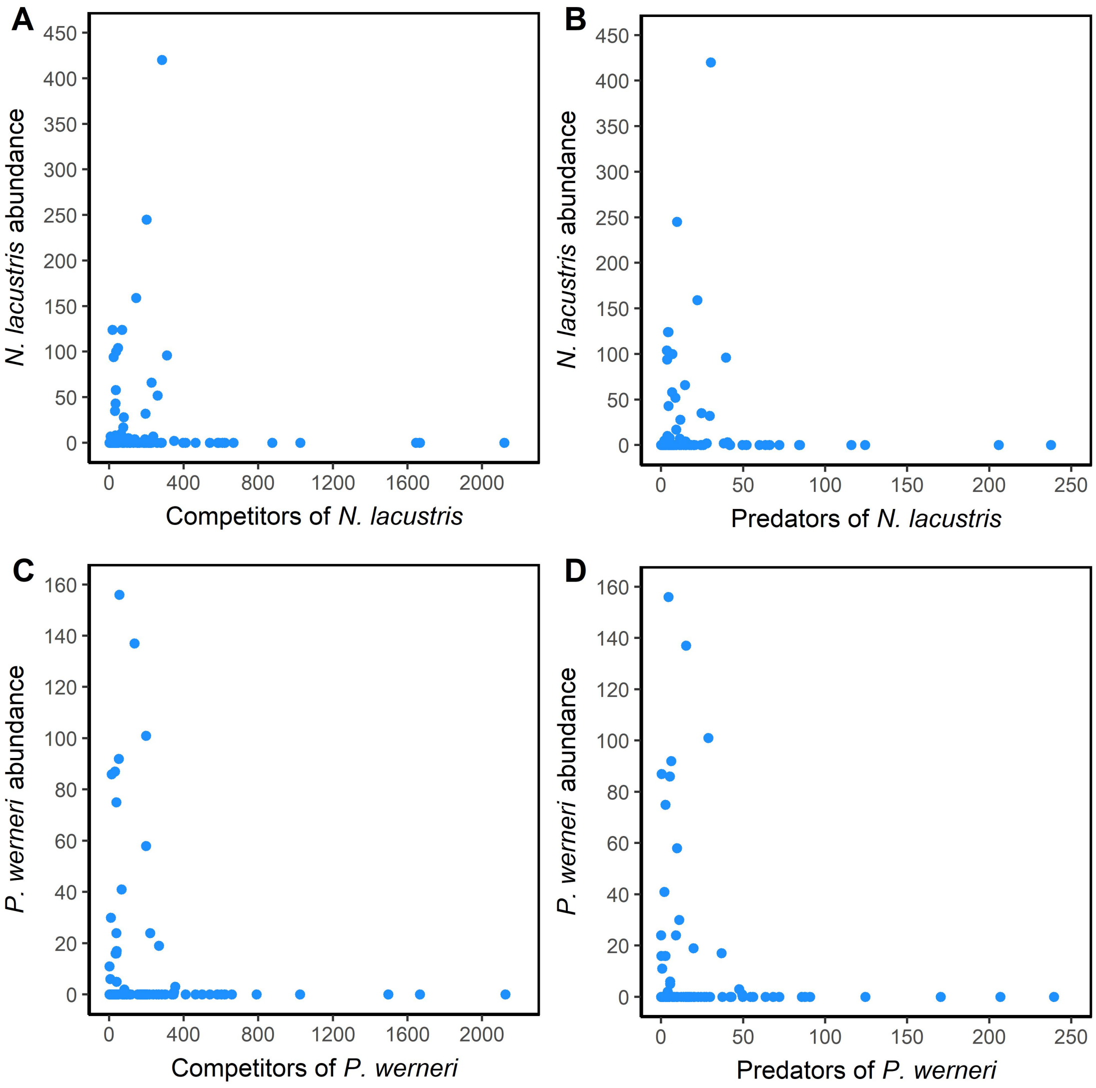


Figure 4.4: *Nemoura lacustris* (A, B) and *Paraleptophlebia werneri* (C, D) abundance relative to the sum of abundance-weighted affinities for food sources that make taxa competitors (A, C) with and predators (B, D) of *N. lacustris* and *P. werneri*.

Of the 12 competitive/predatory taxa, *G. fossarum/pulex* and the bivalve Sphaeriidae were negatively associated with *N. lacustris* (P = <0.001–0.003: **Figure 4.5A**) and *P. werneri* (P = <0.001–0.008: **Figure 4.5B**) abundance, supporting H3. Sphaeriidae were represented by 223 individuals (8 of 9 samples, mean ± SD = 27.9 ± 31.2 individuals per sample) in perennial streams, by 226 individuals (7 of 11 samples, mean ± SD = 32.0 ± 57.7 individuals per sample) in perennial ditches, by 102 individuals (8 of 45 samples, mean ± SD = 12.8 ± 18.1 individuals per sample) in temporary streams and by 9 individuals (5 of 22 samples, mean ± SD = 1.8 ± 0.8 individuals per sample) in temporary ditches. *Nemoura lacustris* and *P. werneri* abundance was higher in, or unaffected by, the presence of all other potential competitors and predators (P = <0.001–0.897: **Figure 4.5**), contrary to H3.

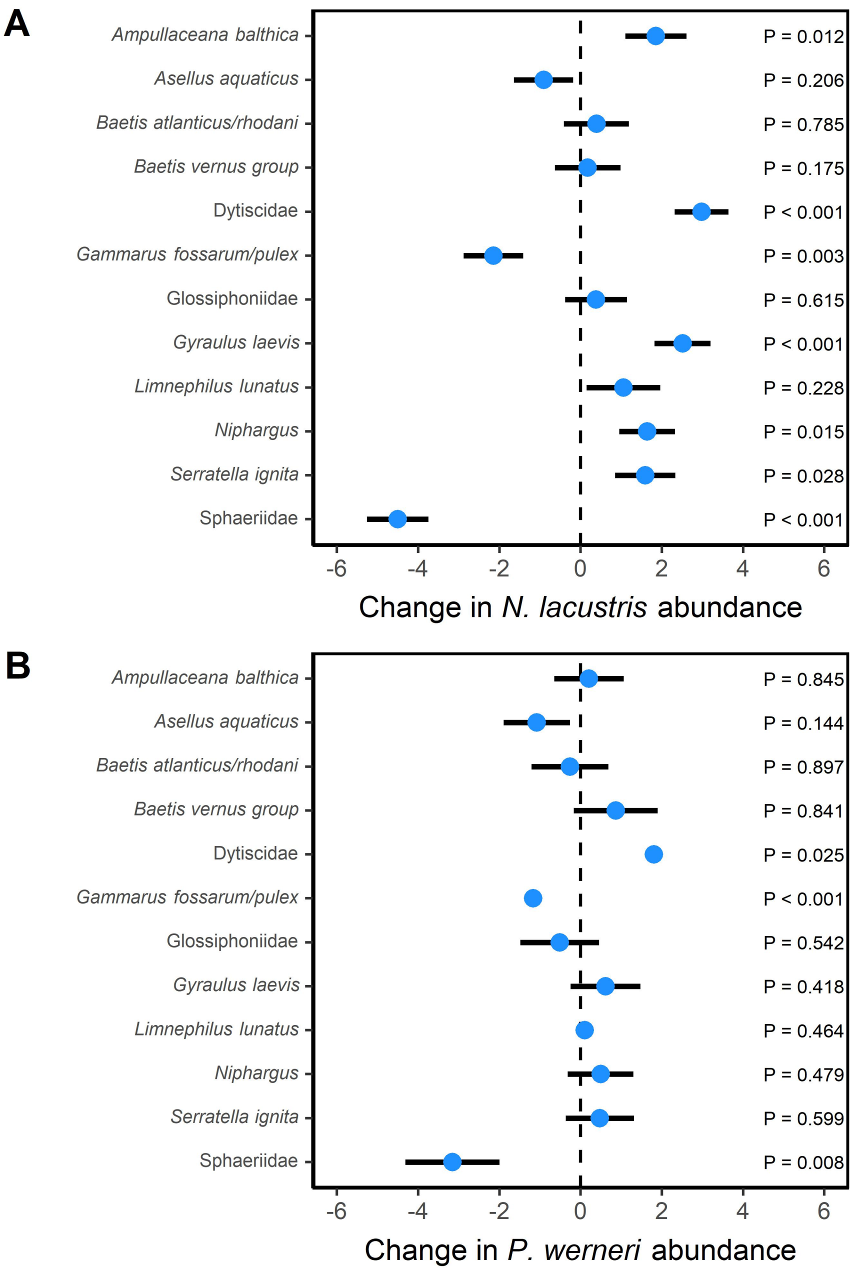


Figure 4.5: The change in *Nemoura lacustris* (A) and *Paraleptophlebia werneri* (B) abundance in the presence of their competitors and predators. The vertical dashed line represents zero (i.e. no change in abundance), the blue circles represent the estimated change in abundance and black horizontal lines represent the standard error around abundance change estimates. Estimates and standard error of changes in abundance are based on negative binomial linear mixed-effects model results, with significance (P values) provided on the right.

The overall potential competition and predation experienced by *N. lacustris* and *P. werneri* was higher in streams than ditches (Estimate ± SE = 1.553 ± 0.510–1.713 ± 0.596, P = 0.002–0.005, R^2 = 0.168–0.329). The competition experienced by *N. lacustris* (Estimate ± SE = -0.986 ± 0.490, P = 0.047, R^2 = 0.221) and predation experienced by *P. werneri* (Estimate ± SE = -1.327 ± 0.435, P = 0.003, R^2 = 0.329) was lower in temporary waterbodies. No interaction between waterbody type and flow permanence regime was a significant driver of the competition or predation experienced by either species (all P >0.05).

4.4 Discussion

Ditches are common in agricultural areas, but their role in supporting the biodiversity of catchments with perennial and temporary streams has not been quantified. I found that ditches with perennial and temporary flow permanence regimes make distinct contributions to landscape-scale biodiversity, mostly by contributing a comparable number of taxa but a different assemblage composition to that in streams, supporting H1. Ditches provide habitat for rare, drying-tolerant specialists, and the occurrence of *P. werneri* in ditches was positively associated with its abundance in streams, supporting H2. *Nemoura lacustris* and *P. werneri* were seemingly unaffected by overall levels of potential competition and predation, contrary to H3, but were negatively associated with individual competitive/predatory taxa that are common in perennial streams, supporting H3. Thus, the extended area and diversity of habitats and lower abundance of potential predators and competitors may allow ditches to contribute to increased landscape-scale biodiversity whilst supporting populations of rare, drying-tolerant specialist species. Collectively, networks of streams and ditches may have the potential to promote resilience to disturbance, such as drying, at sub-catchment to landscape-scales.

4.4.1 H1. The contribution of ditches to landscape-scale biodiversity

Ditches supported a similar number of taxa to streams with comparable flow permanence regimes. This comparability is common, having been reported between ditches and streams (Verdonschot, 1990; Kavanagh & Harrison, 2014), rivers (Gething & Little, 2020) and lakes (Verdonschot et al., 2011). However, some comparative studies report lower richness in ditches than streams (e.g. Williams et al., 2004). My results suggest this lower richness in ditches may be an artefact of the flow permanence regime, and not reflect a difference between waterbody types (also see Davies et al., 2008b). In particular, Williams et al. (2004) notes that ditches support drying-tolerant species, highlighting that their ditches likely had a temporary flow permanence regime. Thus, the lower richness in ditches observed by Williams et al. (2004) is consistent with the lower richness I observed in temporary ditches relative to perennial streams and perennial ditches. This influence of ditch flow permanence regime is also supported by correlations between richness and water depth (Shaw et al., 2015), with deeper ditches being less likely to dry out. Thus, ditches and streams are likely capable of supporting a comparable number of taxa when confounding factors, such as flow permanence regime, are accounted for.

Although supporting a comparable number of taxa, the composition of assemblages in streams and ditches differed, possibly because of environmental differences between the waterbody types (Armitage et al., 2003). The specific environmental variables that drive compositional differences are likely location-specific, with conductivity, water temperature and dissolved oxygen concentrations influencing composition in some studies (e.g. Gething, 2021), but not in others (e.g. Leslie et al., 2012; Rolke et al., 2018). Here, I detected no differences in pH, conductivity or water temperature between ditches and streams, suggesting other factors such as shading (Shaw et al., 2015), flow regime (Armitage et al., 2003) or physical habitat structure (i.e. sediment and vegetation composition: Armitage et al., 2003; Verdonschot et al., 2012; Whatley et al., 2014; Gething et al., 2020) may have been responsible for the observed compositional differences.

Ditches often support taxa which are not found elsewhere in a catchment (Painter, 1999; Watson & Ormerod, 2004; Williams et al., 2004; Rolke et al., 2018). The occurrence of unique taxa may reflect differences in environmental conditions (Armitage et al., 2003), small-scale differences in habitat structure (Verdonschot et al., 2012; Gething et al., 2020), the differing cast of predators/competitors and/or interactions with such predators/competitors between streams and ditches. For example, the amphipod *Niphargus* typically lives in groundwater (Johns et al., 2014), but had an affinity for temporary ditches. This affinity may reflect that temporary ditches in the study area are periodically dredged, potentially exposing patches of the underlying chalk and allowing *Niphargus* to be washed out of the aquifer by upwelling groundwater (Claret et al., 1999; Morhun et al., 2022). Once washed into ditches, *Niphargus* may subsequently survive in higher abundance because competitive/predatory taxa, such as the amphipod *G. fossarum/pulex*, are less common, as observed in temporary stream assemblages (Punchard & House, 2009; White et al., 2018; Aspin & House, 2022; Miliša et al., 2022). Similarly, Odonates, which prefer slow flowing or standing water (Extence et al., 1999), were only found in ditches, suggesting ditches provided slow flowing/standing water habitats that were not found in streams.

The richness, assemblage composition and unique taxa supported differed between perennial and temporary ditches, consistent with the differences typically reported between perennial and temporary streams (Storey & Quinn, 2008; Santos & Stevenson, 2011; White et al., 2018). Differences between flow permanence regimes in addition to differences in assemblage composition between waterbody types thus imply that ditches with temporary and perennial flow permanence regimes made distinct contributions to landscape-scale biodiversity, supporting H1. The comparable LCBD of waterbody types suggests that the magnitude of these compositional differences (i.e. contributions to biodiversity) were similar among streams and ditches with perennial and temporary flow permanence regimes.

4.4.2 H2. The role of ditches in supporting drying-tolerant specialists in streams

The resilience of populations to disturbance depends upon the characteristics of the disturbance (i.e. onset rate, frequency, intensity, duration) and upon traits including the dispersal strength of the species present (Bogan et al., 2017; Cunillera-Montcusí et al., 2021). *Nemoura lacustris* and *P. werneri* are from orders with limited dispersal abilities (Tachet et al., 2010; Schmidt-Kloiber & Hering, 2015; Sarremejane et al., 2017b), with adult *Paraleptophlebia submarginata* being incapable of aerially dispersing to adjacent catchments (approx. 2 km based on **Figure 1** in Masters et al., 2007). Consistent with Masters et al. (2007), Jackson & Resh (1989) observed that the number of adult *Paraleptophlebia debilis* decreased significantly between 5 m and 150 m from a stream and for nemourid stoneflies, 90% of adults travelled <60 m from the stream (Petersen et al., 1999). Thus, in the study area, if not for ditches, the lower drainage densities than those studied by Masters et al. (2007) would likely mean that stream populations of drying-tolerant specialists are isolated from populations in the nearest stream by their limited dispersal abilities. Such isolation shapes aquatic assemblages (Cañedo-Argüelles et al., 2015; Swan & Brown, 2017), because extreme events, such as prolonged/intense dry phases (Sarremejane et al., 2021) or successive wet years that allow competitors and predators to colonise usually temporary reaches (Punchard & House, 2009; Aspin & House, 2022), may result in the loss of drying-tolerant specialists with limited opportunities for subsequent re-colonisation from adjacent temporary streams. Thus, populations of drying-tolerant specialists in ditches may represent a key source of post-disturbance colonists for temporary streams, with exchanges of *P. werneri* between the stream and ditches (i.e. the positive association between *P. werneri* occurrence in ditches and abundance in the stream) potentially promoting sub-catchment-scale resilience of this drying-tolerant specialist to disturbance (e.g. intense localised drying: Dodemaide et al., 2018; Iwamoto et al., 2022).

Nemoura lacustris abundance was not influenced by the occurrence of ditch populations, suggesting that stream and ditch populations within the same sub-catchment are somewhat isolated from one another, contrary to H2. Associations between stream abundances and ditch occurrences of *P. werneri* but not *N. lacustris* may reflect that *Nemoura* have a lower affinity for aerial dispersal than *Paraleptophlebia* (Tachet et al., 2010; Schmidt-Kloiber & Hering, 2015; Sarremejane et al., 2017b), and thus populations of *N. lacustris* are potenitally isolated over shorter distances. A high proportion of ditches (18 of 22 ditches) were hydrologically connected to streams potentially allowing colonisation by juvenile *Nemoura*, which have a greater propensity for active aquatic dispersal than *Paraleptophlebia* (Tachet et al., 2010; Schmidt-Kloiber & Hering, 2015). However, the absence of a relationship between their occurrence/abundance again suggests that stream and ditch populations of *Nemoura* are more isolated from one another than stream and ditch populations of *Paraleptophlebia*, and may have occurred if barriers to aquatic dispersal (e.g. culverts: Vaughan, 2002; Wild et al., 2011) prevented movements of *N. lacustris*. The weak dispersal abilities of *N. lacustris* may be balanced by a greater resistance to drying (Tierno de Figueroa & López-Rodríguez, 2005; Bauernfeind & Soldán, 2012; Tapia et al., 2018; White et al., 2018), and potentially other pressures that manifest via similar stressors (**Under pressure: aquatic macroinvertebrate responses to agriculture in temporary streams**), than *P. werneri*.

Paraleptophlebia werneri's greater capacity for aerial dispersal than *N. lacustris*, in addition to increasing resilience within a sub-catchment, may allow ditches to act as stepping stones between streams/sub-catchments (Cañedo-Argüelles et al., 2015; Patrick et al., 2021), further buffering *P. werneri* populations against disturbance. The occurrence of *N. lacustris* populations in a stream and ditches means that extinction in one channel does not necessarily mean extinction within the sub-catchment. Collectively, therefore, asynchronies in landscape-scale disturbances between streams and ditches, such as intense drying in one of the two waterbody types (Dodemaide et al., 2018; Iwamoto et al., 2022), may mean that catchments with ditches contain a greater area and diversity of habitats than catchments without ditches (Armitage et al., 2003; Herzon & Helenius, 2008). This environmental heterogeneity may in turn promote the survival of aquatic invertebrate assemblages that include drying-tolerant specialists by allowing non-spatially coordinated responses to landscape-scale disturbances (Sarremejane et al., 2021).

4.4.3 H3. The influence of competitors and predators on the abundance of drying-tolerant specialists

Paraleptophlebia werneri and *N. lacustris* were seemingly unaffected by overall levels of potential competition, contrary to H3, possibly because they are generalists that use multiple food sources (i.e. detritus, dead plant material and living microphytes: Tachet et al., 2010; Schmidt-Kloiber & Hering, 2015) and were thus not tied to a specific limiting resource. Similarly, overall levels of potential predation did not influence the abundance of either drying-tolerant species, contrary to H3. This may reflect that potential predation, as calculated based on documented genus-level food preferences, did not correlate with the actual predation pressure. In particular, *G. fossarum/pulex* are frequently predatory (MacNeil et al., 1997; Kelly et al., 2002; Dick et al., 2013), but this is not well reflected in their documented food preferences (Tachet et al., 2010; Schmidt-Kloiber & Hering, 2015). Alternatively, the effects of predation on populations of drying-tolerant specialists was too weak to be detected (e.g. because few predators were capable of colonising temporary reaches: Punchard & House, 2009; Aspin & House, 2022).

Both drying-tolerant species were negatively associated with *G. fossarum/pulex* and Sphaeriidae. *Gammarus fossarum/pulex* is rheophilic, preferring well-oxygenated, perennial/near-perennial waterbodies (Maltby, 1995; White et al., 2018; Miliša et al., 2022), and cannot colonise the upstream reaches of temporary streams that exceed the distances they are capable of dispersing during a flowing phase/where subsurface drying limits their survival (Wright et al., 1984; Armitage & Bass, 2013; White et al., 2018; Aspin & House, 2022). Similarly, Sphaeriidae were more abundant in perennial waterbodies, consistent with White et al. (2018) and Miliša et al. (2022), but see Stubbington et al. (2016) and Chadd et al. (2017). Thus, the negative association between drying-tolerant specialists and competitors/predators such as *G. fossarum/pulex* and Sphaeriidae may be in part driven by independent responses to the same hydrological drivers (i.e. a site's flow permanence). However, *P. werneri* and *N. lacustris* occur in perennial waterbodies (Wright et al., 1998; Prenda & Gallardo-Mayenco, 1999; Salmela, 2013), suggesting flow permanence regime is not solely responsible for the negative relationship between taxa that are typically found in perennial and temporary reaches. For example, temporary ditches can provide refuge from competition and predation for fish and invertebrates (Colvin et al., 2009; Leslie et al., 2012). *Gammarus fossarum/pulex* are highly abundant generalists, who frequently predate upon a range of taxa (MacNeil et al., 1997; Kelly et al., 2002; Dick et al., 2013) and therefore strongly influence macroinvertebrate assemblage composition (Kelly et al., 2006). Thus, the negative association with *G. fossarum/pulex* may also reflect that drying-tolerant specialists have a limited tolerance for competition with/predation by abundant generalists, and not simply a specific requirement for a dry phase to complete the lifecycle. In this regard, drying-tolerant specialists and the taxa they are positively associated with (e.g. *Niphargus*, *S. ignita*) may use "predation refuges", in which the the abundance of drying-sensitive predators/competitors (i.e. *G. fossarum/pulex*) is limited (Peckarsky, 1983; Fritz & Dodds, 2005).

4.4.4 Conclusions

Given their distinct contributions to landscape-scale biodiversity, and their potential to increase resilience to disturbance, ditches with temporary and perennial flow permanence regimes should receive greater attention from those seeking to enhance aquatic biodiversity. A key characteristic of ditches that likely allows them to enhance biodiversity is the provision of habitats with unique environmental conditions and differing levels of competition and predation relative to other waterbodies in the catchment. Thus, to enhance the biodiversity of catchments that include perennial and temporary streams, monitoring and management activities should consider the landscape context of such stream networks by including ditches and other waterbodies. In particular, connectivity between habitats for species with aquatic and aerial dispersal strategies should be a focus of management activities to promote the resilience of landscape-scale metacommunities across stream and ditch networks with a range of flow permanence regimes.

Author contributions

Parts of this chapter are published as: **Gething, K. J.**, Sykes, T., Biondi, G., Macadam, C. and Stubbington, R. (2021) Ditching misconceptions: rare temporary stream specialists in man-made habitats. *Freshwater Biological Association News*, 83, 14–18. https://irep.ntu.ac.uk/id/eprint/44941

Kieran J. Gething conceptualised the study (lead), performed investigation (lead), curated the data, designed the methodology, performed formal analysis, wrote the original draft, administered the project and reviewed and edited the manuscript (equal). Tim Sykes performed investigation (supporting) and reviewed and edited the manuscript (equal). Giulio Biondi and Craig Macadam reviewed and edited the manuscript (equal). Rachel Stubbington conceptualised the study (supporting) and reviewed and edited the manuscript (equal).

5 Why did the arthropod cross the river channel - to get to the other side?

5.1 Introduction

Terrestrial arthropods such as ground beetles are key to the functioning of riparian ecosystems (Ramey & Richardson, 2017), and support adjacent aquatic and terrestrial ecosystems via trophic subsidies (Nakano & Murakami, 2001; Owens et al., 2022), occupying roles as decomposers, consumers, predators and prey (Webb et al., 2017). However, they are increasingly threatened by human-caused habitat fragmentation (Shepherd, 2013), which reduces connectivity, leaving isolated communities less resilient to extreme events (Van Looy et al., 2019) such as drought or floods. In addition to human-caused habitat fragmentation, terrestrial arthropod communities are influenced by natural features such as topography and elevation (Musthafa et al., 2021), which can impede dispersal and colonisation. However, the role of smaller, temporally variable natural barriers in shaping riparian arthropod communities is rarely quantified.

Temporary streams, those which sometimes dry, comprise more than half of the global river network and are present on every continent (Datry et al., 2014b; Messager et al., 2021). As streams dry, temporary stream habitats can be colonised by diverse and abundant assemblages of riparian arthropods (Steward et al., 2011; Corti & Datry, 2016). In contrast, perennial and flowing temporary streams represent barriers between communities in parallel riparian zones, with an arthropod's capacity to disperse across the channel (and thus maintain connectivity between communities on opposite banks; hereafter, cross-channel communities) being determined by an individual's inundation tolerance (Kolesnikov et al., 2012) and dispersal mode (e.g. terrestrial, aerial), and stream hydrology and morphology (e.g. the width, depth and velocity of the water: Lindroth, 1992).

Narrow, linear habitat features with sparse surface vegetation (e.g. roads, railway tracks, bare ground) are barriers to terrestrial and aerial dispersal (Mader, 1984; Mader et al., 1990; Lövei et al., 1998; Andersson et al., 2017), encouraging longitudinal movements along rather than lateral movements across such a linear features (Mader et al., 1990). Temporary streams may have similar effects, particularly during flowing phases, because the extent of ground-based dispersal across the channel is likely influenced by flow conditions (Lindroth, 1992). Although water is no physical barrier to aerial dispersers, it might be perceived as such (Lövei et al., 1998; Andersson et al., 2017) and when individuals do disperse by flight it is resource intensive, dependent upon life stage (Matalin, 1994), and influenced by environmental conditions (e.g. weather) and the relative favourability of the source and its surrounding habitats (Lövei & Sunderland, 1996).

Riparian arthropods in unfavourable habitats move further and more frequently than those experiencing favourable conditions (Lövei & Sunderland, 1996). Thus, although dispersal is resource intensive and linear features encourage longitudinal movement, the relative favourability of habitat conditions may trigger taxa to disperse into, and ultimately across, temporary streams. Drying and dry temporary streams often contain food resources, such as stranded and emerging insects (O’Callaghan et al., 2013a), and may contain fewer competitors than nearby riparian habitats (Sánchez-Montoya et al., 2020). Thus, drying and dry temporary streams may be more favourable than riparian zones, encouraging movement into the channel (Steward et al., 2022), with the temporal stability of in-channel conditions, the barrier posed by any remaining water and an individual’s capacity for dispersal determining their subsequent movement into either their original or the parallel riparian zone.

Riparian arthropod communities exhibit strong lateral zonation near rivers (Paetzold et al., 2005; Bates et al., 2007; Sánchez-Montoya et al., 2016), potentially driven by species-specific inundation tolerances (O'Callaghan et al., 2013a). Additionally, longitudinal changes in flow (and co-varying factors, e.g. sediment composition, vegetation characteristics) influence arthropod community composition (e.g. McCluney & Sabo, 2012; Sánchez-Montoya et al., 2016), with riparian zones in headwater reaches supporting communities of generalists (*sensu* Gooderham et al., 2007; Devictor et al., 2008), which become more specialised with distance downstream (Eyre et al., 2001a, 2001b). Communities in dry temporary streams may also exhibit spatial zoning, but such zoning also varies through time (e.g. Sánchez-Montoya et al., 2020) because the lateral and longitudinal extent of flow varies across diel to multi-year timescales (e.g. Burt, 1979; Claret & Boulton, 2003; Bunting et al., 2021).

In the riparian zones of perennial rivers, microhabitats (e.g. riparian vegetation, gravel banks) and food resources (emerging aquatic insects) are relatively stable over time, allowing terrestrial arthropod communities to specialise (Hering et al., 2004; Paetzold et al., 2005; Ramey & Richardson, 2017). Although temporally stable on their respective banks, the distribution of microhabitats and resources may differ between parallel riparian zones in perennial reaches (e.g. if banks have different land uses/management practices). Thus, the combination of a permanent barrier that promotes longitudinal rather than lateral movements (Mader et al., 1990) and the potentially different microhabitats/resource provision on each side of the river may discourage cross-channel dispersal, especially by ground-dwelling organisms, in perennial reaches. Such isolation and specialisation to site-specific conditions can result in greater spatial variability in community composition (Hubbell, 2001; Sánchez-Montoya et al., 2020; Hu et al., 2022), i.e. high spatial beta (β) diversity (Whittaker, 1960). In contrast, partial or complete drying in temporary streams means that communities in parallel riparian zones are intermittently connected. Such connectivity may foster less variability between cross-channel communities (i.e. low spatial β diversity), which are comprised of mobile, generalist species that can exploit new in-channel and cross-channel opportunities (Eyre et al., 2001a, 2001b; Gooderham et al., 2007).

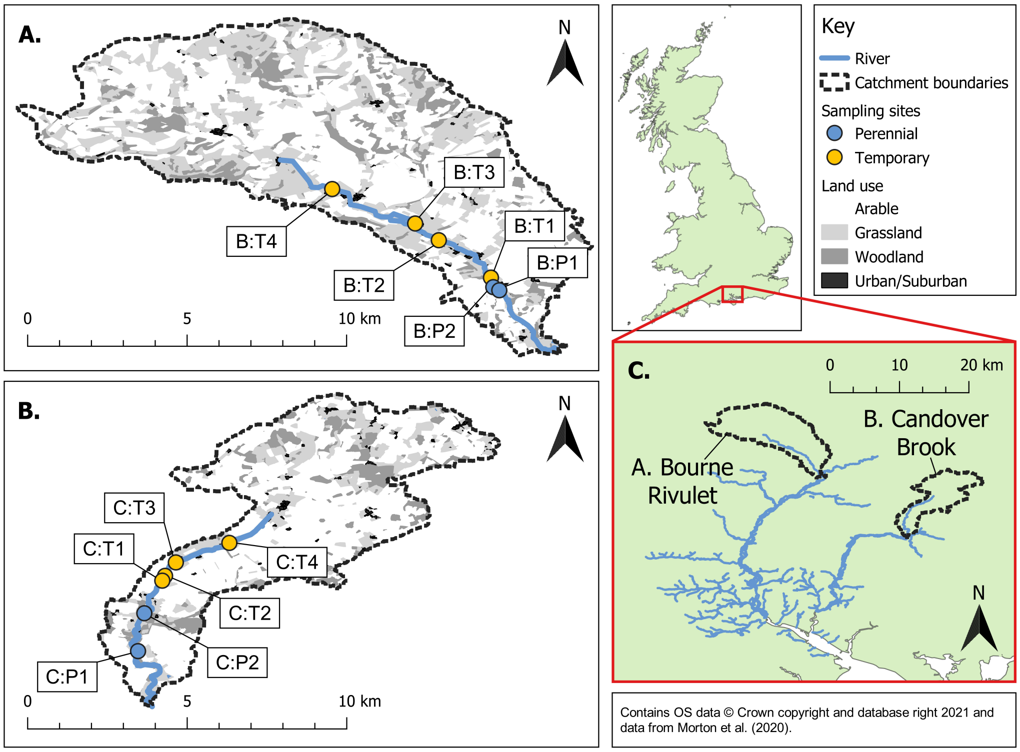
I assessed how riparian communities responded to declining flows and drying along a gradient of flow permanence from perennial to seasonally intermittent in two headwater streams. I hypothesised that: (H1) cross-channel communities are less variable (i.e. have lower β diversity) in temporary than perennial reaches, due to antecedent opportunities for mixing across dry channels, (H2) cross-channel communities become less similar from upstream to downstream, reflecting upstream to downstream drying patterns, and (H3) cross-channel communities become less variable as the stream dries, because the water's decreasing width and depth are a diminishing barrier to cross-channel dispersal.

5.2 Methods

5.2.1 Data collection

Study area

This study was conducted in the catchments of the Candover Brook and the Bourne Rivulet, Hampshire, UK. Hampshire has a temperate oceanic climate (Cfb: Kottek et al., 2006), with mean (± SD) annual minimum and maximum air temperatures of 6.1 ± 3.9°C and 15.0 ± 5.7°C, respectively and a mean annual rainfall of 754 mm (Met Office, 2022). Land use in both catchments is dominated by arable agriculture (>50%, **Figure 5.1A** and **B**: National River Flow Archive, 2021) and pasture (>28%) with few urban areas (<5%). The catchments are underlain by a chalk aquifer, which causes the upper reaches of both streams to dry during summer when groundwater levels are low (Sear et al., 1999).



Contains OS data © Crown copyright and database right 2021 and data from Morton et al. (2020).

Figure 5.1: Sampling sites and land use in the (A) Bourne Rivulet and (B) Candover Brook catchments, (C) tributaries of the Rivers Test and Itchen, respectively. Codes on A and B indicate the river name (B, Bourne; C, Candover), the flow permanence regime (P, perennial; T, temporary) and the site number (1–4).

Six sampling sites adjacent to each stream spanned 7.3 km and 5.6 km of the Candover Brook and the Bourne Rivulet, respectively. Sampling sites were selected to be representative of conditions in the wider reach. On each stream, the two sites furthest downstream were located in perennial reaches, and the upper four sites in seasonally intermittent reaches (**Figure 5.1A** and **B**). All of the sites, except one on each stream, had comparable land uses on both banks: mown grassland, pasture or wetland (**Table 13.1**). At these sites, the comparable land uses extended ≥6 m laterally from the water's edge, which included the full bank face and at least 4 m of the terrestrial area surrounding the channel. The Bourne Rivulet site B:P2 (**Figure 5.1A**) had woodland on one bank and mown grassland on the other. The Candover Brook site C:T3 (**Figure 5.1B**) had wet woodland on one bank and a mown grass verge with a road paralleling the channel at a distance of ~4 m on the other. Bank slopes were <45° at all sites, except the right bank of B:T3, where the two pitfall traps farthest downstream were adjacent to a 90° slope formed of concrete slabs and the four traps furthest upstream were adjacent to a 30° slope (**Table 13.1**).

Study design and sampling

On each stream, I sampled all six sites on four equally spaced dates between April and July 2021 (see **Figure 5.2**). I made observations of the width and depth of water in the channel at each site relative to previous visits. To supplement these observations of change over time, I sourced discharge data from the closest downstream gauging station in the National River Flow Archive (NRFA). For the Bourne Rivulet, this was located approx. 12 km downstream of B:P1 on the River Test (NRFA station 42024: National River Flow Archive, 2022a). For the Candover Brook, the gauging station was 3 km downstream of C:P1 (NRFA station 42009: National River Flow Archive, 2022b).

I sampled invertebrates by pitfall trapping, broadly following Drake et al. (2007). Pitfall traps are buried plastic cups (8-cm diameter, 10-cm height), with the lip of the cup being level with the surrounding substrate. At each site, I set six pitfall traps at intervals of 2 m on each bank. These traps were between 0.25 m and 3 m from the water's edge during the first visit and remained in the same location throughout the study. I 1/3 filled the cups with an ethylene glycol–water mix to preserve invertebrates that fell into the traps from the surrounding surface substrates. After 15–16 days, I collected and pooled the six traps from each side of the channel (i.e. a left and right sample were collected by pooling the six traps from their respective sides of the channel). In total, I set 576 individual pitfall traps (2 streams × 6 sites per stream × 2 samples per site × 6 pitfall traps per sample × 4 dates), and subsequently pooled them into 96 samples. Prior to identification, I discounted the left and right bank samples from the fourth visit to B:T4 (**Figure 5.1A**) due to disturbance of the pitfall traps by livestock, leaving 94 samples.

Ground beetles (Coleoptera: Carabidae) are a common family in riparian ecosystems (e.g. Sadler et al., 2004; Steward et al., 2011) that has well-studied environmental preferences and includes species that employ terrestrial and aerial dispersal (Luff, 2007; Knapp et al., 2020). Therefore, I used ground beetles to represent changes in the terrestrial arthropod community in space and time. I identified ground beetles mostly to species or a species aggregate, with 1.0% and 0.2% of individuals being identified to genus and family, respectively.

5.2.2 Data preparation and analysis

To avoid the inflation of cross-channel variability by taxa identified to multiple taxonomic levels (e.g. *Pterostichus madidus* and *Pterostichus*), I assigned taxa identified above species/species aggregate level to a single most-likely species/species aggregate (*sensu* Cuffney et al., 2007). Because the similarity of communities on each side of the channel is likely moderated by capacity for flight, I used wing morphology as a proxy for a species' ability to fly. I classified species as macropterous (long winged, i.e. able to fly), brachypterous (short winged/wingless, i.e. unable to fly) or polymorphic (some individuals may be capable of flight) using Luff (2007) and Knapp et al. (2020). Using these wing morphology classifications, I produced three versions of the dataset, one including all species (hereafter, the *all species* dataset) one including macropterous species (the *flight capable* dataset) and the other only brachypterous and polymorphic species (i.e. species with a limited or no ability for flight, the *limited flight* dataset).

In preparation for hypothesis testing, I used Sørensen β diversity to represent variability between samples in the all species, flight capable and limited flight datasets. I calculated Sørensen β diversity from species occurrence in each dataset using the betapart package (Baselga et al., 2021). I then extracted the β diversity value comparing samples from the left and right bank for each site and sampling visit. After preliminary analysis, I removed samples from the fourth visit to site B:T1 (**Figure 5.1A**), leaving 92 samples, because the right bank sample contained only a single specimen of *Trechus obtusus*. This species occurred once in the dataset, resulting in high β diversity with its corresponding left bank sample that had a disproportionally large influence on my results.

To test H1–3, I used the β diversity value comparing left and right bank samples as a response variable in linear mixed-effect models built with the lme4 package (Bates et al., 2015). The optimal random effect structure was determined by modelling the response variable with combinations of four potential random intercepts (stream, site, visit number and no random intercept: see Burnham & Anderson, 2002; Brown et al., 2018), and selecting the most parsimonious structure using Akaike's information criterion (AIC). The no random intercept model had the lowest AIC for both the all species and limited flight datasets, and thus I used no random effects. Site had the lowest AIC for the flight capable dataset, but was <2 ΔAIC lower than the no random intercept model (i.e. the models performed comparably: Burnham & Anderson, 2002) and thus no random effects were selected for comparability with the all species and limited flight datasets.

To test whether community composition was less variable in temporary than perennial reaches (H1), I used flow permanence regime (categorical: perennial or temporary) as a fixed effect. To test whether assemblages became more variable along a gradient of drying (i.e. from downstream to upstream, H2), I used downstream position (sites ranked from downstream to upstream, categorical: 1–6) as a fixed effect. To test whether assemblages became less variable as the stream dries (H3), I used visit number (categorical: V1, V2, V3, V4) as a fixed effect. To explore any differences in β diversity among levels of the fixed effects, I partitioned β diversity into replacement (i.e. turnover) or differences in richness (nestedness-resultant dissimilarity) and reran the model while replacing β diversity with 1 of its partitioned components as the response variable (see **Tables 13.4**, **13.5** and **13.6**).

I tested all model assumptions using DHARMa (Hartig, 2020). I visualised variability among left/right sample pairs by non-metric multidimensional scaling (NMDS), using vegan (Oksanen et al., 2019). For all NMDS, I used Sørensen distance matrices in two dimensions over 500 iterations. All analyses were conducted in R v.4.0.3 (R Core Team, 2020).

5.3 Results

5.3.1 In-channel conditions

On the first sampling date, both streams were flowing at all sites. Discharge at the closest downstream gauging station decreased with each visit from 6.4 ± 0.2 (mean ± SD) and 0.7 ± <0.1 m^3/s during V1 to 5.1 ± 0.2 and 0.5 ± <0.1 m^3/s during V4 in the Bourne Rivulet and Candover Brook catchments (**Figure 5.2**: National River Flow Archive, 2022a, 2022b), respectively. Consistent with decreasing discharge in downstream reaches, I observed decreases in the width and depth of water at all sites with each sampling visit. The uppermost site on each stream dried between V3 and V4. Between V1 and V4, dense vegetation encroached from the channel margins toward the centre of the channel at all sites (**Figures 13.1**, **13.2**, **13.3** and **13.4**), often appearing to slow flow velocities and limit solar radiation at the water's surface/channel bed.

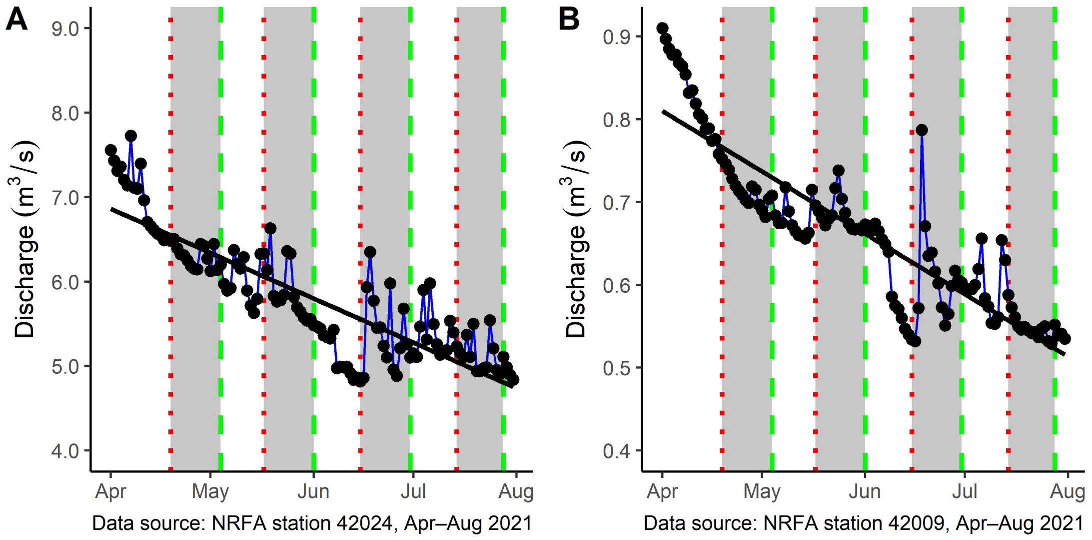


Figure 5.2: Daily discharge during the study period at the closest downstream gauging station to sampling sites in the Bourne Rivulet (A) and Candover Brook (B) catchments. Black circles represent daily discharge, solid blue lines represent changes in discharge between consecutive days, solid black lines represent the trend in daily discharge over the study period and grey shaded areas represent sampling periods. Sampling periods began (i.e. pitfall traps were set) at the dotted red lines and ended at the dashed green lines. Data source: National River Flow Archive (NRFA).

5.3.2 Assemblage summary

In total, 4,236 ground beetles from 82 species were captured, with samples containing 10.5 ± 5.1 (mean ± SD) species and 46.0 ± 41.9 individuals (also see **Table 13.2**). *Nebria brevicollis* (494 individuals), *Agonum emarginatum* (441) and *Pterostichus nigrita/rhaeticus* (378) were the most abundant species overall, comprising 31.0% of all captures. Twenty two species were captured only on 1 bank, all of which occurred in low abundance (2.8 ± 3.2 individuals, range: 1–12). Of the 22 species, *Anisodactylus binotatus* and the Nationally

Scarce *Panagaeus bipustulatus* were captured in both temporary and perennial reaches. *Carabus granulatus* and three species of *Leistus* were captured on 1 bank only in perennial reaches and 16 species, including four species of *Bembidion*, were unique to temporary reaches. The majority of species captured were macropterous (64.6%), followed by polymorphic (24.4%) and brachypterous (11.0%). The flight capable dataset contained 53 species, represented by 2,888 individuals. Samples contained 6.7 ± 3.8 (mean ± SD) species and 31.2 ± 33.9 individuals. Like the all species dataset, the three most abundant species in the flight capable dataset were *N. brevicollis*, *A. emarginatum* and *P. nigrita/rhaeticus*, comprising 45.5% of captures. The limited flight dataset comprised 29 species and 1,348 individuals, with samples containing 3.9 ± 2.0 (mean ± SD) species and 14.7 ± 16.1 individuals. The three most abundant species (*Pterostichus madidus* – 312 individuals, *Pterostichus minor* – 258 and *Bembidion tetracolum* – 187) accounted for 56.2% of captures. Most species in the limited flight dataset were polymorphic (69.0%), with 31.0% being brachypterous.

Beta diversity (i.e. community variability) between left and right samples (see black lines on **Figure 5.3**) was comparable on the Bourne Rivulet (mean ± SD: 0.595 ± 0.187, 0.611 ± 0.210 and 0.614 ± 0.275) and the Candover Brook (0.506 ± 0.175, 0.481 ± 0.197 and 0.555 ± 0.238) for the all species (**Figure 5.3A**), flight capable (**Figure 5.3B**) and limited flight (**Figure 5.3C**) datasets (also see **Table 5.1**). Across all datasets, turnover accounted for a greater proportion of total β diversity on average than nestedness-resultant dissimilarity (**Table 13.3**).

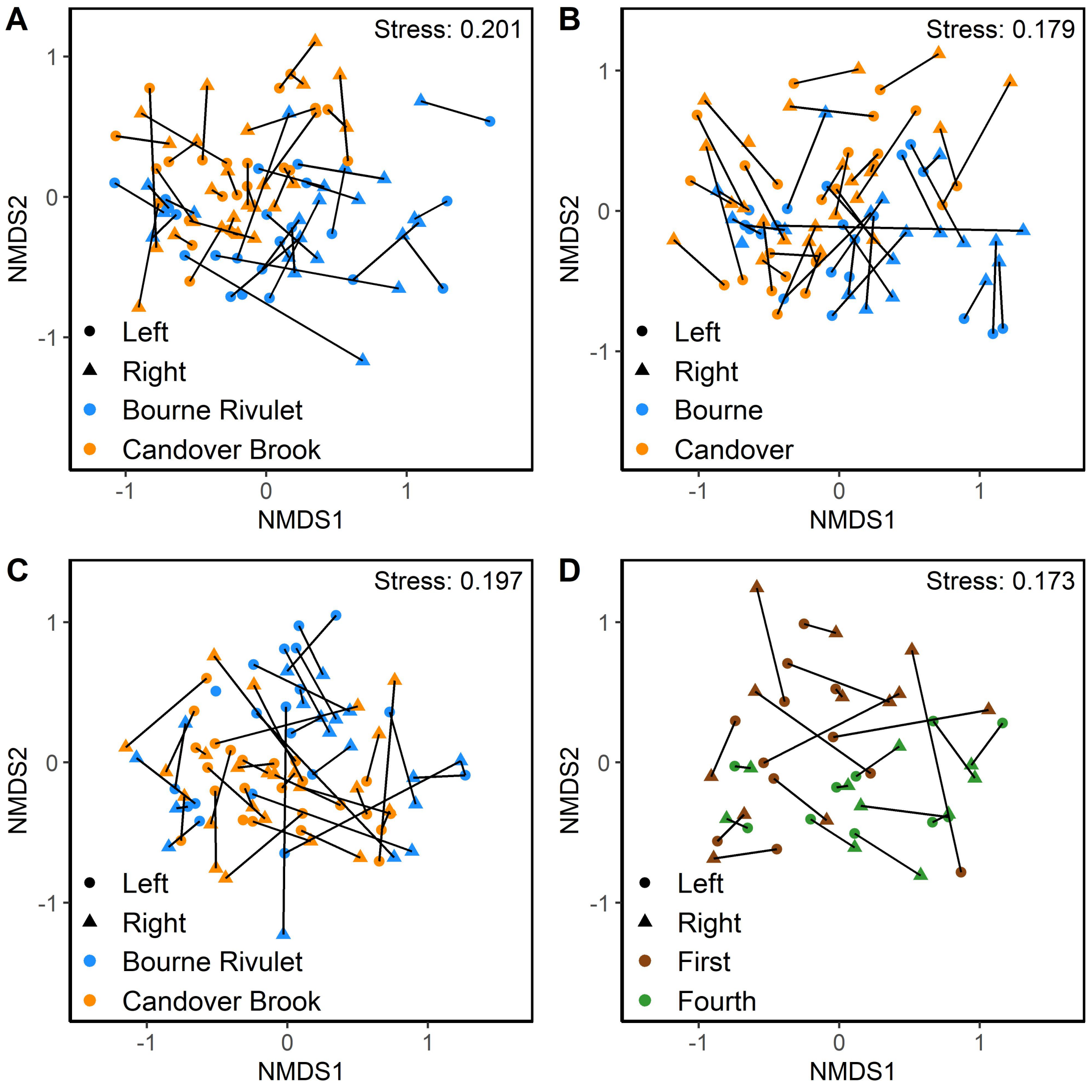


Figure 5.3: Non-metric multidimensional scaling of terrestrial invertebrate assemblage samples from the all species (A), flight capable (B) and limited flight (C and D) datasets, collected on the left (circles) and right (triangles) banks of the Bourne Rivulet (blue) and the Candover Brook (orange) or during the first (brown) and fourth (green) sampling visits.

Table 5.1: Summary statistics of Sørensen beta (β) diversity for the Bourne Rivulet and Candover Brook catchments in the all species, flight capable and limited flight datasets.

Dataset	Catchment	Minimum	Mean ± SD	Maximum
All species	Bourne Rivulet	0.231	0.595 ± 0.187	1.00
	Candover Brook	0.167	0.506 ± 0.175	0.889
Flight capable	Bourne Rivulet	0.00	0.611 ± 0.210	1.00
	Candover Brook	0.167	0.481 ± 0.197	1.00
Limited flight	Bourne Rivulet	0.250	0.614 ± 0.275	1.00
	Candover Brook	0.00	0.555 ± 0.238	0.833

Sites with different land use on each bank (B:P2 and C:T3) did not consistently rank highest for cross-channel β diversity, with B:P2 being ranked joint highest (alongside B:T1 and B:T4) during the second visit in the limited flight dataset for the Bourne Rivulet catchment. Similarly, C:T3 only ranked highest during the second visit in all datasets and joint highest with C:P1 during the third visit in the limited flight dataset for the Candover Brook catchment.

5.3.3 H1. Beta diversity in temporary and perennial reaches

Cross-channel β diversity was comparable in temporary and perennial reaches for the all species ($P = 0.101$, $R^2 = 0.059$: **Figure 5.4A**) flight capable ($P = 0.198$, $R^2 = 0.037$: **Figure 5.4B**) and limited flight datasets ($P = 0.239$, $R^2 = 0.031$: **Figure 5.4C**), contrary to H1. For the all species and flight capable datasets, temporary reaches occupied a greater range of cross-channel β diversity values (i.e. β diversity was less consistent) than perennial reaches (**Figures 5.4A** and **5.4B**). In the flight capable dataset, cross-channel β diversity spanned the maximum range (i.e. 0 to 1, indicating total and no overlap in cross-channel communities, respectively: **Figure 5.4B**). Complete overlap in cross-channel communities occurred at C:T2 during the second visit, with both banks supporting 8 species represented by a total of 78 individuals. Total dissimilarity between cross-channel communities occurred at B:T1 during V1, V2 and V3, with left banks supporting 3, 5 and 4 species while right banks supported 2, 5 and 2 different species. The total number of individuals recorded on both banks at B:T1 was 18, 28, 12 for V1, V2 and V3, respectively.

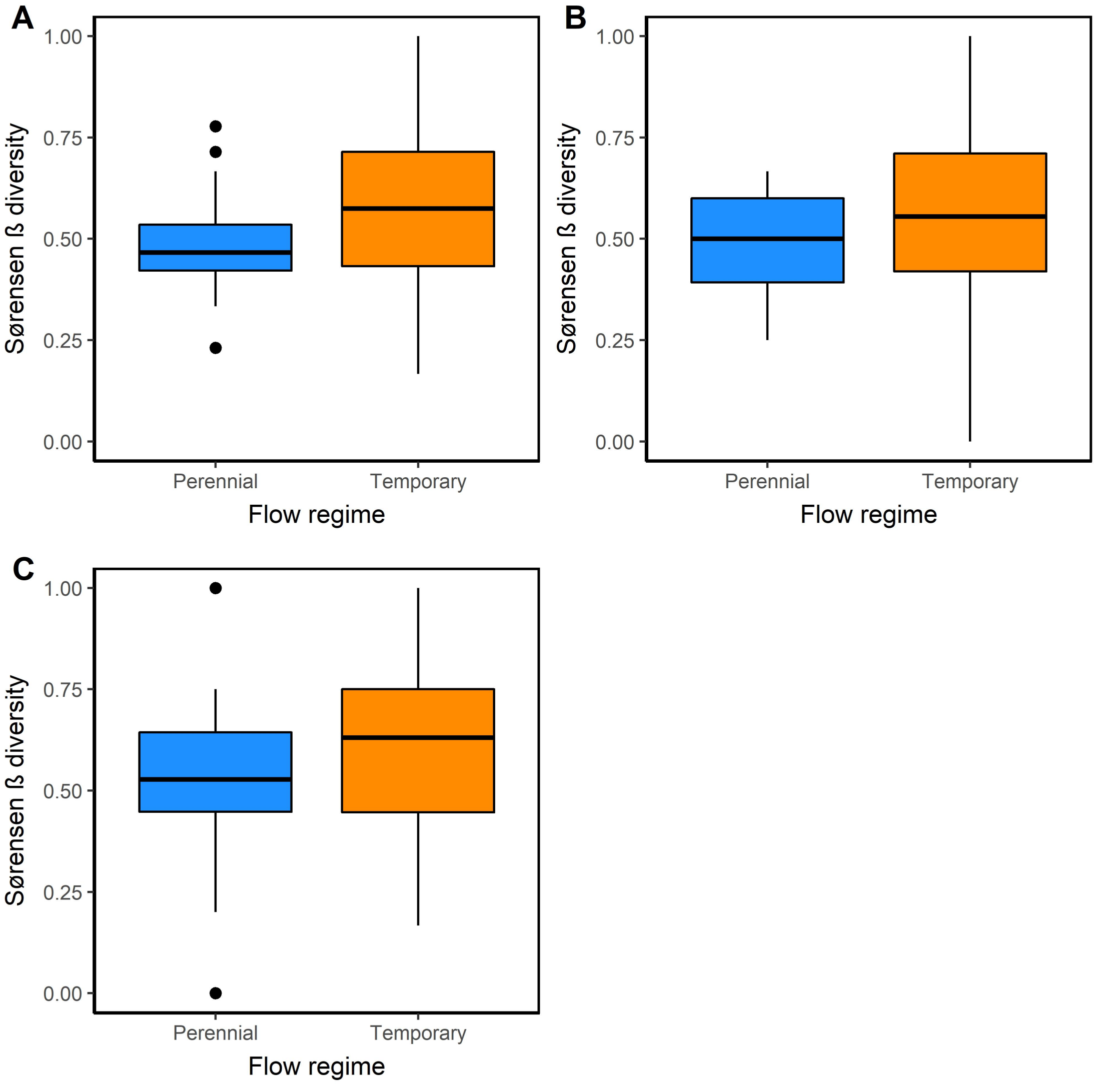


Figure 5.4: Cross-channel Sørensen beta (β) diversity in the perennial (blue) and temporary (orange) reaches of the Bourne Rivulet and the Candover Brook from the all species (A), flight capable (B) and limited flight (C) datasets. The centre line represents the median, boxes represent the interquartile range, whiskers represent the minimum/maximum values which are within 1.5× the interquartile range of the first and third quartiles and filled circles represent outliers.

In the limited flight dataset, perennial reaches had less consistent cross-channel β diversity values than temporary reaches (**Figure 5.4C**). However, this variability was driven by a single species (*Notiophilus biguttatus*) at B:P2, which occurred on the right bank during V2 (3 individuals, cross-channel β diversity: 1) and both banks during V4 (4 individuals, cross-channel β diversity: 0). Similarly, C:P1 during V3 supported two species on the left bank (3 individuals) and a different species on the right bank (1 individual, cross-channel β diversity: 1). Without these low richness and abundance samples from B:P2 and C:T1, temporary reaches would have had less consistent β diversity values in the limited flight dataset (**Figure 5.4C**).

5.3.4 H2. Beta diversity along a drying gradient

Cross-channel β diversity was comparable from upstream to downstream for both the all species ($P = 0.054–0.476$, $R^2 = 0.101$: **Figure 5.5A**), flight capable ($P = 0.111–0.811$, $R^2 = 0.092$: **Figure 5.5B**) and limited flight ($P = 0.178–0.711$, $R^2 = 0.061$: **Figure 5.5C**) datasets, contrary to H2. Although non-significant, cross-channel β diversity trended upward from downstream to upstream (**Figure 5.5**). Cross-channel β diversity was highly variable at downstream position 3:T in all three datasets due to differences between catchments, with B:T1 having a higher cross-channel β diversity of 0.910 ± 0.184 (mean ± SD) relative to 0.371 ± 0.126 at C:T1.

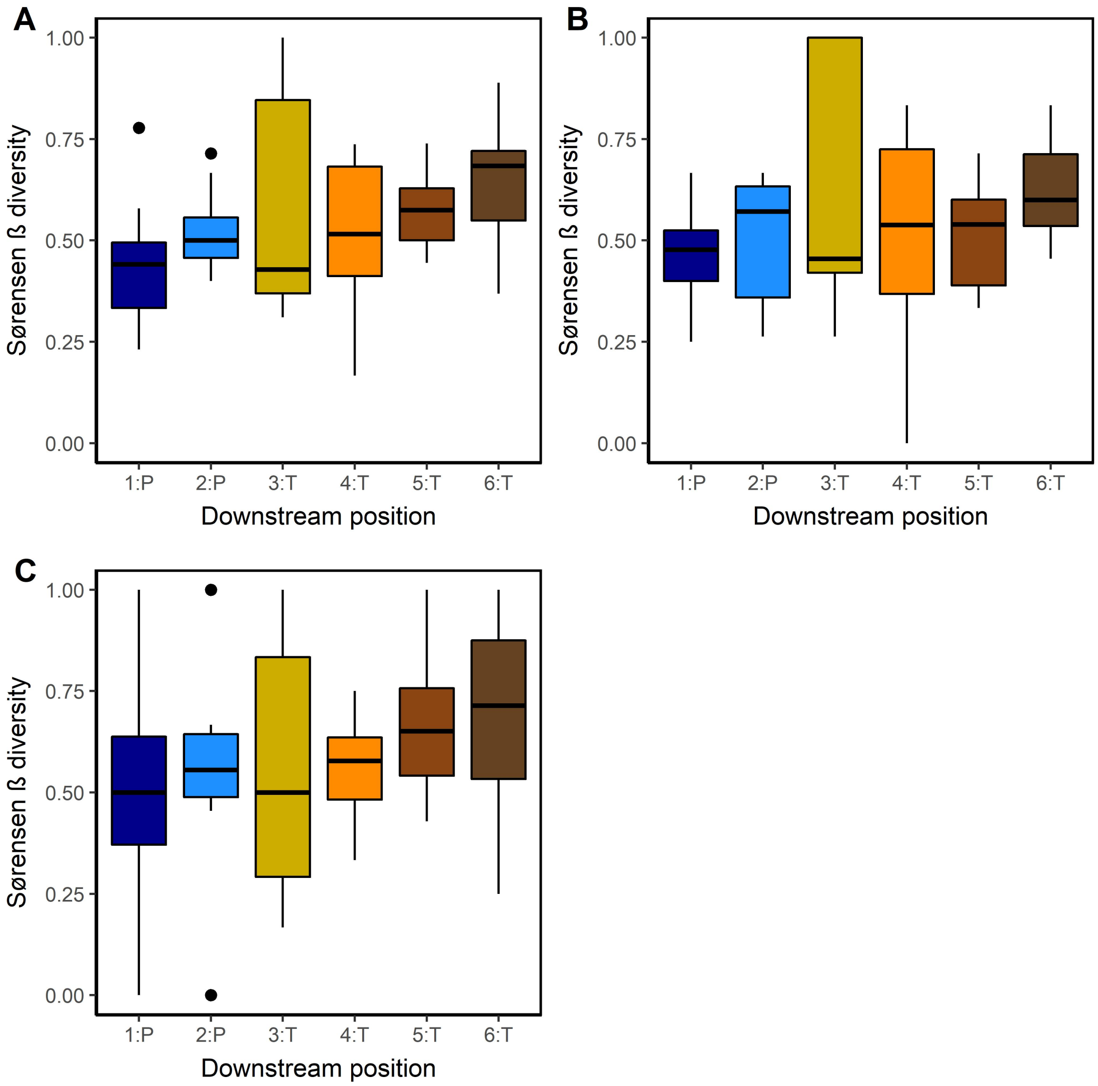


Figure 5.5: Cross-channel Sørensen beta (β) diversity in the Bourne Rivulet and the Candover Brook catchments from downstream (1) to upstream (6) in the all species (A), flight capable (B) and limited flight (C) datasets, where P and T indicate perennial and temporary reaches, respectively.

5.3.5 H3. Beta diversity over time

For the all species and flight capable datasets, cross-channel communities had comparable β diversity during drying (all species: P = 0.273–0.877, R^2 = 0.054, **Figure 5.6A**, flight capable: P = 0.894–0.946, R^2 = 0.001, **Figure 5.6B**), contrary to H3. For the limited flight dataset, cross-channel β diversity was comparable during V1, V2 and V3 (P = 0.768–0.884, R^2 = 0.142: **Figure 5.6C**), whereas cross-channel β diversity was lower during V4 than V1 (Estimate ± SE = -0.240 ± 0.104, P = 0.027: **Figure 5.3D**), supporting H3. Turnover explained these decreases in β diversity between V1 and V4 (Estimate ± SE = -0.294 ± 0.134, P = 0.034, R^2 = 0.129: **Table 13.6** and **Figure 5.7B**). Nestedness-resultant dissimilarity did not differ between V1 and V4 (P = 0.450, R^2 0.107: **Figure 5.7A**).

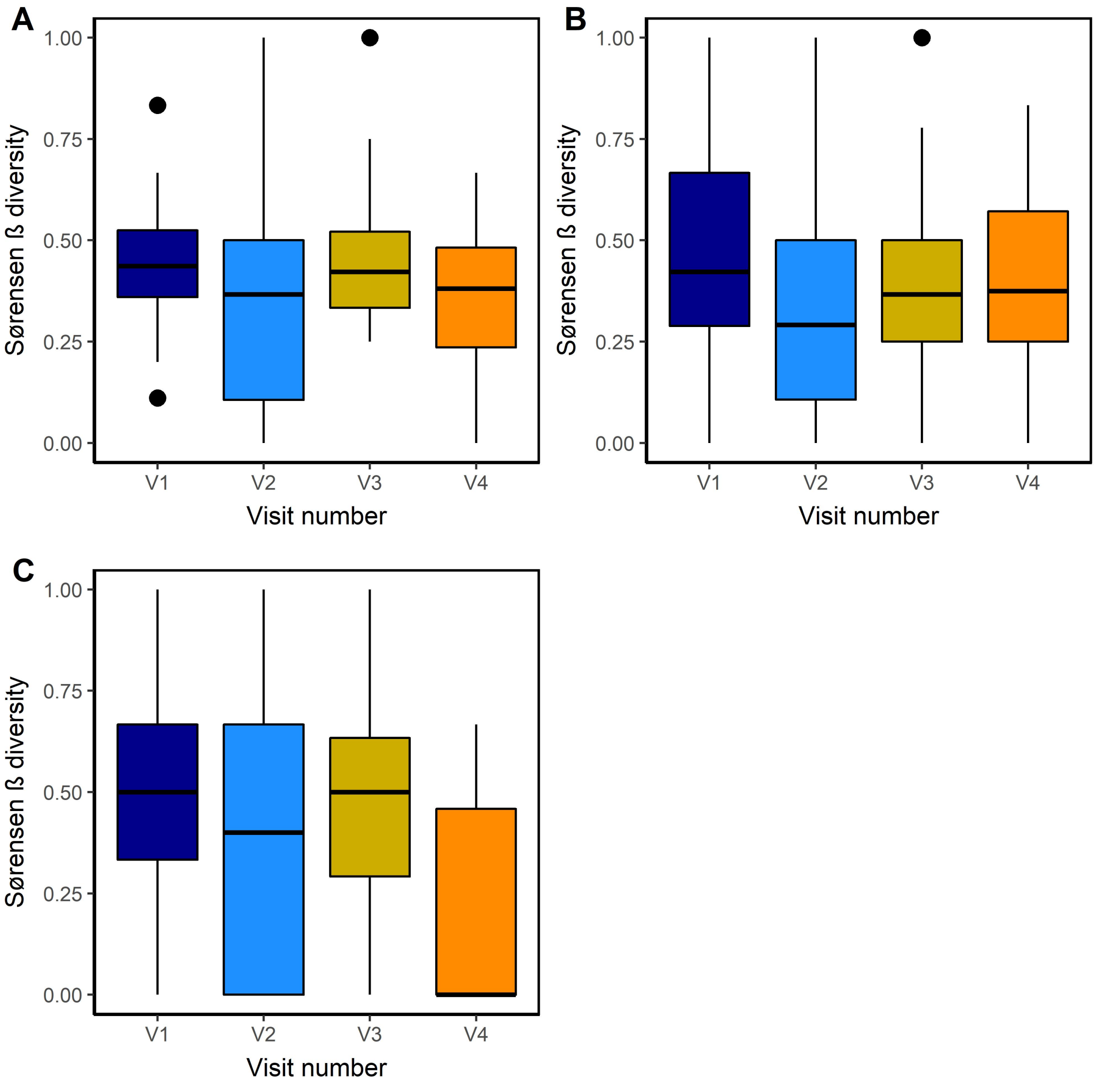


Figure 5.6: Cross-channel Sørensen beta (β) diversity in the Bourne Rivulet and the Candover Brook catchments from the first to fourth sampling visit in the all species (A), flight capable (B) and limited flight (C) datasets.

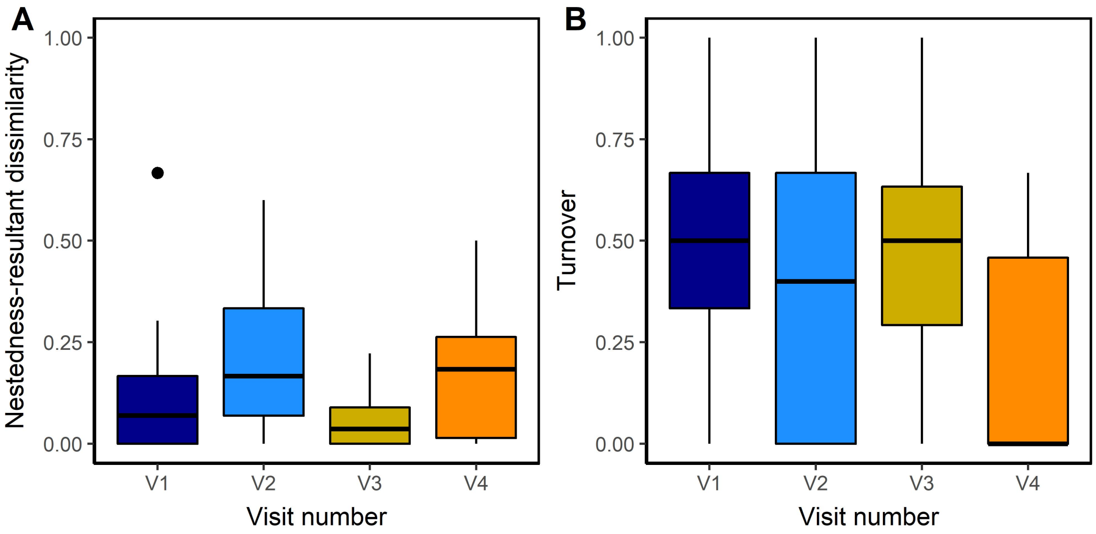


Figure 5.7: Cross-channel Sørensen beta (β) diversity in the Bourne Rivulet and the Candover Brook catchments for the limited flight dataset partitioned into its nestedness-resultant dissimilarity (A) and turnover (B) components.

Pterostichus madidus (brachypterous), the most abundant species in the limited flight dataset, increased in abundance from V1 (5 individuals, 1.4% of captures), to V2 (28, 11.2%), V3 (43, 12.8%) and V4 (236, 57.8%). During V1, *P. madidus* was captured on 1 bank at three sites on the Candover Brook (right C:P2, left C:T2 and left C:T4). During V4, all sites except C:P1 and B:P1 supported *P. madidus* and, at the sites where it was captured, it was present on both banks except at B:P2 and B:T1. I observed a similar pattern throughout the limited flight dataset, with 59 occurrences of a species on only 1 of the two banks during V1, reducing to 35 occurrences of a species on a single bank during V4.

Notable exceptions to this pattern were species with specific habitat (e.g. *Paranchus albipes*, which has an affinity for running water) or resource (e.g. *Badister unipustulatus* and *Bembidion tetracolum*, snail and aquatic insect hunters, respectively) preferences. Between V1 and V4, the abundance of *P. albipes*, *B. unipustulatus* and *B. tetracolum* decreased from 75, 20 and 85 individuals to 4, 1 and 2 individuals, respectively. During V1, 60%, 50% and 50% of sites supporting *P. albipes*, *B. unipustulatus* and *B. tetracolum* did so on both banks, whereas no site supported these species on both banks during V4. Between V1 and V4, 24 species, 10 of which are associated with wetland habitats, were lost (**Table 13.7**). Over the same period, 10 species were gained, 9 of which were associated with open habitats and trees and 1 (*Bembidion dentellum*) was wetland associated (**Table 13.7**).

5.4 Discussion

Terrestrial arthropods support riparian ecosystem functioning (Ramey & Richardson, 2017), and have communities shaped by seasonal changes in resource provision (Paetzold et al., 2005; Greenwood & McIntosh, 2010), habitat availability/suitability (Paetzold et al., 2008; Sprößig et al., 2020) and connectivity with nearby communities (Shepherd, 2013). Here, I assessed how cross-channel riparian communities around seasonally intermittent streams responded to declining flows and drying (which I hypothesised to be a diminishing barrier to cross-channel dispersal) along a gradient of flow permanence. Cross-channel β diversity was comparable in temporary and perennial reaches and along the drying gradient, contrary to H1 and H2. This comparability suggests that opportunities for mixing across dry channels do not reduce community variability by increasing cross-channel connectivity. Cross-channel β diversity of species capable of flight remained comparable during drying, suggesting their dispersal was not limited by in-channel conditions, contrary to H3. However, the cross-channel β diversity of species with limited flight abilities decreased during drying, suggesting that drying allows greater connectivity between assemblages of non-flying taxa on parallel banks, supporting H3. Collectively, these findings suggest that wet and dry channels can represent similar barriers to dispersal by terrestrial arthropods and thus temporary streams, similar to perennial streams (e.g. Bates et al., 2007; O'Callaghan et al., 2013a), may play a key role in structuring their surrounding terrestrial invertebrate communities.

5.4.1 H1. Cross-channel beta diversity in temporary and perennial reaches

Cross-channel β diversity was comparable regardless of flow permanence regime, contrary to H1, suggesting that seasonal drying events did not increase community similarity in temporary relative to perennial reaches. This may be because, although dry channels are no physical barrier to aerial or terrestrial dispersal, a range of invertebrate taxa avoid crossing linear features (e.g. roads and hedgerows: Mader, 1984; Mauremooto et al., 1995; Andersson et al., 2017). This avoidance may occur because open areas, such as roads or temporary streams before vegetation encroachment, increase predation risks (Brose, 2003; Steward et al., 2022). Additionally, dispersal across unvegetated channels may be discouraged by harsh conditions (e.g. high solar radiation, wind: Yilmaz et al., 2008; Steward, 2012; Langhans & Tockner, 2015), with the abrupt changes in such conditions between in-channel and riparian habitats exerting strong species sorting effects (*sensu* Leibold et al., 2004) on riparian communities. Vegetation may offer shelter from such harsh environmental conditions (e.g. Sánchez & McCollin, 2015), but may also be a barrier to dispersal (Mauremooto et al., 1995; Thomas et al., 1998; Garcia et al., 2000). As encroaching vegetation becomes established in the channel, its density can increase resistance to movement (Heydemann, 1957; Thomas et al., 2006; Allema et al., 2019), representing another gradient along which species may be filtered (i.e. sorted: Leibold et al., 2004) in cross-channel movement attempts. Species capable of flight may have been better able to avoid harsh wet and dry phase in-channel conditions (e.g. inundation, temperature: Lindroth, 1992; Steward, 2012; Langhans & Tockner, 2015), but flight is resource intensive (Lövei & Sunderland, 1996) and, given the comparable habitats on both sides of the channel at most sites, may not have been sufficiently incentivised by habitats/resources on the opposite bank. Thus, invertebrates may perceive wet and dry stream channels as similar barriers to dispersal, fostering comparable cross-channel β diversity in temporary and perennial reaches.

The comparable β diversity of perennial and temporary reaches may alternatively indicate that wet and dry streams are no barrier to cross-channel dispersal (i.e. the community spanned the channel, and was not a metacommunity—two communities partitioned by the channel but connected by dispersal). In particular, species capable of flight may have crossed the channel throughout the study. Additionally, over the study period, vegetation encroached upon the channel and flow velocities declined (possibly related *sensu* Schoelynck et al., 2012; Gurnell et al., 2016) in both temporary and perennial reaches. Collectively, these physical changes may have promoted movement between parallel riparian zones regardless of flow permanence regime, by increasing the proportion of individuals capable of swimming across the channel or allowing invertebrates to climb across the channel on encroaching vegetation (Mundy et al., 2000; Hannam et al., 2008; Riddick, 2008). Flight, climbing or swimming may thus have promoted cross-channel dispersal, resulting in comparable β diversity. Although crossings by flight, climbing or swimming may have allowed cross-channel movement, the studied communities have likely assembled over longer time periods. Over such longer periods, exchanges between parallel riparian zones may have occurred passively (e.g. with invertebrates rafting across the channel on debris: Corti & Datry, 2012; Fleming et al., 2021) or actively, with invertebrates flying across or walking upstream, crossing the dry channel and then walking back down to perennial reaches over multi-generational range expansions and contractions.

5.4.2 H2. Cross-channel beta diversity along a drying gradient

Beta diversity was comparable along the upstream to downstream drying gradient, contrary to H2. Although non-significant, I observed the opposite trend to that hypothesised, with cross-channel β diversity being higher at upstream than downstream sites. This upward trend in β diversity may reflect increasing environmental heterogeneity along the drying gradient (Datry et al., 2016a; Moody & Sabo, 2017; Ruhí et al., 2017), and highlights that community variability occurs both between (Moody & Sabo, 2017) and within sites, with sites which more readily transition between wet and dry phases over time (i.e. those furthest upstream in this study) supporting more variable cross-channel communities. Moody & Sabo (2017) and Sánchez-Montoya et al. (2020) observed that β diversity between sites with contrasting flow regimes was driven by unique species, which did not occur at other sites. Similarly, I observed a greater occurrence of species unique to 1 bank in temporary reaches (Moody & Sabo, 2017; Sánchez-Montoya et al., 2020), suggesting that temporary flow permanence regimes may drive greater cross-channel β diversity, consistent with the theory of patch dynamics (Leibold et al., 2004; Thorp, 2009). However, I studied twice as many sampling sites in temporary relative to perennial reaches, potentially enabling detection of this upward trend in β diversity and unique species in temporary reaches. This highlights that, with greater replication or a longer drying gradient, differences in cross-channel β diversity may be detected.

The downstream to upstream increase in β diversity may reflect that water is the impetus for, and not a barrier to, dispersal. Aquatic food sources (e.g. Paetzold et al., 2005; Greenwood & McIntosh, 2010) and species-specific inundation tolerances likely influence the lateral and longitudinal distribution of terrestrial species around rivers (Eyre et al., 2001b; Bates et al., 2007; O'Callaghan et al., 2013a). For example, some brachypterous species such as *B. tetracolum* are common in riparian habitats (Lott, 2003; Luff, 2007), with the *Bembidion* genus containing strong swimmers (Joy, 1910; Andersen, 1968) that feed on emerging aquatic insects (Hering & Plachter, 1997). Thus, the cross-channel distribution of species such as *B. tetracolum* may be influenced by the presence rather than absence of water because, although an absence of water may facilitate terrestrial cross-channel movements, the resource incentive to remain in or around the channel is lost.

Where the incentive of water availability is lost, longer dry periods and encroaching terrestrial vegetation often means that dry headwater channels resemble surrounding terrestrial habitats. Such upstream habitats typically support generalist species (Eyre et al., 2001a, 2001b), with body types that can navigate dense vegetation (i.e. *strong wedge-pushers*, like *P. madidus*: Evans & Forsythe, 1984; Evans, 1994; Lott, 2001), and which can exploit in-channel opportunities during and immediately after drying (i.e. "clean-up crews": Williams, 2006; Steward et al., 2022). Once any aquatic resources are depleted, assemblages in and around the channel are likely a random subset of patchily distributed species from surrounding habitats (i.e. they occur in the channel due to mass effects: Leibold et al., 2004; Moody & Sabo, 2017). Such species are likely captured while moving in search of resources or breeding partners (Lövei & Sunderland, 1996; Matalin, 2003; Lagisz et al., 2010), potentially accounting for the upward trend in β diversity with distance upstream. Thus, the presence and flow characteristics of water at a site may reduce cross-channel β diversity at perennial, downstream relative to temporary, upstream sites by providing a relatively stable resource around which communities can assemble in space and time.

Beta diversity at the two sites (B:P2 and C:T3) with different land uses on each bank often supported cross-channel communities that were equally or less dissimilar from one another than those at sites with comparable land uses. This comparability suggest that around rivers, a factor other than land use, such as proximity to water (Bates et al., 2007; O'Callaghan et al., 2013a), is more influential in determining the composition (and thus the collective β diversity) of cross-channel communities.

5.4.3 H3. Cross-channel beta diversity during drying

Cross-channel β diversity remained comparable in the all species and flight capable datasets as streams dried, contrary to H3. This comparability likely reflects that species capable of flight could move between banks regardless of in-channel conditions, allowing them to cross the channel throughout the study period (i.e. they were a single community). In contrast, cross-channel β diversity decreased during drying in the limited flight dataset, supporting H3 and suggesting that drying may increase connectivity between parallel riparian zones. Over the study period, decreasing water levels may have made cross-channel dispersal easier for non-flying species (i.e. a factor causing speices-sorting, possibly water in the channel, was weakened/removed), with vegetation encroachment during later visits slowing flow and reducing solar radiation at the channel bed (Steward, 2012; Langhans & Tockner, 2015).

The increased occurrence of non-flying species between V1 (April) and V4 (July) likely reflects a seasonal increase in abundance, which was likely concurrent with an increase in spatial extent as such species spread from overwintering, hatching or larval habitats. For example, increases in the abundance of *P. madidus* can trigger movement in search of resources (Desender et al., 1994; Lövei & Sunderland, 1996; Bennewicz & Barczak, 2020), competitor-free space (Lenski, 1984; Loreau, 1990; Reznikova & Dorosheva, 2004) or egg-laying sites (Rijnsdorp, 1980; van Huizen, 1990; Zhang et al., 1997). The increased occurrence of such brachypterous, wedge-shaped species on both banks (instead of 1 bank), particularly in temporary reaches, also suggests that concurrent declining flows may have allowed dispersal into parallel riparian zones. Thus, although in-channel conditions likely determine the frequency of cross-channel dispersal, resource availability, population dynamics and species-specific life histories may also influence cross-channel β diversity once barriers to dispersal are sufficiently diminished.

The stable nestedness-resultant dissimilarity and relative importance of turnover in driving decreased cross-channel β diversity between V1 and V4 suggests that species colonising from one bank replace those on the newly colonised bank, consistent with previously observed changes in community composition during drying (McCluney & Sabo, 2012; Corti & Datry, 2014; Sánchez-Montoya et al., 2016). This replacement may reflect that, as barriers to ground-based dispersal decline during drying, generalist species such as *P. madidus* colonise and outcompete more specialised species such as *B. unipustulatus* and *B. tetracolum* on the opposing bank, eventually reducing the number of wetland associated species in the community. Generalist species are often more common in upstream assemblages (Eyre et al., 2001a, 2001b), where the streams are theoretically weakest as barriers to dispersal in space and time. Thus, the environmental variability of the streams over time, particularly at upper sites which dried between V3 and V4, may favour generalist species which can better cope with changing conditions (*sensu* Devictor et al., 2008; Datry et al., 2014a). However, the decline of wetland associated species coincided with drying, and *B. unipustulatus* and *B. tetracolum* may have declined in response to a loss of key resources (e.g. aquatic prey), similar to the absence of aquatic-resource reliant beetles alongside ephemeral steams observed by Moody & Sabo (2017).

5.4.4 Conclusions

As temporary streams—the globe's most common lotic waterbody type (Datry et al., 2014b; Messager et al., 2021)—become more prevalent under predicted climatic shifts (Sauquet et al., 2021; Tramblay et al., 2021; Zhang et al., 2023), my study is the first to explore how cross-channel riparian communities respond to river drying. I provide insights as to how more extensive drying may shape such communities, and thus potentially alter ecosystem functioning throughout river networks and their surrounding terrestrial habitats. I found that the environmental heterogeneity of temporary reaches over the study period may have allowed them to support more unique species overall (Moody & Sabo, 2017; Sánchez-Montoya et al., 2020). However, for species with limited flight capabilities, declining flows likely increased cross-channel connectivity, resulting in the replacement of specialised wetland species by generalists (Eyre et al., 2001a, 2001b). Thus, to balance access to key resources such as water with the cross-channel connectivity communities require for long-term stability, management actions should seek to support natural flow regimes that mitigate climate-driven shifts in spatiotemporal extent of drying events.

6 Working 9 to 5: diurnal variability in invertebrate activity does not compromise ecosystem health assessments in dry stream channels

6.1 Introduction

Temporary streams, which alternate between wet and dry phases, are the world's dominant lotic ecosystem type (Messager et al., 2021) and are becoming more common due to climate change and anthropogenic pressures including abstraction (Chiu et al., 2017; Sauquet et al., 2021). The occurrence of both wet and dry phases mean that temporary stream communities include both aquatic and terrestrial fauna (Corti & Datry, 2016; Steward et al., 2022). Thus, both aquatic and terrestrial assemblages require inclusion in holistic assessments of temporary stream health (Stubbington et al., 2018a). However, fluctuating water levels complicate assemblage sampling in temporary streams (i.e. aquatic sampling methods cannot be applied in the dry phase and vice versa), and they are often excluded from biomonitoring programmes, especially terrestrial assemblages during dry phases (Stubbington et al., 2019). Thus, the effectiveness of in-channel dry-phase sampling methods and how terrestrial assemblages may be more readily characterised remains unclear.

Temporary stream communities include groups that rapidly colonise dry channels, are taxonomically diverse and are responsive to a range of environmental stressors, making them ideal biomonitors (Maelfait & Hendrickx, 1998; Rainio & Niemelä, 2003; Koivula, 2011). For example, ground beetles (family: Carabidae) are common in riverine environments including dry streams (e.g. Steward et al., 2011), and differ among sites with varying shade (Thiele, 1977c) and sediment composition (Eyre et al., 2001b; Baiocchi et al., 2012), potentially enabling inference of human impacts on ecosystem health. However, ground beetles entering drying and dry stream channels may also be influenced by natural environmental variability, in particular factors relating to intermittence, including the amount of water remaining in the channel (Bates et al., 2007), the availability of aquatic food resources (O'Callaghan et al., 2013a) and the duration of a dry period (Rosado et al., 2015; Bunting et al., 2021). These intermittence related factors influence species-specific colonisation rates (Bates et al., 2006; Kolesnikov et al., 2012), and thus overall composition. Additionally, post-colonisation activity patterns are further moderated by diurnal/diel cycles and associated temperature shifts (Luff, 1978; Tuf et al., 2012). Thus, characterisation of relationships between terrestrial invertebrate assemblages and human impacts need to take intermittence and short-term (e.g. diurnal) variability into account.

Terrestrial temporary stream invertebrate assemblages are typically sampled using two methods: hand searching and pitfall trapping (e.g. Corti & Datry, 2016; Bunting et al., 2021). Pitfall traps are typically left in place for 7–28 days and collect ground-dwelling species that fall into traps while walking over surface sediments (Siewers et al., 2014). In contrast, hand searches often last 30–60 minutes (Webb et al., 2022), during which a range of taxa, including aerially active species that fly rather than walk between in-channel habitats, are captured (Alexander, 2014; Bunting et al., 2021). Thus, both methods are needed to capture a representative assemblage (Andersen, 1995; Gobbi et al., 2018; Webb et al., 2022), requiring two visits, to set and retrieve pitfall traps, which can be problematic for managers and regulators. In addition to differences in duration and taxa captured between sampling methods, variability introduced by the application of each method may also influence assemblage characterisation (Corti et al., 2013). For example, invertebrate activity fluctuates in response to temperature (Tuf et al., 2012; Saska et al., 2013) and each method may sample a different assemblage during the hottest/coolest part of the day. Therefore, the sampling strategy used to characterise terrestrial assemblages may influence inferences of ecosystem health.

Citizen scientists can increase the collection of data used to assess the health of under-represented ecosystems such as temporary streams. Citizen scientists can produce high-quality datasets that rival those collected by professionals (Kosmala et al., 2016); however, the taxonomic diversity of terrestrial invertebrates means that identifying all groups to lower (i.e. family to species) taxonomic levels is challenging, time-consuming and potentially expensive. Thus, determining an identification level that balances sufficient characterisation of terrestrial assemblages and their responses to environmental conditions with the time and skill sets offered by citizen scientists could promote more frequent and widespread dry phase biomonitoring.

I assessed diurnal variability in the capacity of two methods (hand searching and pitfall trapping) to characterise terrestrial invertebrate assemblages and their responses to environmental conditions in dry temporary stream channels. I hypothesised that: (H1) diurnal changes in environmental conditions (e.g. temperature) and associated changes in invertebrate activity alter assemblages characterisation by the sampling methods; and (H2) these methods can distinguish invertebrate assemblages responses to stressors indicative of human activity despite the effects of intermittence. For each hypothesis, I also assess the influence of level of identification on characterisations of assemblages and their responses to environmental conditions, because identification to the minimum taxonomic level that provides useful ecological information may allow citizen scientists to more easily monitor dry-phase assemblages.

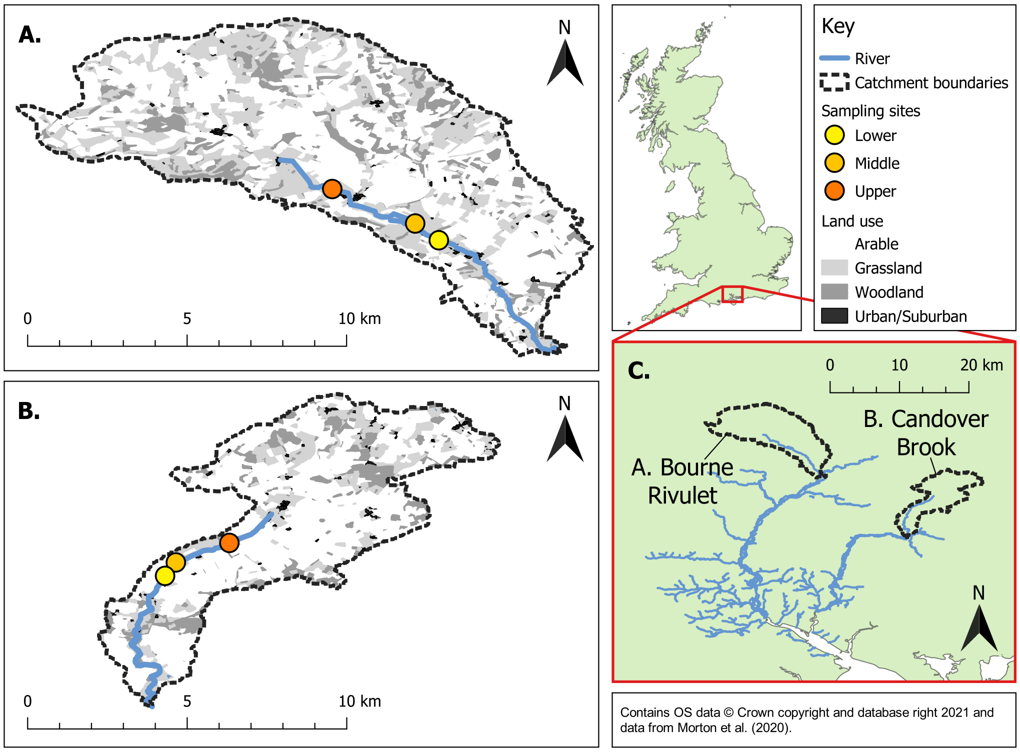
6.2 Method

6.2.1 Study area

This study was conducted in Hampshire, UK, which has a temperate oceanic climate (Cfb: Kottek et al., 2006) with mean (± SD) annual minimum and maximum air temperatures of 6.1 ± 3.9°C and 15.0 ± 5.7°C, respectively and a mean annual rainfall of 754 mm (Met Office, 2022). The study area is underlain by a chalk aquifer, meaning that surface stream flows are controlled primarily by groundwater levels (Sear et al., 1999). When groundwater levels are low, the upper reaches of many streams dry out (Berrie, 1992; Sear et al., 1999). In the study area, dry phases typically occur between late-spring and mid-autumn, but can last from 1 month to several years depending on the longitudinal position of a site in the network (Bunting et al., 2021).

During July 2022, I sampled two streams, Bourne Rivulet and Candover Brook. Their catchments have a comparable amount of arable (Bourne Rivulet and Candover Brook: 50.4% and 51.4%), grassland (mostly pasture: 29.0% and 28.4%), woodland (13.5% and 14.1%) and urban/suburban (3.4% and 4.0%) land use (**Figure 6.1A** and **B**: National River Flow Archive, 2022a, 2022b). I defined sampling sites as an approx. 20 m length of the channel, where in-channel characteristics were representative of the habitats in the wider reach. On each stream, I sampled three sites with temporary flow permanence regimes. The Bourne Rivulet lower and middle sites and the middle and upper sites were separated by 1.2 km and 3.6 km, respectively. The Candover Brook sites were separated by 0.9 km and 2.0 km, respectively. The site locations were selected because, based on observations by the Environment Agency (a regulatory body in England), the upper, middle and lower sites on the Bourne Rivulet typically dry at a similar time (i.e. ±1 week) to their corresponding upper, middle and lower site on the Candover Brook. Sites on both streams dry from upstream to downstream and, at the time of sampling, had been dry for approx.

1–6 weeks. The sites are all in or immediately (i.e. <350 m) downstream of pastures occupied by livestock which have direct access to the channel. The sites receive runoff from roads and pastoral and arable agriculture from upstream reaches during flowing phases, and are mown during dry phases.



Contains OS data © Crown copyright and database right 2021 and data from Morton et al. (2020).

Figure 6.1: Sampling sites and land use in the (A) Bourne Rivulet and (B) Candover Brook catchments, (C) tributaries of the Rivers Test and Itchen, respectively.

6.2.2 Data collection

To characterise environmental conditions that may be influenced by human activities, I visually estimated the relative proportions of each sediment grain-size class (i.e. % gravel, sand and silt to the nearest 5%) at each site. At the channel bed of each site, before collecting each invertebrate sample, I visually estimated shading (% cover to the nearest 10%), and recorded relative humidity (%) and air temperature (°C) at three evenly spaced points. The triplicate readings of humidity and temperature were used to calculate a mean summarising the environmental conditions that correspond to each invertebrate sample.

At each site, I sampled terrestrial invertebrates using two methods, hand searching and short-duration (5–6 hours) pitfall trapping. Briefly, I conducted 30-min hand searches in three periods: in the morning (06.00–07.30), at midday (12.00–13.00) and in the evening (17.00–18.30). Hand searches involved manual disturbance of all habitats between the base of the banks in a 10-m long section of the channel bed and collection of invertebrates using an aspirator (n = 25, 3–6 samples per site). The number of hand search samples per site varied between 3 and 6 because some sites/sampling periods were attended by two researchers, each completing their own hand search in different longitudinally adjoining sections of the channel with comparable habitat conditions. I retained all samples to maximize my characterisation of the assemblages present, and account for the potential variability in my analyses, as detailed below.

Less than 5 m away from the hand search area(s), in a section of the channel with comparable habitat conditions, I set pitfall traps in the morning by burying six plastic cups (8 cm diameter, 10 cm height) in the channel bed, with the cup lip level with surface sediments, and 1/3 filling them with preservative. I emptied the pitfall traps at midday and pooled the contents of the six cups into a single ‘morning’ sample. The traps were then reset at midday and collected in the evening following the same procedure, creating one ‘afternoon’ sample (total n = 12, i.e. one morning and one afternoon sample per site). I identified invertebrates to the lowest practical resolution, with 23, 1, 52 and 24% of individuals identified to species, genus, family and order, respectively.

6.2.3 Data preparation

To avoid artificially altering assemblage composition, I assigned taxa identified to multiple levels (e.g. *Porcellio scaber* and *Porcellio*) to the single most-likely taxon (*sensu* Cuffney et al., 2007).

To test H1–2, I calculated taxa richness (the number of taxa per sample) and activity density (the number of individuals per sample, hereafter ‘abundance’: see Adis, 1979), and summarised assemblage composition (i.e. taxa abundance per sample, hereafter ‘taxa composition’) as a log+1 transformed Bray-Curtis dissimilarly matrix. To characterise the influence of taxonomic resolution on support for each hypothesis, I also calculated family richness (the number of families or higher taxa per sample, where the higher taxon was morphologically distinct, e.g. Hymenoptera other than Formicidae) and order richness (the number of orders per sample). I summarised family and order assemblage composition (i.e. family/order abundance per sample, hereafter ‘family composition’ and ‘order composition’, respectively) as log+1 transformed Bray-Curtis dissimilarly matrices.

6.2.4 Data analysis

To assess the diurnal variability in metrics (i.e. taxa, family and order richness, and abundance) and their capacity to characterise assemblage responses to environmental conditions, I applied a linear mixed-effects modelling (LMM) approach using the R package lme4 (Bates et al., 2015). To meet model assumptions of residual normality (as tested using the DHARMa package:

Hartig, 2020), I log+1 transformed the response variables (richness and abundance). To account for potential sources of additional variability, I modelled richness and abundance with combinations of two potential random factors (hand search sampler and catchment: see Burnham & Anderson, 2002; Brown et al., 2018), and selected the most parsimonious structure using Akaike's information criterion corrected for small sample sizes (AICc). The final structure for richness and abundance models included catchment and sampler, respectively, as a random effect. To determine whether the time of sampling influenced captures by pitfall traps and hand searching (H1), I used sampling period, method and their interaction as predictors (i.e. fixed effects).

To test whether the effects of drying and stressors indicative of human impacts on assemblages can be distinguished (H2), I first used stepwise variance inflation factor analysis to identify collinear abiotic variables (i.e. each grain-size class, shade, relative humidity and temperature, threshold = 3: Zuur et al., 2010). Silt was negatively and positively associated with gravel and shade, respectively. Temperature was negatively correlated with humidity. Therefore, I excluded gravel, humidity and shade from statistical analyses.

To include the effects of drying in the model, I ordered sites from upstream to downstream as a categorical variable (hereafter 'longitudinal position'). Longitudinal position was favoured over a continuous variable (e.g. the absolute distance between sites) because the longitudinal rate of drying (and the associated effects of intermittence on colonisation rates) differs between catchments. The final model included dry phase duration (here represented by longitudinal position) and two-way interactions between longitudinal position and silt, sand and temperature as predictors. For all LMMs, I distinguished the variance explained by the predictors and random factor using marginal (R^2M) and conditional (R^2C) R^2, calculated using the MuMIn package (Bartoń, 2020).

To assess diurnal variability in assemblage composition and its response to environmental conditions, I ran permutational multivariate analysis of variance (PERMANOVA: Anderson, 2017) over 9,999 iterations using the vegan package (Oksanen et al., 2019). For both hypotheses, PERMANOVA predictors followed the structure of predictors outlined for LMMs, used the log+1 transformed Bray-Curtis dissimilarly matrix as a response and included a permutation scheme restricted by catchment. To account for the influence of multiple hand search samplers on compositional analyses, I also ran all PERMANOVAs including only samples collected by the primary hand searcher (who collected samples from all sites during all sampling periods). The reported results refer to analyses of all samples, except where a result differs due to the inclusion of the additional hand search sampler, in which case I report the results of both analyses.

To determine whether significant PERMANOVA results represented true differences in assemblage composition or variability among levels of categorical predictors (i.e. differences in multivariate dispersion among methods, sampling periods and longitudinal positions), I used permutational analyses of multivariate dispersions (PERMDISP2: Anderson, 2006). I calculated dispersion within levels of each predictor (e.g. between hand search samples and between pitfall trap samples in the method predictor), and tested for differences in dispersion using a one-way analysis of variance.

I identified the contribution of each taxon to dissimilarity between categorical predictor levels using similarity percentage analysis (SIMPER: Clarke, 1993) over 9,999 permutations. I considered a taxon as driving differences if SIMPER P <0.05 and contributions to overall differences were ≥5%. For H2, I used Pearson product-moment correlations to characterise relationships between widespread taxa (i.e. those occurring in ≥10 samples) and continuous abiotic predictors (i.e. silt, sand and temperature).

I visualised assemblage composition in relation to method, sampling period and longitudinal position using two-dimensional non-metric multidimensional scaling (NMDS) ordinations based on log+1-transformed Bray-Curtis distance matrices over 500 iterations. Continuous abiotic predictors were applied to NMDS ordinations using envfit (Oksanen et al., 2019).

I conducted all analyses in R v.4.0.3 (R Core Team, 2020).

6.3 Results

Abiotic conditions varied among catchments, longitudinal positions and periods (**Table 6.1**). Silt ranged from 40–80% of total sediment at lower sites and 20–55% at middle sites, being consistently higher in the Candover Brook than the Bourne Rivulet. Upper sites in both catchments had a comparable (30%) amount of silt. Sand comprised 10–20% and 20–40% of total sediment at lower and upper sites, being higher in the Bourne Rivulet. At middle sites, sand ranged from 20–40%, being higher in the Candover Brook. Temperatures ranged from 11.8–29.5°C, with a mean (± SD) of 15.6 ± 2.9°C in the morning, 25.2 ± 2.7°C at midday and 25.7 ± 2.9°C in the evening.

Table 6.1: Mean ± SD air temperature, relative humidity and shade at all sites, sites in the Bourne Rivulet and Candover Brook catchments, sites at lower, middle and upper longitudinal positions and during morning, midday and evening sampling periods.

	Air temperature (°C)	Relative humidity (%)	Shade (%)
All sites	22.2 ± 5.5	59.4 ± 14.7	56.7 ± 35.8
Bourne Rivulet	22.3 ± 5.4	59.0 ± 15.6	33.3 ± 30.8
Candover Brook	22.0 ± 5.9	59.8 ± 14.6	80.0 ± 23.5
Lower	22.4 ± 5.1	61.6 ± 13.7	66.7 ± 44.6
Middle	20.9 ± 6.0	61.5 ± 19.1	48.3 ± 46.2
Upper	23.2 ± 6.2	55.2 ± 12.1	55.0 ± 5.5
Morning	15.6 ± 2.9	77.0 ± 7.6	53.3 ± 42.7
Midday	25.2 ± 2.7	52.0 ± 8.0	65.0 ± 32.7
Evening	25.7 ± 2.9	49.3 ± 7.1	51.7 ± 36.6

I recorded 1,768 individuals from 72 taxa, with an average (mean ± SD) of 11.6 ± 4.0 taxa and 47.8 ± 29.2 individuals per sample. The most abundant orders were Coleoptera (beetles: 432 individuals, 24.4% of total abundance), Araneae (spiders: 331, 18.7%) and Hymenoptera (sawflies, wasps, bees and ants: 259, 14.7%: **Figure 6.2**).

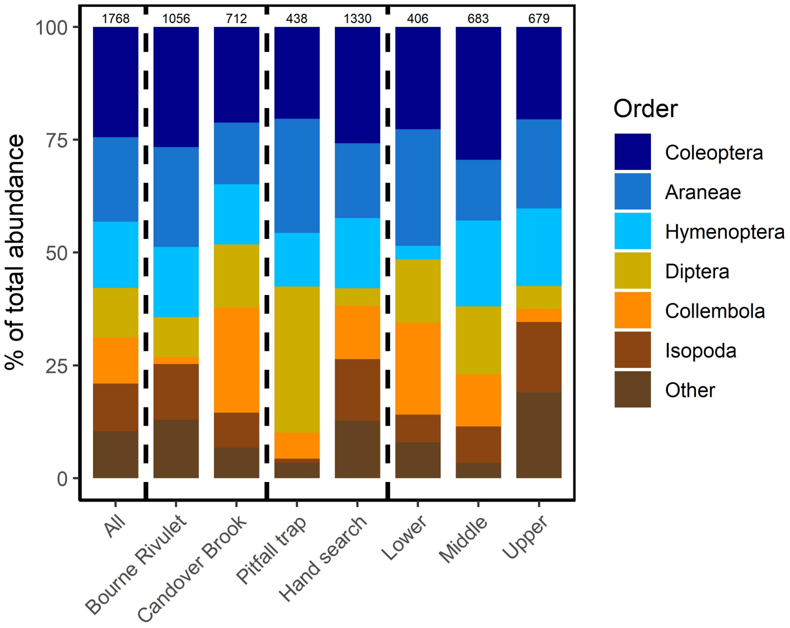


Figure 6.2: The relative abundance of orders collected in the channel, with vertical bars representing all samples and samples collected per catchment, method and longitudinal position. Values at the top of each bar represent the number of individuals.

6.3.1 H1. Diurnal variability of sampling methods

Taxa richness was comparable between pitfall trap (mean ± SD: 10.0 ± 2.7 taxa) and hand search (12.4 ± 4.3) samples ($P = 0.911$: **Figure 6.3A**), and among sampling periods ($P = 0.142$–0.843, $R^2M = 0.115$, $R^2C = 0.268$: **Figure 6.3C**), contrary to H1. Patterns were comparable at taxa, family and order level, with method and sampling period having no effect on richness (all $P > 0.05$: see **Supplementary material – Working 9 to 5: diurnal variability in invertebrate activity does not prevent ecosystem health assessments in dry stream channels**). Similarly, abundance was comparable between methods ($P = 0.770$: **6.3B**) and among sampling periods ($P = 0.059$–0.611, $R^2M = 0.072$ and $R^2C = 0.419$: **Figure 6.3D**).

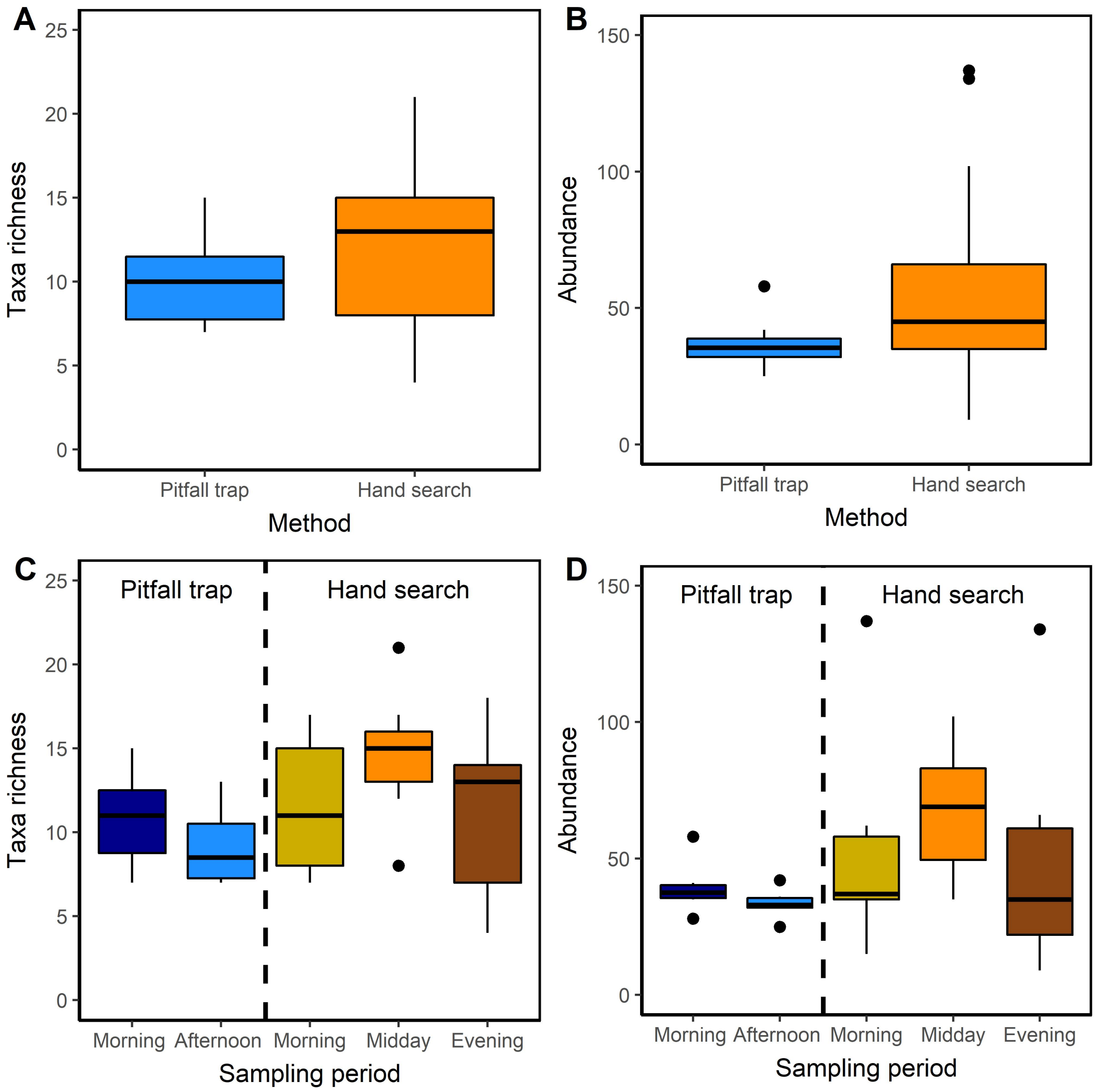


Figure 6.3: The taxa richness (A and C) and abundance (B and D) of assemblages sampled by pitfall trapping and hand searching methods (A and B) and sampled by pitfall trapping in the morning and afternoon, and by hand searching in the morning, midday and evening sampling periods (C and D). The centre line represents the median, boxes represent the interquartile range, whiskers represent the minimum/maximum values which are within 1.5× the interquartile range of the first and third quartiles and filled circles represent outliers.

Taxa composition differed between hand search and pitfall trap samples (PERMANOVA: F (1) = 4.059, P <0.001, R^2 = 0.108), with assemblages being more consistently characterised by pitfall trapping (PERMDISP2: F (1) = 31.089, P <0.001: **Figure 6.4A**). Differences between methods were driven by adult Diptera (true flies, SIMPER: 12.9% of dissimilarity, P <0.001), which were captured more frequently by pitfall trapping (mean ± SD individuals per sample: 11.7 ± 6.2) than hand searching (1.8 ± 2.0). Hand search samples plotted in two areas (**Figure 6.4A**): samples with negative NMDS1 scores were collected from four sites (upper Candover Brook and all Bourne Rivulet sites) with less shading (mean ± SD: 34 ± 26% of the site) and silt (28 ± 7% of total sediment) than samples with positive NMDS1 scores (96 ± 7 and 71 ± 13%, respectively). The taxa composition of pitfall trap and hand search samples was unaffected by sampling period (F (3) = 0.550, P = 0.91, R^2 = 0.044: **Figure 6.4B**), contrary to H1. No differences in dispersion among sampling periods was detected for pitfall trapping (P = 0.644) or hand searching (P = 0.332–0.882). Family and order level compositional responses to method (PERMANOVA: P <0.001) and sampling period (PERMANOVA P >0.05) were comparable to taxa level responses (**Supplementary material – Working 9 to 5: diurnal variability in invertebrate activity does not prevent ecosystem health assessments in dry stream channels**).

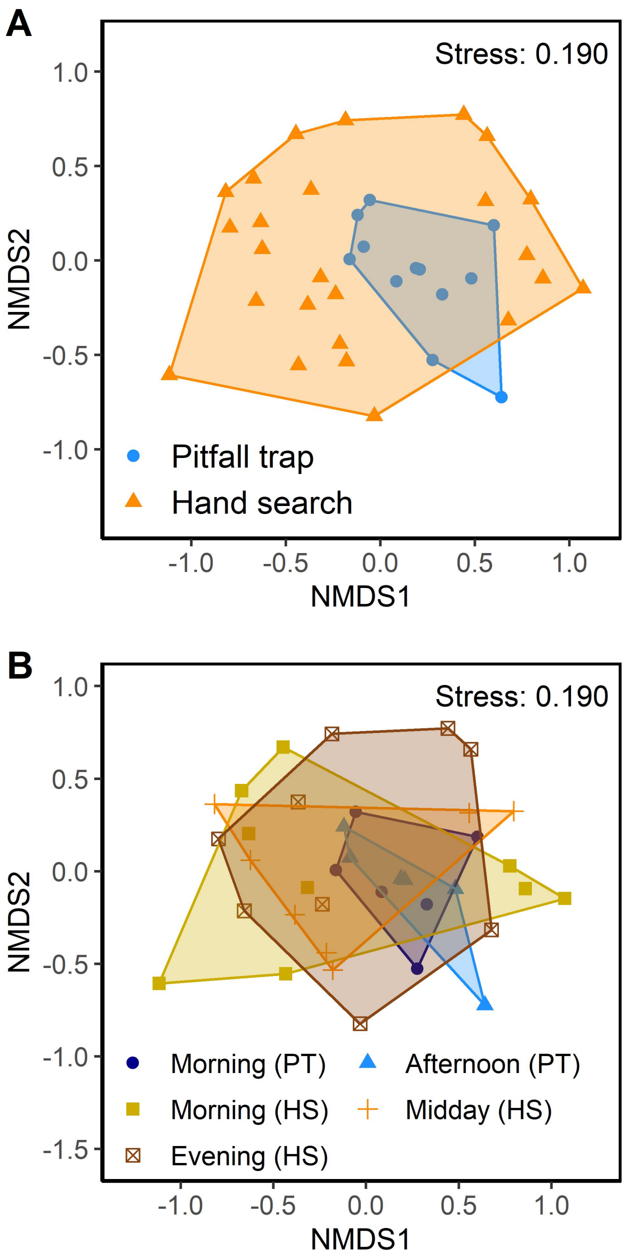


Figure 6.4: Non-metric multidimensional scaling of terrestrial invertebrate taxa composition sampled (A) by hand searching and pitfall trapping, and (B) by pitfall trapping (PT) in the morning and afternoon, and by hand searching (HS) in the morning, midday and evening sampling periods.

6.3.2 H2. Detecting responses to anthropogenic stressors despite drying

Longitudinal position (a proxy for dry phase duration), silt, sand and temperature had no effect on taxa richness (all P = 0.095–0.978, R^2M = 0.255, R^2C = 0.613: **Figure 6.5**) or abundance (all P = 0.157–0.745, R^2M = 0.217, R^2C = 0.487: **Figure 6.6**), contrary to H2. Like taxa richness, family and order richness was not affected by longitudinal position, silt, sand or temperature (all P >0.05: **Supplementary material – Working 9 to 5: diurnal variability in invertebrate activity does not prevent ecosystem health assessments in dry stream channels**).

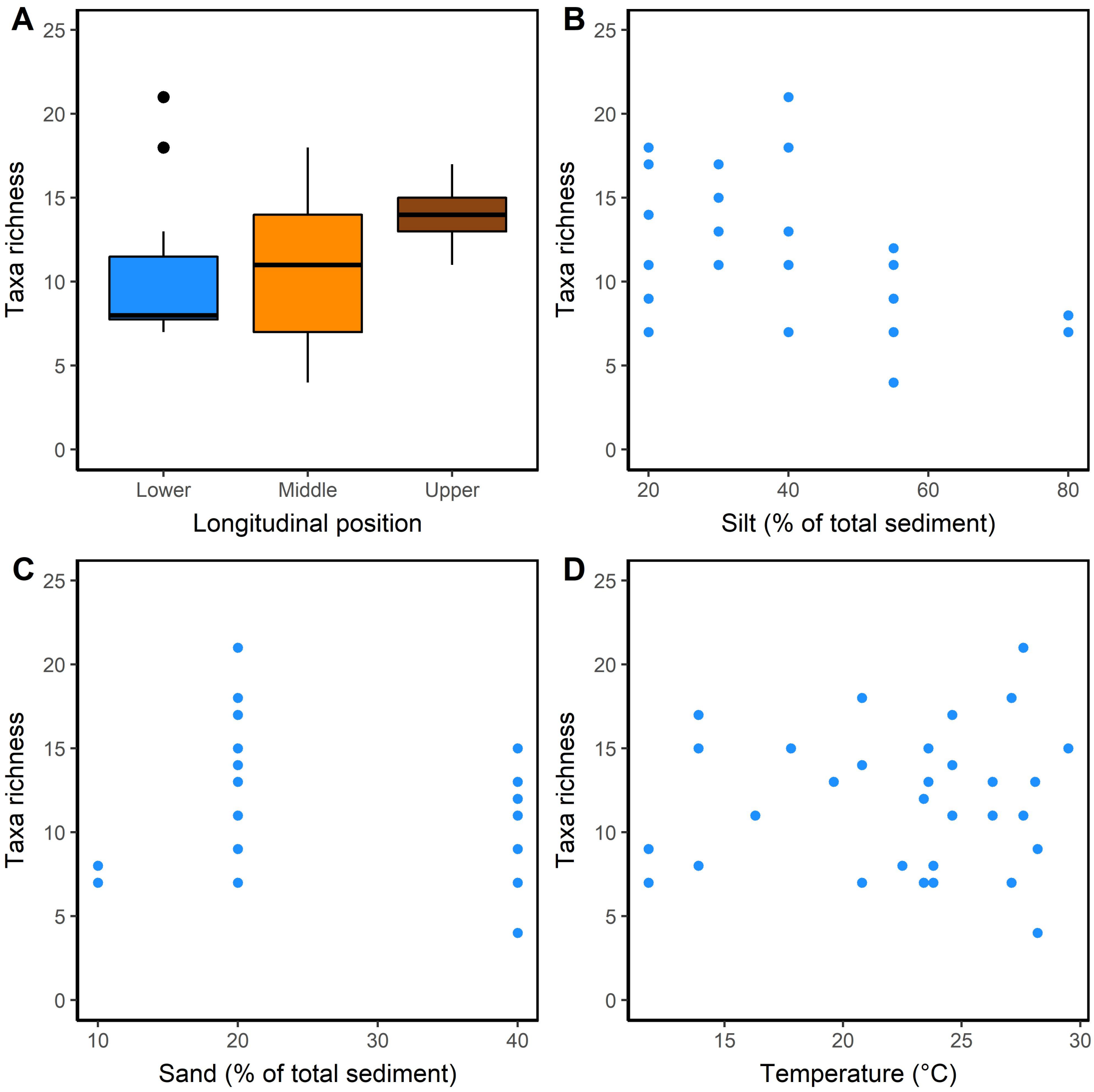


Figure 6.5: The taxa richness sampled at differing longitudinal positions (A) and relationships between taxa richness and silt as a proportion of total sediment (B), sand as a proportion of total sediment (C) and air temperature at the channel bed (D).

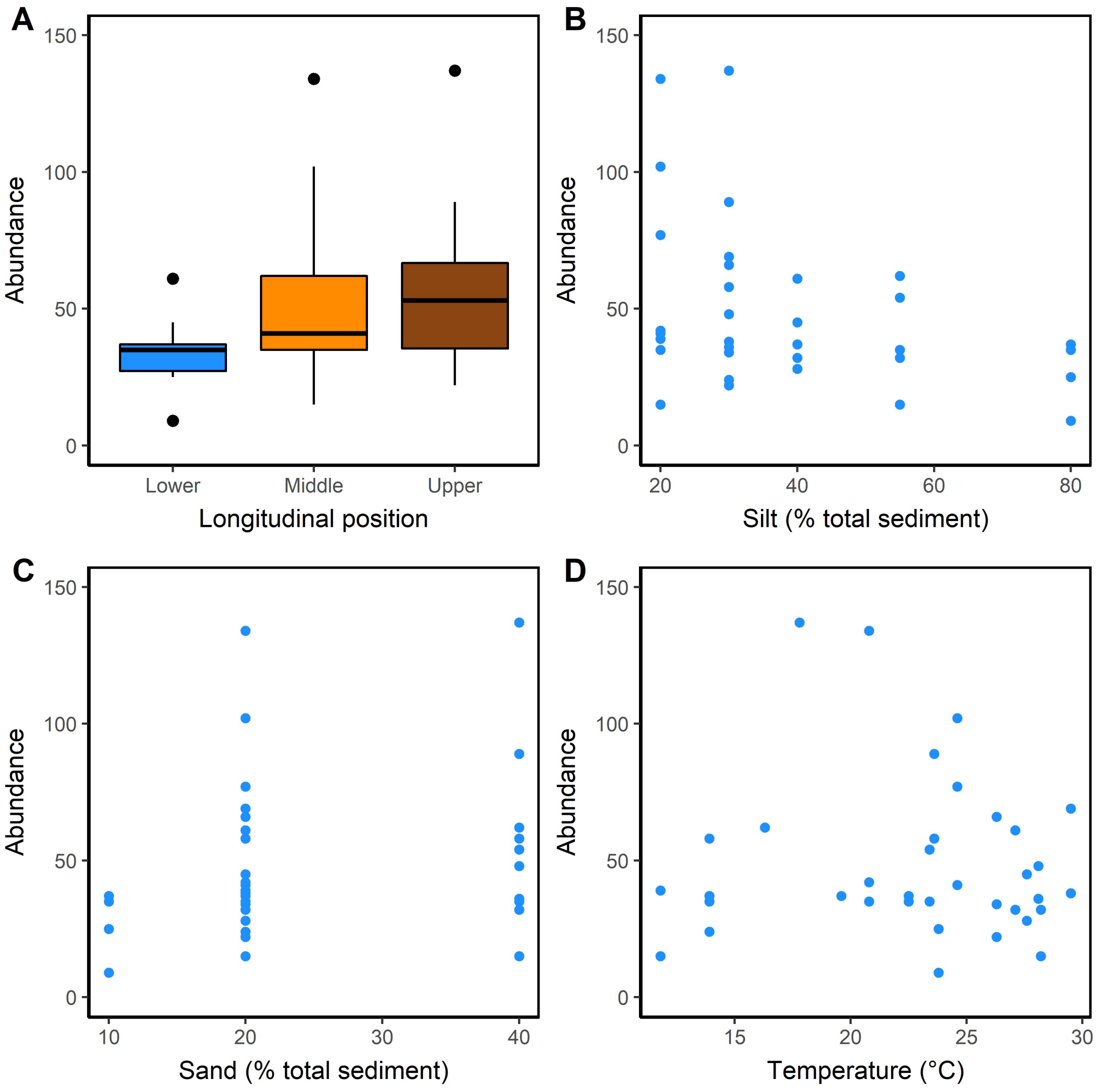


Figure 6.6: The abundance of invertebrates sampled at differing longitudinal positions (A) and relationships between abundance and silt as a proportion of total sediment (B), sand as a proportion of total sediment (C) and air temperature at the channel bed (D).

Taxa composition, but not multivariate dispersion, differed between upper, middle and lower sites (PERMANOVA: F (2) = 5.697, P <0.001, R^2 = 0.198, PERMDISP2: F (2) = 2.059, P = 0.143: **Figure 6.7A**). Compositional differences between upper and middle sites were caused by the spider family Lycosidae (SIMPER: 8.3% of dissimilarity, P <0.001, **Table 6.2**), whereas differences between middle and lower sites were caused by spider family Linyphiidae (8.1%, P = 0.026), the beetle family Staphylinidae (7.0%, P = 0.003) and adult Diptera (10.1%, P = 0.029, **Table 6.2**). Differences between upper and lower sites were driven by Lycosidae (9.8%, P <0.001), Linyphiidae (7.8%, P = 0.046) and the millipede family Craspedosomatidae (6.2%, P = 0.008, **Table 6.2**). Taxa, family and order composition responded comparably to longitudinal position (**Supplementary material – Working 9 to 5: diurnal variability in invertebrate activity does not prevent ecosystem health assessments in dry stream channels**).

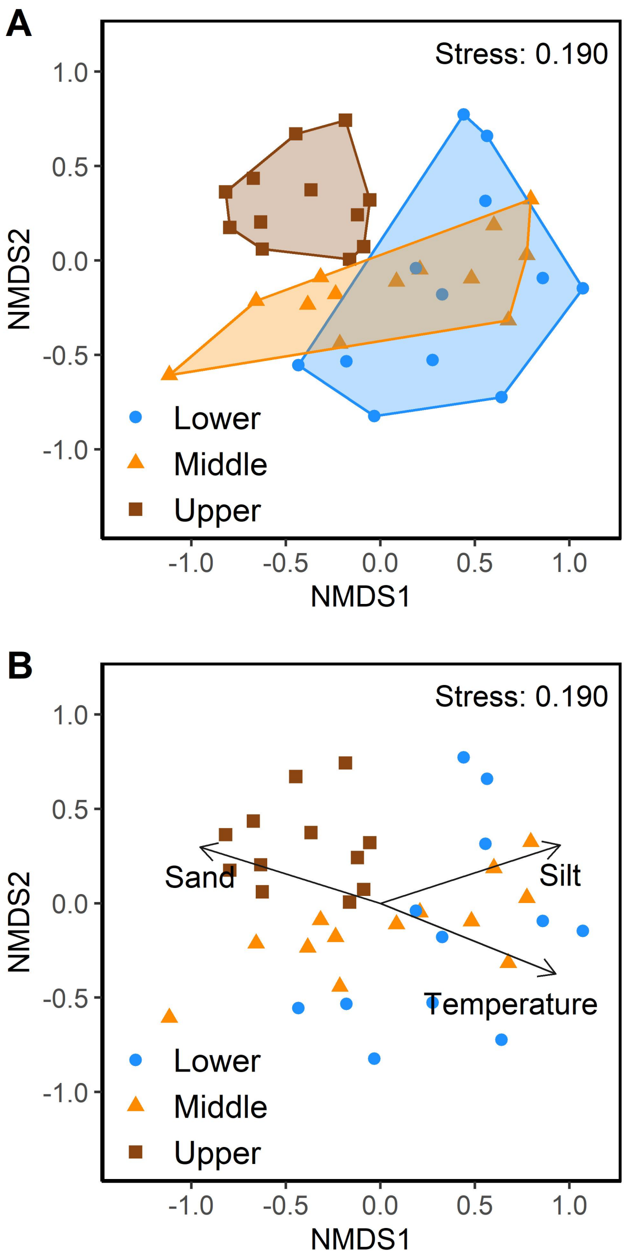


Figure 6.7: Non-metric multidimensional scaling of terrestrial invertebrate taxa composition as captured (A) at lower, middle and upper sites (i.e. longitudinal position), and (B) in relation to longitudinal position, silt, sand and temperature gradients.

Table 6.2: Mean ± SD abundance of taxa contributing to differences among lower, middle and upper sites.

Taxon	Lower	Middle	Upper
Lycosidae	0.6 ± 1.0	2.2 ± 4.6	9.4 ± 5.6
Linyphiidae	7.8 ± 7.0	4.8 ± 5.0	1.8 ± 3.1
Staphylinidae	1.9 ± 2.1	7.8 ± 12.7	2.4 ± 2.1
Diptera (adult)	4.8 ± 6.2	7.5 ± 7.2	2.5 ± 3.2
Craspedosomatidae	0.7 ± 0.9	0.5 ± 0.8	8.6 ± 23.2

Silt and temperature influenced taxa composition (PERMANOVA: F (1) = 3.080–8.033, P = <0.001–0.004, R^2 = 0.053–0.139: **Figure 6.7B**), but sand had no effect (F (1) = 2.269, P = 0.079, R^2 = 0.039). No interaction between longitudinal position and silt, sand or temperature was detected (P = 0.139–0.206). Silt positively correlated with Collembola (springtail) abundance (Pearson's *r* = 0.520, P = 0.001, n = 28), and negatively correlated with Lycosidae (*r* = -0.453, P = 0.005, n = 21) and Formicidae (ant, *r* = -0.436, P = 0.007, n = 23) abundance. Both Lycosidae and *P. scaber* (woodlouse) abundance positively correlated with sand (*r* = 0.403, P = 0.013, n = 21 and *r* = 0.361, P = 0.028, n = 15, respectively). The abundance of no taxon correlated with temperature.

When re-analysed to include data collected by only the primary hand searcher, no significant relationship between temperature and taxa composition was detected (F (1) = 1.920, P = 0.066, R^2 = 0.043), but all other relationships were comparable. Taxa, family and order composition responded comparably to silt, sand and temperature (**Supplementary material – Working 9 to 5: diurnal variability in invertebrate activity does not prevent ecosystem health assessments in dry stream channels**).

6.4 Discussion

Terrestrial temporary stream invertebrate assemblages are often excluded from biomonitoring programmes (Stubbington et al., 2019) because sampling can be resource intensive for regulators, manager and citizen scientists, requiring multiple site visits (sometimes up to 28 days apart: Drake et al., 2007; Jung et al., 2019). Therefore, I assessed the effectiveness of two short-duration, dry-phase sampling methods for characterising terrestrial temporary stream invertebrate assemblages and their responses to environmental stressors that may indicate human impacts. I found that characterisations of biodiversity using metrics (i.e. richness and abundance) were comparable when using hand searching or pitfall trapping at any time of day, and among sites with different longitudinal positions (a proxy for dry phase duration), silt, sand and temperatures, contrary to H1 and H2. This comparability suggests these metrics may be insufficient to detect the effects of natural and anthropogenic stressors on dry-phase assemblages. Assemblage composition differed between methods, but not among sampling periods, suggesting diurnal activity patterns (e.g. those driven by temperature changes: Tuf et al., 2012) need not hinder assemblage characterisation in dry temporary streams, contrary to H1. Differences in assemblage composition were detected among sites with differing drying durations, silt, sand and temperatures, suggesting that the effects of natural and anthropogenic stressors can be detected despite the effects of intermittence (H2).

6.4.1 H1. Differences in captured assemblages between methods and sampling periods

The richness, abundance and composition of invertebrate assemblages captured was comparable throughout the day, contrary to H1 and suggesting that samples collected at any time of day may provide comparable assemblage characterisations, despite potential responses to diurnally variable environmental conditions (e.g. temperature: Tuf et al., 2012; Saska et al., 2013). The lack of diurnal differences among pitfall trapped assemblages may partly reflect that morning and afternoon samples captured similar assemblages around midday. In contrast, hand searches were more temporally distinct, being conducted for 30 minutes in the morning, at midday and in the evening, and thus their comparable assemblages are likely a truer representation of the in-channel communities present at different times of day. Their comparability may reflect that air temperatures were relatively high, being consistently above 11°C which correlates with higher development rates, activity and hunting among terrestrial invertebrates (Tuf et al., 2012; Vangansbeke et al., 2015;

Fricke et al., 2022), allowing individuals to become and remain active from morning to evening. Similarity among sampling periods may also have been influenced by the 76% of individuals that were identified to family or above, obscuring differences that could have been detected with a finer taxonomic resolution. However, invertebrate responses are typically consistent between species and family level (Pik et al., 1999; Timms et al., 2013) and no taxon from groups that were identified to species or genus (e.g. Carabidae) was influential in driving overall dissimilarity.

Richness and abundance were comparable between hand searched and pitfall trapped assemblages, suggesting—subject to comparable sampling effort—either method may provide similar estimates of such metrics, which could be used for basic comparisons between sites or habitats (Fleishman et al., 2006). A lack of consistent differences between methods is commonly reported (e.g. Zanetti et al., 2016; Privet et al., 2020) and the observed comparability in this study may reflect an incidental comparability of effort between the shorter (0.5 h), active hand searches and the longer (5–6 h), passive pitfall traps. Regardless of cause, comparable richness and abundance values here and in other studies (e.g. Moorhead & Philpott, 2013; Croft-White et al., 2021) can mask differences in assemblage composition. Thus, inferences of ecosystem health in temporary streams should be made from assemblage composition as characterised using a consistent sampling approach that includes both pitfall trapping and hand searching (e.g. Webb et al., 2022).

Differences in the assemblages captured by pitfall trapping and hand searching likely reflect taxon-specific differences in abundance, habitat preferences and biological traits (e.g. Lang, 2000; Engel et al., 2017). For example, the taxon responsible for the greatest proportion of dissimilarity (adult Diptera) are motile fliers, making them difficult to collect using aspirators during hand searches. Thus, a standardised multi-method approach (e.g. Webb et al., 2022) should be used to maximise characterisations of assemblages composition in dry temporary streams. However, one method may be sufficient to detect variability attributable to human influences, as demonstrated by the differing composition of hand search samples from sites with different amounts of shade and silt. Similarly, pitfall traps may capture the majority of taxa captured by active searching methods (e.g. hand searching, quadrat sampling) if left in place for longer durations (Corti et al., 2013), and thus may also allow inference of environmental variability (e.g. Eyre et al., 2001b).

6.4.2 H2. Distinguishing the effects of drying from stressors indicative of human impacts

Any differences in assemblage composition caused by environmental conditions were not detected by metrics, contrary to H2. Despite such difficulties in distinguishing the effects of drying and other stressors (Stubbington et al., 2022c), however, hand searching and pitfall trapping detected both the influence of dry phase duration (represented here by longitudinal position) and stressors that can indicate human impacts on assemblage composition, supporting H2. The taxa influenced by longitudinal position often differed from taxa influenced stressors indicative of human impact, potenitally enabling distinction of different environmental effects. For example, spiders and millipedes were most responsive to longitudinal position, with Lycosidae and Craspedosomatidae preferring upstream habitats and Linyphiidae preferring downstream habitats. This may reflect that more recent water loss at downstream sites favour Linyphiidae, which may prefer moist sediments (Hayes, 2022), prey upon aquatic invertebrates (Power & Rainey, 2000; Kato et al., 2004), have a high inundation tolerance (Hayashi et al., 2015) and a greater ability to colonise newly dry habitat (being capable of aerially dispersing by “ballooning”: Adis & Junk, 2002; Bell et al., 2005; Blandenier, 2009), relative to Lycosidae and Craspedosomatidae. Sites with a higher proportion of silt typically supported fewer Formicidae and Lycosidae, likely reflecting their use of interstitial spaces for hunting or shelter from predation and heat (Uetz, 1979; Sosiak & Barden, 2021).

Indices, such as the BMWP-style indices used in aquatic biomonitoring (Armitage et al., 1983), are often used to infer human impacts on an ecosystem. The taxon-specific preferences to longitudinal position, silt and sand detected here highlight that such biomonitoring indices could potentially be developed or existing indices (e.g. Solascasas et al., 2022) adapted to characterise terrestrial assemblage responses to a range of impacts in dry temporary streams. However, taxa that are responsive to both inundation and other human-impacted environmental conditions (e.g. Formicidae, which respond to inundation *and* silt: Hertzog et al., 2016) may confound responses to any such index. Thus, further taxa whose responses to human impacts can be detected despite any concurrent response to flow permanence require identification.

6.4.3 Implications for monitoring and further study

The methods' ability to distinguish the effect of intermittence from stressors indicative of human impacts highlight that, like aquatic assemblages and physical habitat characteristics (e.g. Gething et al., 2022; Stubbington et al., 2022c), terrestrial assemblages have the potential to contribute to ecosystem health assessments (Steward et al., 2018; Marshall et al., 2020; Hayes, 2022). However, further research on whether the habitat preferences of terrestrial taxa are transferable to dry temporary streams is required to enable the development of dry-phase biomonitoring indices that indicate assemblage responses to natural and anthropogenic stressors (e.g. moisture availability, nutrient enrichment, channel modification). Further research is also needed on the colonisation of dry and drying channels, and the subsequent spatiotemporal arrangement of terrestrial assemblages in temporary streams. For example, terrestrial assemblages remain in distinct lateral zones relative to the waterline during wet phases (Bates et al., 2007), but how long it takes this zonation to breakdown during/after drying is unclear. Additionally, this study considered samples collected throughout the day but many terrestrial invertebrates are nocturnal (e.g. Luff, 1978) further highlighting that the spatiotemporal dynamics of terrestrial assemblages during and after drying could be key in determining when, where and how to collect representative samples.

To promote the inclusion of terrestrial assemblages in assessments of ecological health, sampling procedures should maximise usable ecological information while minimising the time and resources expended (Stenzel et al., 2017; Hoffmann et al., 2019). Differences in the assemblages captured by pitfall trapping and hand searching suggest that using one of the two methods is not an option for increasing efficiency, and that both methods are needed to comprehensively characterise dry-phase assemblages (Andersen, 1995; Gobbi et al., 2018; Bunting et al., 2021). Longer sampling periods more robustly characterise assemblages (Niemelä, 1990), although better characterisations can also be obtained by increasing the spatial, rather than temporal, extent of surveys (e.g. by setting more pitfall traps: Lövei & Magura, 2011). Thus, the comparability of samples collected throughout the day suggest that shorter sampling durations (i.e. <1 d) may be applied to characterise terrestrial assemblages and their responses to environmental conditions when time or resources prevent longer sampling periods, with more traps/searching a wider area being a potential way to compensate for these shorter sampling periods (Lövei & Magura, 2011).

Taxa, family and order level information provided consistent support for/against each hypothesis, suggesting that coarser identification levels may be sufficient, enabling samples to be processed more quickly and with less training. Comparable richness and abundance despite differences in environmental conditions (e.g. drying duration) have been reported in the study area (Bunting et al., 2021). However, such comparability suggests that finer levels of identification may be required to elucidate environment–assemblage relationships, because such metrics do respond to drying (McCluney & Sabo, 2012), sediment composition (Sadler et al., 2004; Baiocchi et al., 2012) and temperature (Müller et al., 2015; Liu et al., 2021). Thus, although less comprehensive than longer, spatially extensive multi-method samples identified to species level, monitoring using multiple methods over shorter periods with an intermediate level of identification may provide managers, regulators and citizen scientists with opportunities to increase the representation of terrestrial assemblages in ecosystem health assessments for temporary streams.

7 Living on the edge: predicting invertebrate richness and rarity in disturbance-prone aquatic–terrestrial habitats

7.1 Introduction

Inundation by water—from gradual rewetting to major flood events—characterises disturbance in aquatic–terrestrial habitats. Inundation promotes high rates of trophic exchange and high habitat heterogeneity at small spatial scales, fostering unique invertebrate communities (Sabo et al., 2005; Soininen et al., 2015; Schindler & Smits, 2017), which include rare and specialist species (Ramey & Richardson, 2017). However, anthropogenic activities are altering the hydrological and morphological characteristics of aquatic–terrestrial habitats, reducing or eliminating inundation-prone areas and their associated communities (Paetzold et al., 2008; Kennedy & Turner, 2011). Effective monitoring strategies are thus needed to characterise and protect biodiversity within aquatic–terrestrial habitats.

Aquatic–terrestrial riverine habitats are inherently difficult to biomonitor due to temporal variability in events such as inundation (Bates et al., 2006; O'Callaghan et al., 2013a; Sarneel et al., 2019). For example, mobile, inundation-tolerant ground beetles (Coleoptera: Carabidae) colonise newly dry habitats within days (Bates et al., 2007; O'Callaghan et al., 2013a). However, less-mobile species avoid recently inundated habitats (O'Callaghan et al., 2013a). Thus, the outcome of terrestrial biomonitoring in disturbance-prone habitats depends on species-specific responses to events like inundation. Additionally, unpredictable inundation can render standard terrestrial sampling techniques ineffective. For example, passive sampling devices (e.g. pitfall traps) left in aquatic–terrestrial habitats for days-to-weeks may be lost if water levels rise. Equally, rapid bioassessment methods (e.g. ground searching: Webb et al., 2022) can only be used when in-channel habitats are not inundated. Thus, the relative timing of inundation and sampling events influence both sampling success and the species captured, hindering estimation of biodiversity.

Difficulties in characterising communities within aquatic–terrestrial riverine habitats leave them largely excluded from biomonitoring programmes (Skoulikidis et al., 2017; Stubbington et al., 2018a). However, terrestrial invertebrates respond predictably to long-term average habitat conditions (Rainio & Niemelä, 2003; Koivula, 2011), and habitat survey data may thus enable estimation of assemblage characteristics such as taxonomic richness, rarity and composition. Professional habitat survey protocols (e.g. Agency, 2017) are typically complex, requiring equipment and extensive training to complete, which makes them unsuited to the widespread and frequent assessments needed to characterise aquatic–terrestrial riverine habitats. However, simpler standardised habitat surveys that can be conducted with limited training and equipment have been developed for citizen scientists (e.g. Shuker et al., 2017). Such habitat survey data can be used to calculate simple, unimetric indicators that characterise key habitat features such as water availability, or be combined into multimetric indicators that summarise overall conditions (Gurnell et al., 2020a). Many such habitat indicators represent features that influence terrestrial fauna, such as habitat complexity, which increases both alpha and beta diversity (Lassau et al., 2005; Lengyel et al., 2016), and could thus enable prediction of invertebrate assemblage characteristics in aquatic–terrestrial riverine habitats.

I evaluated whether habitat indicators can predict metrics characterising terrestrial invertebrate assemblages, and could thus be used to increase their representation in biomonitoring programmes. Specifically, I selected terrestrial beetles (**Table 15.1**) to represent invertebrate assemblages, as a ubiquitous, abundant and diverse group within aquatic–terrestrial riverine habitats (Sadler et al., 2004) which have a wide range of well-known habitat preferences (Rainio & Niemelä, 2003; Webb et al., 2018) and which respond to multiple environmental drivers (e.g. moisture, shade, temperature: Koivula, 2011). In addition, some terrestrial beetles are specialists that rely on aquatic–terrestrial riverine habitats for survival (Bates et al., 2005), many of which are rare (Webb et al., 2018) and thus require effective monitoring and protection.

Beetle assemblage composition differs both spatially between and temporally within aquatic–terrestrial habitats. I therefore selected biotic metrics that characterise assemblages regardless of compositional differences (e.g. taxonomic richness), to allow application of my predictive method beyond the habitats tested herein. I hypothesised that habitat indicators can be used to predict beetle assemblage taxonomic richness and conservation status (i.e. rarity) in aquatic–terrestrial riverine habitats (H1). I tested this hypothesis in two habitat types: exposed riverine sediments (ERS) and temporary streams. ERS are fluvially deposited sediments within river channels with perennial flow (Sadler et al., 2004; Bates et al., 2005), whereas temporary streams are those in which surface sediments periodically dry. Both are widespread (O'Callaghan et al., 2013b; Datry et al., 2014b), biodiverse (Sadler et al., 2004; Corti & Datry, 2016) and increasingly threatened by anthropogenic activities (Paetzold et al., 2008; Acuña et al., 2014). I also compared the performance of different habitat indicators, and hypothesised that more complex multimetric indicators can characterise variability in faunal ERS metrics more effectively than unimetric indicators (H2).

7.2 Method

7.2.1 Data collection

ERS dataset

I used data collated by Buglife (an invertebrate conservation charity) and

Natural England (an advisory body to the U.K. government) from baseline surveys that aimed to characterise the beetle fauna of ERS. The dataset comprises 91 terrestrial beetle assemblage samples collected between May and July in 2003–2019 at 39 ERS sites on nine rivers in England and Wales. Sites were approx. 5–10 m in length and were positioned to maximise the diversity of fauna sampled (see Drake et al., 2007). All sites were rural, being surrounded by arable land, pasture and/or semi-natural scrubland (**Figure 15.1**), with >80% of samples collected from sites which are nationally protected for their wildlife, geomorphology or geology (Natural England, 2021).

Samples were collected by pitfall trapping (n = 34) or ground searching (n = 57: Webb et al., 2022). Pitfall traps comprised buried plastic cups (8 cm diameter, 10 cm height), with the cup lip level with the sediment surface. To preserve beetles, each trap contained 100 ml ethylene glycol and 5 ml detergent. At each site, seven to 10 traps set 2 m apart were left in place for 14 days. On retrieval, all traps from a site were pooled into one sample. Ground searches lasted 1 h, during which time all habitats between the base of the bank and the water's edge along approximately 10 m of the channel were manually disturbed and all organisms were collected using an aspirator. Terrestrial beetles were identified to species level and recorded as present.

I used the Modular River Survey (MoRPh: Shuker et al., 2017) to characterise the physical habitat at each site from five to 10 photographs taken by field surveyors at the time of beetle sampling to depict bank-top land use, bank features and the beetle sampling area. MoRPh surveys are usually conducted in the field, but the type and extent of habitat features can be quantitatively estimated using photographs (Hill et al., 2005) and photographs are used to remotely verify MoRPh data (Gurnell et al., 2020a). Thus, given the large number of photographs from each site, which were taken by trained ecologists seeking to record habitat conditions, the photographs provide an adequate record of habitat conditions from which to complete a MoRPh survey.

Minor site-specific features may have been absent or unidentifiable from the photographs, aligning with MoRPh's exclusion of features covering <5% of the survey reach in the calculation of indicators.

I calculated three standardised indicators that represent habitats from the water's edge to 10 m lateral to the bank top from the MoRPh data using Gurnell et al. (2020b). I selected each indicator based on evidence that the habitat conditions it characterises can influence beetle assemblage responses (**Table 15.2**). Habitat complexity (hereafter, HabComplex) is a multimetric indicator calculated from four unimetric components: (1) the type and extent of wood habitat (Wood, e.g. fallen trees, exposed roots); (2) the type and extent of bank-top water features (WatFeat, e.g. ponds, side channels); (3) the type and extent of natural bank-face features (Bank face, e.g. vegetated bars, riverine cliffs) and (4) the type and extent of natural bank profiles (Profiles, e.g. overhanging, gentle). The other two indicators are unimetric, characterising the number of riparian and bank-face vegetation morphotypes (VegMorph, i.e. short grass/herbs, tall grass/herbs, scrub/shrubs, trees/saplings) and the type and extent of anthropogenic land cover (AnthroCover, e.g. industrial buildings, residential buildings, grazed land, plantation woodland). During calculation, the MoRPh method scales indicators so the probable range of values is 0 (extremely low) to 10 (extremely high: Gurnell et al., 2020b).

Temporary stream dataset

I combined two temporary stream datasets. The first dataset, published in Bunting et al. (2021), was collected from five sites in one dry stream (Candover Brook) in south central England between June and September 2019 (**Figure 15.2**). The catchment is dominated by arable and pastoral agriculture (51% of total catchment land use), with minimal urban areas (4%). Based on observations from site visits by the Environment Agency (a regulatory body in England), sites had dried 2–181 weeks (±1 week) prior to sampling. Beetles were collected by ground searching (n = 5) and pitfall trapping (n = 10) as described for the ERS dataset, except pitfall traps were left in place for 7 days, not 14 days. The second dataset was collected from one site in each of two dry streams (the Rivers Misbourne and Ver) north of London, England between May and September 2019 (**Figure 15.3**). These sites were within or in direct proximity to urban areas which comprise 16%–19% of land use, with wider catchment land uses being primarily arable and pastoral agriculture (34%–51%). Sites had dried 1–220 weeks before sample collection. Beetles were sampled by pitfall trapping (n = 8) as described for the ERS dataset; no ground searching was undertaken. For all temporary stream sites, MoRPh surveys were conducted in the field at the same time as beetle sampling. Terrestrial beetles were identified predominantly to species level (61% of individuals), except some small and ambiguous specimens which were resolved to genus (11%) or family (28%).

7.2.2 Data analysis

Data preparation

In calculating metrics to test H1–2, I considered pooled pitfall trap samples as comparable regardless of the number of individual pitfall traps they contained because increased sampling effort (i.e. deploying more traps) has a limited impact on capture rates (Brose, 2002; Webb et al., 2022). I also considered pooled pitfall traps and ground searches as comparable, because both methods can capture a similar number of taxa (e.g. Melbourne, 1999; Phillips & Cobb, 2005; Zanetti et al., 2016; Privet et al., 2020).

To test H1–2, I calculated two biological metrics: taxonomic richness (i.e. the number of taxa per sample, using the vegan package: Oksanen et al., 2019) and the sum of species quality scores (sSQS), an index of conservation status (Webb et al., 2018). To avoid inflation of these biotic metrics, I assigned beetles in the temporary stream dataset that were identified to multiple taxonomic levels to a most likely taxon (Cuffney et al., 2007). To calculate sSQS, I obtained a score for each species based on their threat and rarity status from a national invertebrate conservation database (*Pantheon*: Webb et al., 2018). Scores range between 1 and 32, with higher values indicating rarer, more threatened species (**Table 15.3**). I assigned a value of 1 (common native species) to unscored native species and specimens identified to genus or family. To caluclate sSQS, I summed scores for all taxa in a sample. I also identiifed specialist species (e.g. wood specialists) using Pantheon, and noted their method of capture.

I used stepwise variance inflation factor analysis (Zuur et al., 2010; threshold = 3, using the usdm package: Naimi et al., 2014) to identify collinear fixed effect variables. HabComplex was collinear with its four components, which were therefore not included in the same models.

Predicting terrestrial invertebrate richness and conservation status

To explore the ability of habitat indicators to predict taxonomic richness and conservation status in ERS, I used a cross-validation modelling process, whereby different randomly selected parts of the dataset were used to train and test model outcomes over 500 iterations (Refaeilzadeh et al., 2009). To train the initial model, I selected a random subset of 70 samples, with the remaining 21 samples being used to verify the results. I repeated this random selection for each iteration (i.e. 500 times) to quantify the effect of variability within and between the training and verification subsets. I calculated differences (mean ± standard error) in richness and sSQS between training and verification subsets for each iteration.

I used each subset to train negative binomial generalised linear mixed-effect models (NB-GLMMs, using the lme4 package: Bates et al., 2015). I selected NB-GLMMs because exploratory analyses highlighted the response variables (i.e. richness and sSQS) were non-normally distributed and overdispersed. I used HabComplex, VegMorph and AnthroCover as fixed effects to predict richness and sSQS. I determined the optimal random effect structure by modelling richness and sSQS with combinations of two potential random factors (sampling site and method: see Burnham & Anderson, 2002) and selecting the most parsimonious structure using Akaike's information criterion (AIC). The final structure for both richness and sSQS training models included only method as a random intercept.

I used models derived from each of the 500 training subsets to predict richness and sSQS for their respective verification subset. To test whether habitat indicators can predict assemblage characteristics (H1), I determined the number of subsets with predicted richness and sSQS values that were significantly correlated with observed values using Pearson product-moment correlations. I then summaried the strength of correlations between observed and predicted values for each subset using Pearson's *r* and reduced major axis regression (RMA, using the lmodel2 package: Legendre, 2018). I selected RMA because observed richness and sSQS values were not truly independent (i.e. uninfluenced by external factors, such as temperature during sampling). Thus, RMA, which allows for variability in both the observed and predicted values, was more appropriate to summarise agreement between the two values than more widely used regression methods (Harper, 2016).

Tables 7.1, **15.4** and **15.5** present the minimum, maximum, mean, standard error (SE) and standard deviation (SD) (i.e. 'summaries') of the strength (RMA slope, where 1 indicates perfectly correlated variables, and Pearson's *r*) and significance (Pearson's p) of correlations over the 500 subsets. **Table 7.1** presents summaries of RMA slope for subsets with significant Pearson correlations, because RMA cannot robustly summarise non-significant relationships (as tested using a Pearson correlation: Legendre & Legendre, 2012). These summaries encompass >88% of predictions, offer more robust estimates of the strength of the relationship between observed and predicted values than Pearson correlations and are independent of the testing of H1 (i.e. I tested H1 using the number of subsets with a significant Pearson correlation, not the strength of RMA slopes from only subsets with a significant Pearson correlation). **Table 15.4** presents summaries of RMA slope for subsets with non-significant Pearson correlations for comparison with significantly correlated subsets (**Table 7.1**), but should not be considered as evidence for assessing correlation strength. To allow comparisons across all subsets regardless of significance, **Table 15.5** includes summaries of Pearson's *r* for all subsets.

Due to the limited number of temporary stream samples (n = 23), I used all ERS samples to train a new NB-GLMM following the structure outlined for ERS. I then used this training model to predict richness and sSQS for all temporary stream sites and for rural (i.e. Candover Brook) temporary stream sites only, based on their habitat indicator values. I assessed the agreement between observed and predicted values using ranged major axis regression (RaMA: Legendre & Legendre, 2012; Legendre, 2018), which scales variables prior to regression, thus accounting for differences in taxonomic resolution between ERS and temporary stream datasets.

Characterisation of richness and sSQS by multimetric and unimetric indicators

To test whether the multimetric habitat indicator characterised variability in ERS richness and sSQS more effectively than unimetric indicators (H2), I developed a NB-GLMM for each habitat indicator with richness or sSQS as the response variable and method as a random intercept. I identified the habitat indicator best characterising variance in richness and sSQS using AIC, and I considered models with ΔAIC < 2 as comparable. I calculated marginal and conditional R^2 (R^2m and R^2c) to quantify the variance explained by each model (using the MuMIn package: Bartoń, 2020).

I performed all analyses in R (R Core Team, 2020), and used the DHARMa package (Hartig, 2020) to check the assumptions of all NB-GLMMs.

7.3 Results

7.3.1 Habitat indicators

In ERS, all indicators except Bank face, Profiles and WatFeat occupied the lower range (<5) of values, with Bank face and Profiles being the only indicators exceeding the range of probable MoRPh values (maximum: 12.5). In temporary streams, HabComplex, VegMorph and AnthroCover values were comparable to those in ERS, except one site with a VegMorph value of 4.5 (ERS VegMorph maximum + 0.5) and another site with an AnthroCover value of 6.0 (ERS AnthroCover maximum + 2.0).

7.3.2 Assemblage composition

The ERS assemblages comprised 344 species from 22 families. Most species were rove beetles (Staphylinidae: 43.9%) and ground beetles (Carabidae: 28.2%), with the remaining 20 families comprising 27.9%. Richness varied between 2 and 60 (mean ± SE: 22 ± 1.4) species per sample. *Bembidion tetracolum*, *Gastrophysa viridula* and *Paranchus albipes* were the most common species, occurring in 53%–68% of samples. Individual species quality scores ranged from 1 (common) to 16 (Nationally Rare/Scarce and IUCN Endangered: IUCN, 2021) with a mean of 1.6 ± 0.1, and sSQS from 2 to 66 (28 ± 1.8) per sample. Wood specialists *Barynotus moerens*, *Glischrochilus hortensis* and *Phyllobius glaucus* each occurred in three to five samples, across seven sites at which the Wood indicator ranged from 0 to 1.4, and were only captured by pitfall trapping. These species were not recorded at five sites with comparable or higher Wood indicator values (0–2.9) at which only ground searching was undertaken.

Temporary stream samples contained 114 taxa from 18 families. Most taxa were ground beetles (46.5%) and rove beetles (31.6%), with the remaining 21.9% including 16 families. Richness varied between 2 and 27 taxa (12 ± 1.9) per sample. Individual species quality scores ranged from 1 to 8 [Nationally Rare/Scarce and IUCN Vulnerable; IUCN (2021)] with a mean of 1.2 ± 0.1, and sSQS from 2 to 33 (14 ± 2.1) per sample.

7.3.3 Predicting taxonomic richness and conservation status in ERS

Five of the 500 ERS iterations were discounted because one of the two sampling methods was represented by insufficient samples to generate accurate estimates. Of the remaining 495 models, 444 (90%) and 438 (88%) predictions of richness and sSQS, respectively, were significantly correlated with observed values from their verification subset, supporting H1. The maximum, mean ± SE and SD of RMA slopes were comparable for richness and sSQS (**Table 7.1**, also see **Table 15.5** for corresponding Pearson correlation summaries). Predicted richness and sSQS were on average 0.2 ± 0.1 and 0.3 ± 0.1 lower than observed values, respectively, with predictions of sSQS being more variable than predictions of richness (SD = 14.9 and 11.3, respectively).

Table 7.1: Descriptive statistics summarizing significant reduced major axis (RMA) slopes and associated Pearson product-moment correlation p-values assessing agreement between predicted and observed richness and sum of species quality scores (sSQS) for terrestrial beetle assemblages sampled from exposed riverine sediments.

		Minimum	Mean ± SE	Maximum	SD
Richness	RMA slope	0.251	0.638 ± 0.009	1.422	0.200
	Pearson's p	0.001	0.009 ± 0.001	0.049	0.011
sSQS	RMA slope	0.258	0.629 ± 0.008	1.405	0.187
	Pearson's p	0.001	0.009 ± 0.001	0.049	0.011

7.3.4 Predicting taxonomic richness and conservation status in temporary streams

In temporary streams, predicted and observed values were not correlated for richness (RaMA: slope = −0.185, p = 0.352) or sSQS (slope = −0.446, p = 0.267; **Figure 7.1A** and **C**), contrary to H1. Rural temporary stream assemblages had richness values of 2–25 (mean ± SE: 14 ± 2.0) and sSQS values of 2–31 (16 ± 2.3), whereas in the more urban assemblages, both metrics were lower, ranging from 2 to 7 (4 ± 0.7). As such, only rural temporary stream assemblages were comparable to those in equivalent ERS samples (i.e. pitfall trap samples: richness 13–59 [31 ± 1.8], sSQS 13–66 [39 ± 2.6]). Removing the more urban samples resulted in correlations between values predicted for rural ERS sites and observed in rural temporary stream sites, for both richness and sSQS (richness slope = 0.906, p = 0.003, sSQS slope = 1.007, p = 0.010; **Figure 7.1B** and **D**), supporting H1. Richness and sSQS in rural temporary streams were over-predicted (richness +5, sSQS +17; **Figure 7.1B** and **D**), likely due to the higher taxonomic resolution of the ERS training samples.

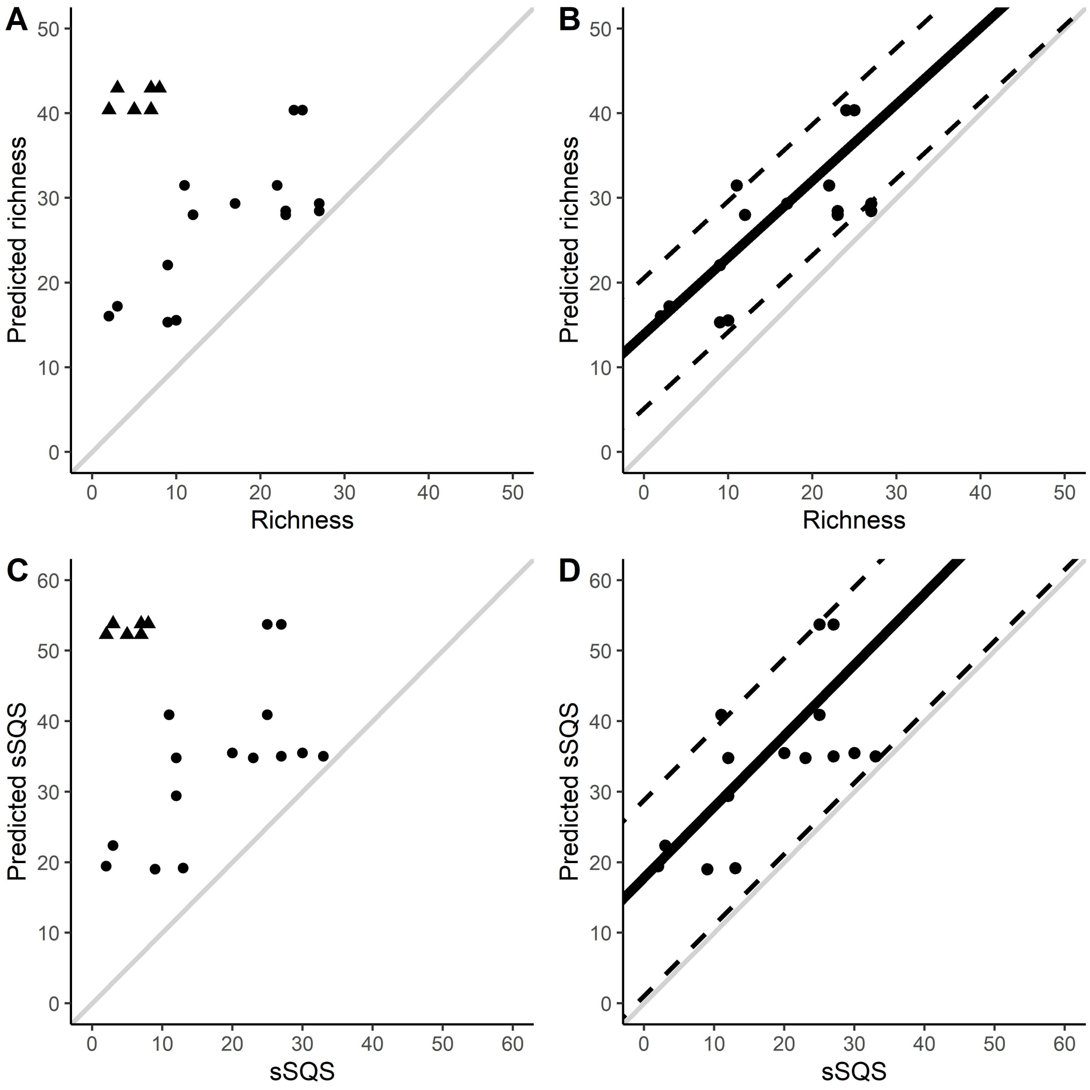


Figure 7.1: The relationship between observed and predicted taxonomic richness (A, B) and sum of species quality scores (sSQS: C, D) for temporary streams including (A, C) and excluding (B, D) assemblages from more urban sites. Triangles and circles represent assemblages from more urban and rural sites, respectively. Grey lines indicate the optimal 1:1 correlation, and solid and dashed black lines indicate the observed correlation and 95% confidence interval

Characterisation of richness and sSQS by multimetric and unimetric indicators

Richness and sSQS responded to two habitat indicators, increasing with both the multimetric indicator HabComplex and the unimetric indicator WatFeat (**Figure 7.2**). HabComplex had a 3.7× and 4.4× greater effect than WatFeat on richness and sSQS, respectively. HabComplex and WatFeat each explained 6% of the variance in richness, with other indicators accounting for ≤2% (R^2m) and method for ≥20% (R^2c). HabComplex and WatFeat explained 7% and 5% of the variance in sSQS, respectively, with other indicators accounting for ≤2% (R^2m) and method for ≥19% (R^2c). Contrary to H2, the unimetric WatFeat best characterised differences in taxonomic richness, but characterisations by the multimetric HabComplex were comparable (i.e. <2 ΔAIC from the WatFeat model). HabComplex best characterised differences in sSQS, and was not comparable to the WatFeat model (ΔAIC > 2), supporting H2. To assess the influence of the two samples with HabComplex values <1 (**Figure 7.2A** and **C**), I reran the richness and sSQS models with these values removed. Models with and without these values had comparable relationship strength (change: ≤0.06), significance (≤0.003), goodness of fit (≤0.01) and relative ranking in terms of AIC. Although non-significant, Wood and Bank face had marginally stronger relationships with sSQS (estimate ± SE: 0.07 ± 0.06 and 0.06 ± 0.04) than richness (0.04 ± 0.06 and 0.05 ± 0.04).

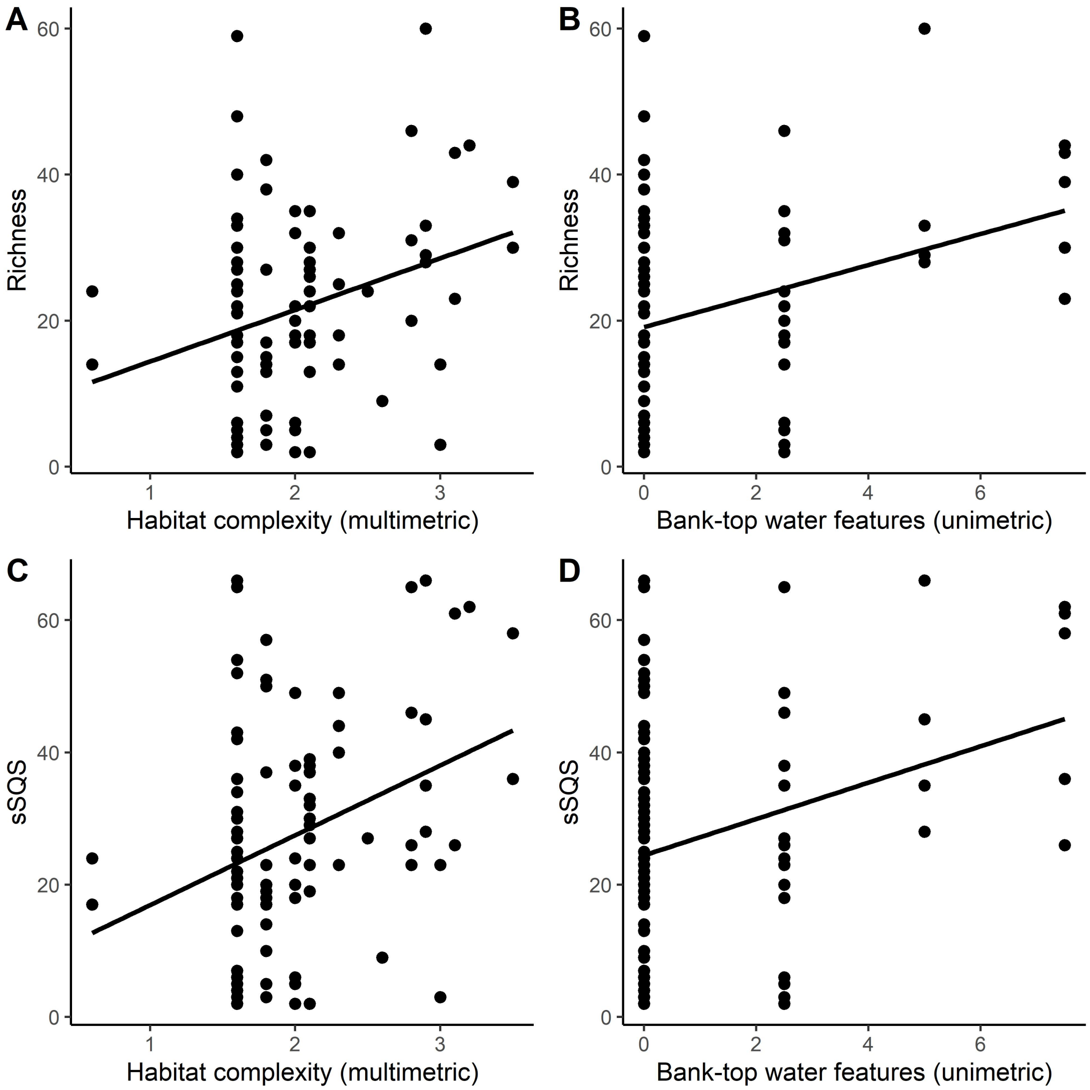


Figure 7.2: The relationship between richness (A, B) and the sum of species quality scores (sSQS: C, D) and the multimetric indicator habitat complexity (A, C) and the unimetric indicator representing the type and extent of bank-top water features (B, D) for terrestrial beetle assemblages sampled from exposed riverine sediments.

7.4 Discussion

Aquatic–terrestrial riverine habitats support unique terrestrial biodiversity (Sabo et al., 2005; Soininen et al., 2015; Schindler & Smits, 2017), but can be difficult to biomonitor due to temporally variable faunal responses to environmental conditions (Bates et al., 2006; O'Callaghan et al., 2013a). To address this challenge, I explored two frequently inundated riverine habitats, ERS and temporary streams, to evaluate whether indicators based on habitat survey data could predict metrics characterising terrestrial invertebrate assemblages. In ERS, significant correlations between observed and predicted taxonomic richness and sSQS, an index of conservation status, suggest that habitat indicators can predict these assemblage characteristics, supporting H1. Correlations between observed and predicted richness and sSQS in rural temporary streams also supported H1 and suggested that predicted assemblage characteristics may enable assessment of biodiversity in a range of aquatic–terrestrial riverine habitats, not just ERS. However, predictions including more urban temporary streams were uncorrelated with observed richness and sSQS, suggesting that better representing human pressures such as land use in habitat indicators could improve future predictions. The effectiveness of unimetric and multimetric habitat indicators (H2) differed for richness and sSQS, suggesting that both may enable monitoring of terrestrial assemblages in aquatic–terrestrial riverine habitats.

7.4.1 Predicting characteristics of terrestrial invertebrate assemblages

Correlations between observed and predicted values of taxonomic richness and sSQS in both ERS and rural temporary streams suggest that standardised habitat indicators may be able to predict assemblage characteristics in a range of frequently inundated habitats. Such correlations reflect similar habitats in ERS and rural temporary streams (i.e. relatively undisturbed semi-vegetated gravels: **Figures 15.1** and **15.3**), and thus similar assemblage characteristics.

Furthermore, the capacity of my habitat indicators (which include the 10 m lateral to the channel) to characterise ERS and rural temporary stream assemblages characteristics suggests that these in-channel assemblages may assemble from nearby riparian zones (Steward et al., 2011, 2022; Corti & Datry, 2016). These similar assemblage characteristics likely arise because ERS, dry temporary streams and adjacent riparian zones have key habitat features in common, such as exposed damp sediments and riparian vegetation that encroaches into the channel as streams dry (Räpple et al., 2017). Thus, biotic metrics (e.g. richness and rarity) predicted from habitat indicators may enable assessment of terrestrial biodiversity in ERS, temporary streams and their adjacent riparian zones by allowing inference of terrestrial assemblage characteristics when time-restricted sampling campaigns coincide with periods of inundation. However, relationships require characterisation in a more comprehensive range of temporary stream habitat types and landscape settings to further enhance predictions.

No relationship was detected between observed and predicted richness or sSQS values in more urban temporary streams, likely because (1) urban land use led to habitat conditions (e.g. compacted sediments: **Figure 15.3**) that decreased richness relative to rural sites (Martinson & Raupp, 2013) and (2) small-scale differences in habitat characteristics, such as sediment composition, were not detected by the reach-scale habitat indicators used, reducing the accuracy of predictions made from ERS samples. Additionally, 10% and 12% of ERS richness and sSQS predictions were uncorrelated with observed values because their training subsets were less representative of verification subsets, and thus could not be accurately predicted. These uncorrelated cases highlight that training datasets which incorporate a full range of habitat conditions and species occurrences could improve prediction of biotic metrics such as richness and sSQS.

7.4.2 Improving future predictions: evaluating characterisations of terrestrial invertebrate assemblages

I identified positive relationships between richness and both the multimetric HabComplex and unimetric WatFeat indicators. These relationships align with well-known beetle responses to habitat complexity (Lengyel et al., 2016; Staudacher et al., 2018) and water availability (Lassau et al., 2005), increasing confidence that habitat indicators can be used to represent species–habitat relationships. However, the lack of response to VegMorph, AnthroCover, Wood, Bank face and Profiles contrasts with established relationships between assemblage composition, including its taxonomic richness, and vegetation characteristics (e.g. complexity and composition: Greenwood et al., 1995; Rouabah et al., 2015), agriculture and urbanization (French et al., 2001; Martinson & Raupp, 2013; Magura & Lövei, 2021), the type and distribution of woody habitats (Hering et al., 2004; Seibold et al., 2016) and bank face features (e.g. side bars and bank profile: Ramey & Richardson, 2017; Sprößig et al., 2020). Thus, assemblage responses may have been masked by both the methods of beetle sampling and of recording these habitat characteristics.

Contrary to H2, WatFeat characterised variability in richness more effectively than HabComplex, but differences were slight. As the only unimetric indicator eliciting a biotic response, WatFeat likely drove the relationship between richness and HabComplex. The marginally weaker performance of the multimetric indicator may thus reflect its inclusion of three non-significant habitat indicators (Bank face, Profiles, Wood), which obscured responses to WatFeat. In contrast, HabComplex best characterised variability in sSQS, supporting H2, and likely reflecting the marginally better performance of two additional components of the multimetric indicator (Wood and Bank face). A multimetric indicator's values depend upon each unimetric component contributing to effects on the response variable, and identification of unimetric indicators that effectively characterise species–habitat relationships is therefore fundamental to accurate, consistent predictions.

Some unimetric indicators calculated using habitat data may be too simplistic to represent species–habitat relationships. For example, VegMorph summarises vegetation complexity as the number of morphotypes (Gurnell et al., 2020b), which does not represent vegetation cover, composition or structural diversity, all of which influence beetle distributions (Brose, 2003; Schaffers et al., 2008). Additionally, some beetles require specific habitat resources (e.g. saproxylic taxa on decaying wood: Fowles et al., 1999; Alexander, 2004), which were excluded from calculation of my indicators if covering <5% of the survey area. This coarse characterisation of some habitat features may have prevented identification of relationships with biotic assemblages.

I calculated indicators based on a reach-scale habitat survey, and their detection of beetle responses may have been limited by the differing spatial scales at which habitats are surveyed and at which beetles respond to environmental conditions. For example, although habitat indicators including AnthroCover suggested that ERS and more urban temporary stream survey areas were comparable, catchment-wide urban land uses may have reduced beetle richness and sSQS in temporary streams, for example by disconnecting sites from potential colonist sources (Niemelä & Kotze, 2009). In contrast, VegMorph represents the structural richness of plant communities within a survey area, and was likely too coarse to detect beetle responses to variability in plant densities and community composition within and between habitat patches, which influence beetle movement and predation risk (Heydemann, 1957; Allema et al., 2019).

Biotic sampling is essential in mapping assemblage responses to environmental drivers, here represented by habitat indicators. The biotic assemblages analysed herein were sampled using two well-tested, widely used methods: ground searching and pitfall trapping (Skvarla & Dowling, 2017; Ramírez-Hernández et al., 2018). However, these methods preferentially capture different species, and species with different conservation statuses (Bunting et al., 2021; Webb et al., 2022), potentially hindering characterisation of species–habitat relationships. For example, the wood specialists *B. moerens*, *G. hortensis* and *P. glaucus* were caught only by pitfall trapping. These species may have been absent from the five sites (where the Wood indicator ranged from 0 to 2.9) at which only ground searching was undertaken, or present but not sampled, reducing responsiveness to the Wood indicator.

Over-estimation of richness and sSQS in rural temporary streams by ERS training samples (identified to mixed and species level, respectively) highlights taxonomic resolution as an additional source of variance that can potentially hinder prediction of assemblage characteristics and characterisation of species–habitat relationships. Therefore, new samples collected to improve prediction of assemblage characteristics from habitat indicators should be collected using a standard multi-method protocol (e.g. Webb et al., 2022) and be identified to the taxonomic resolution at which predictions are required, to avoid introducing variability which could obscure biotic responses.

7.4.3 Applications and future directions

This study demonstrates that indicators calculated from habitat survey data may be used to predict terrestrial invertebrate assemblage characteristics. However, these predictions are currently only sufficient to provide managers with coarse assessments of key assemblage metrics such as richness. While I focused on beetles as a model group, invertebrate taxa including true bugs, true flies and ants contribute to the biodiversity of both ERS and temporary streams (Steward et al., 2022) and respond predictably to habitat conditions (e.g. Mulieri et al., 2011; Buczkowski & Richmond, 2012). Thus, future biodiversity assessments that include a range of terrestrial invertebrate taxa may be used alongside those from aquatic monitoring programmes to provide more comprehensive assessments of the biodiversity within aquatic–terrestrial riverine habitats (Bunting et al., 2021).

Further developing my predictive approach could, for example, enable more precise habitat-survey-based predictions of assemblage characteristics for beetles and other invertebrate taxa, allowing preliminary assessment of habitat quality by managers, researchers and citizen scientists outside of invertebrate survey seasons, or when site access is not safe or practical. Development of sufficiently accurate predictive models could also enable identification sites at which predicted richness and rarity (or other metrics) are higher or lower than expected based on habitat conditions, informing implementation of conservation and management interventions. In practice, a large and representative training dataset will be required to further improve predictions. Citizen science initiatives have the capacity to collect large, high-quality biological and environmental datasets (e.g. Ratnieks et al., 2016; Shuker et al., 2017; Brooks et al., 2019) and may thus enable both generation of this training dataset and application of predictive techniques to increase my understanding of the biodiversity within aquatic–terrestrial riverine habitats.

Author contributions

This chapter is published as: **Gething, K. J.**, Hayes, C., Webb, J., Sykes, T., England, J. and Stubbington, R. (2022) Living on the edge: predicting invertebrate richness and rarity in disturbance-prone aquatic–terrestrial habitats. *Ecological Solutions and Evidence*, 3, e12196. https://doi.org/10.1002/2688-8319.12196

This chapter was short-listed for the 2022 Ecological Solutions and Evidence Georgina Mace Prize and also appears in the 2023 virtual issue by that name.

Kieran J. Gething conceptualised the study (lead), curated the data, designed the methodology, performed formal analysis, wrote the original draft, administered the project and reviewed and edited the manuscript (equal). Chloe Hayes and Jonathan Webb performed investigation (equal) and reviewed and edited the manuscript (equal). Tim Sykes and Judy England reviewed and edited the manuscript (equal). Rachel Stubbington conceptualised the study (supporting) and reviewed and edited the manuscript (equal).

8 Integrative discussion

Chapters 3–7 detail studies on the aquatic (Chapters 3 and 4) and terrestrial (Chapters 5–7) invertebrate assemblages found in winterbournes—temporary streams emerging from the chalk aquifer in south England—and associated habitats, namely ditches, perennial reaches and riparian zones, collectively addressing Objectives 1–4 (see Chapter 1). Chapters 3 and 4 explore how land use influences aquatic assemblages, investigating the effects of agricultural intensity on entire assemblages and temporary stream specialist species (Chapter 3). Chapter 4 builds upon this agricultural context by assessing the role of ditches (i.e. artificial drainage channels that are common in agricultural landscapes) and connectivity between ditches and streams in supporting the resilience of populations of temporary stream specialists. Research in Chapter 5 assesses the connectivity between cross-channel terrestrial assemblages during drying. Chapters 6 and 7 consider adapted methods for characterising in-channel terrestrial assemblages during dry and wet phases, respectively. Here, I detail how Chapters 3–7 individually and collectively advance our understanding of how flow permanence, connectivity and anthropogenic pressures influence riverine ecology, in particular in temporary streams. I then apply the findings to make recommendations on how to effectively monitor and manage the aquatic–terrestrial communities supported by temporary streams (Objective 4). Finally, I identify outstanding and novel questions raised by this research.

8.1 Objective 1: Characterise and compare the response of biotic communities to different types and intensities of human impacts in temporary streams

Whilst my finding that flow permanence is a key driver of aquatic assemblages (Chapters 3 and 4) in temporary streams is well-known (e.g. Matthaei et al., 2010; Leigh & Datry, 2017), my research also contributes to a limited body of evidence demonstrating that adaptations to temporary flow promote cotolerance of anthropogenic pressures (e.g. agriculture, Chapter 3, Storey, 2016; Loskotová et al., 2023) due to common stressors. Chapter 3 presents the first study to demonstrate that both temporary stream assemblages and their specialist species may be cotolerant of drying and agricultural land use pressures. This resistance to co-occurring natural and anthropogenic pressures may mostly reflect a tolerance of low dissolved oxygen concentrations among temporary stream organisms (*sensu* Vinebrooke et al., 2004; Storey, 2016) including their specialist species, because assemblage responses to multiple environmental pressures, such as low flows, excess fine sediment and nutrient enrichment, are all correlated with dissolved oxygen concentrations (Jones et al., 2023). Thus, aquatic temporary stream assemblages may be better able to resist the effects of multiple pressures than their perennial counterparts (Hughes et al., 2009; Stubbington et al., 2018a).

Conceptually, the multiple pressures faced by temporary stream communities act as environmental filters, where some taxa pass through the filter and others are prevented from passing through (**Figure 8.1**: Heino et al., 2007). Stronger pressures (e.g. flow permanence in **Figure 8.1A**) select for a smaller subset of the community than weaker pressures (e.g. agriculture in **Figure 8.1A**: Hughes et al., 2009). Thus, although some pressures impose a weaker filter on a community, the assemblage that is present will ultimately reflect the strongest filter acting upon the community. Like Poff (1997), this model proposes multiple nested filters that shape a community, but unlike Poff (1997) it does not assume that these filters are arranged sequentially from weak to strong. Rather, within sites, the strongest environmental filters act first to remove the majority of sensitive taxa, with weaker filters having a limited impact on the community of generalists created by the strongest filter. Generalist taxa are adaptable, capable of surviving in a range of environmental conditions, and thus may be better able to navigate strong filters (**Figure 8.1B**). Temporary streams often contain the subset of taxa found in perennial streams (e.g. Arscott et al., 2010; Datry et al., 2014a; Stubbington et al., 2017b) that can tolerate the stressors associated with drying (e.g. increased fine sediment deposition and nutrient concentrations, decreased dissolved oxygen concentrations: Gómez et al., 2017; von Schiller et al., 2017). When a weaker filter acts via similar stressors, such as agriculture decreasing dissolved oxygen concentrations (**Figure 8.1A**: Allan, 2004; dos Reis Oliveira et al., 2019), the stronger and weaker filters align, potenitally limiting the effect of the weaker filter on the assemblage. This pre-shaping of the assemblage by a stronger filter is a possible mechanism behind the positive cotolerance of multiple pressures suggested by Vinebrooke et al. (2004) and Hughes et al. (2009), and observed in agricultural temporary stream communities by Storey (2016). Thus, temporary stream assemblages may be less affected by agriculture, because it manifests similarly to drying (**Figure 8.1A**), whereas perennial assemblages which are not pre-filtered by drying and become more variable, reflecting assemblages shaped by site-specific agricultural stressors.

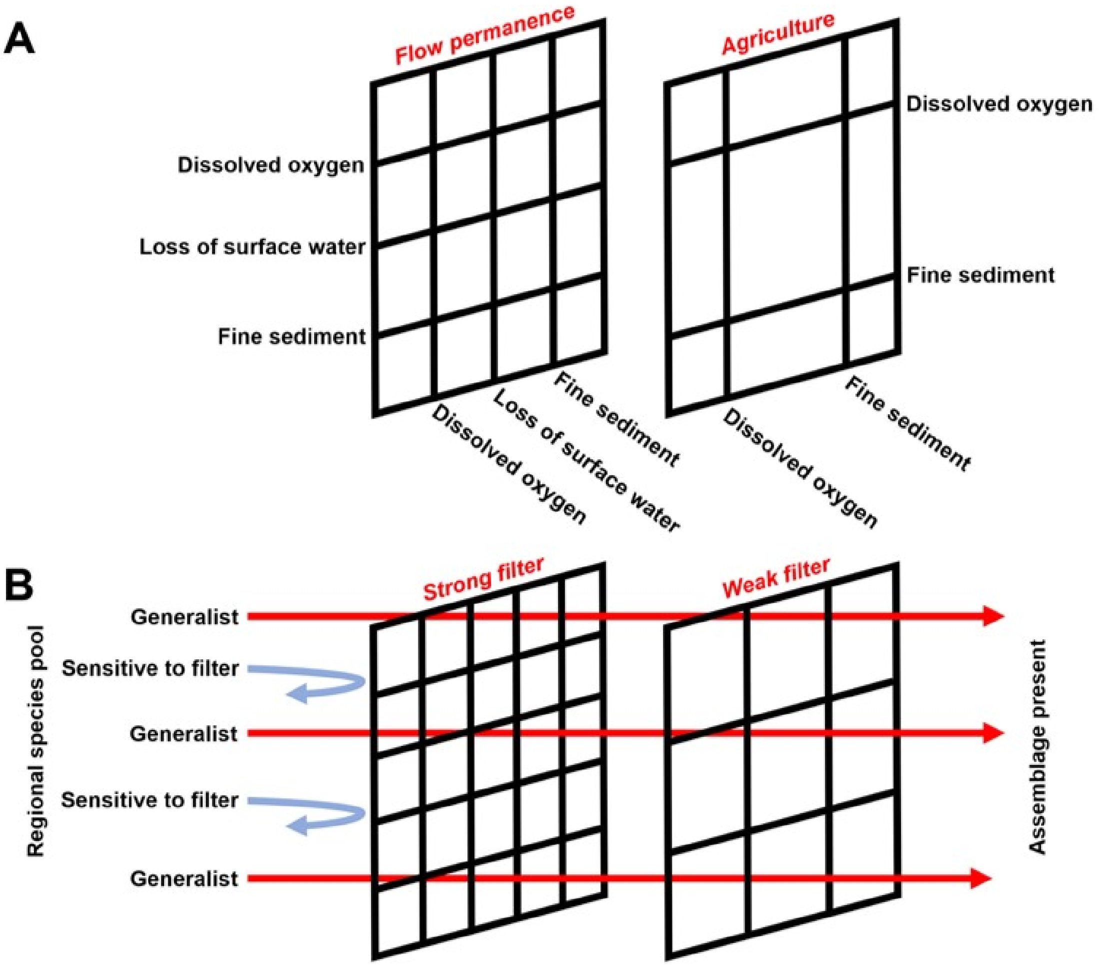


Figure 8.1: Filters shaping the assemblages present in and around temporary streams. Filters (outer black squares) represent pressures, such as flow permanence and agriculture, with stressors such as loss of surface water being represented by black lines within each pressure. Conceptually, pressures act like sieves, with stressors determining the size of holes in the sieve mesh. Generalist taxa are more adaptable, and thus can typically navigate the finer mesh of strong filters. Where the mesh of strong and weak filters align, generalist taxa are seemingly unaffected by the weak filter because they have already navigated the same stressors in the strong filter. Sensitive taxa may theoretically be capable of navigating the larger holes the weak filter, but are removed from the community by the finer mesh of the string filter.

The cotolerance of drying and agriculture by temporary stream specialists such as the stonefly *Nemoura lacustris* and the mayfly *Paraleptophlebia werneri* suggests that—once their flow requirements are met—these species are generalists that can tolerate a wide range of environmental conditions (Errochdi et al., 2014), including anthropogenic pressures. As environmental generalists, temporary stream specialists inhabit both natural and artificial waterbodies (Chalkley, 2006; Tapia et al., 2018; Biondi et al., 2022) and are occasionally found in perennial habitats (e.g. Prenda & Gallardo-Mayenco, 1999; Salmela, 2013), suggesting their association with temporary waters may not be directly driven by flow permanence. In Chapter 4, I find support for the competition/predation theory suggested by Punchard & House (2009) and developed by Aspin & House (2022), by which the occurrence of temporary stream specialists may be driven by the abundance of competitors/predators (e.g. *Gammarus fossarum/pulex*) who progressively become excluded by temporary flow as dry-phase durations increase, rather than the flow permanence itself. Taxon-specific versions of **Figure 8.1** for temporary stream specialists may thus include competitors/predators as biotic filters affecting the occurrence of such taxa in an assemblage, further moderating their responses to human pressures.

As reported in Chapter 6, terrestrial in-channel assemblages also responded to variables influenced by human activities (i.e. silt and temperature), as previously documented by Steward et al. (2018) and Robinson (2019). I extend our understanding by highlighting that, as for aquatic assemblages in agricultural landscapes (Chapter 3), responses to human impacts were weaker than those to flow permanence (Chapter 6, i.e. flow permanence is a stronger filter: **Figure 8.1**). I also found that responses to human impacts were strong and consistent enough to allow predictions of terrestrial assemblage characteristics (i.e. taxonomic richness and conservation value: Chapter 7), demonstrating the potential utility of terrestrial assemblages for inferring ecosystem health in temporary streams.

8.2 Objective 2: Test the role of connectivity in shaping the biotic communities of temporary streams

The occurrence of the Nationally Rare temporary stream specialist *Nemoura lacustris* in ditches was positively associated with its abundance in nearby streams (Chapter 4). This may suggest that lateral exchanges between populations of specialists in ditches and temporary streams support the abundance of catchment-wide populations (**Figure 8.2**). This association provides the first evidence that other waterbodies in a catchment, in particular artificial waterbodies which experience differing anthropogenic pressures and differing flow permanence regimes to nearby temporary streams, may have the potential to support the persistence of temporary stream specialist populations (e.g. via rescue effects: Brown & Kodric-Brown, 1977; Leibold et al., 2004).

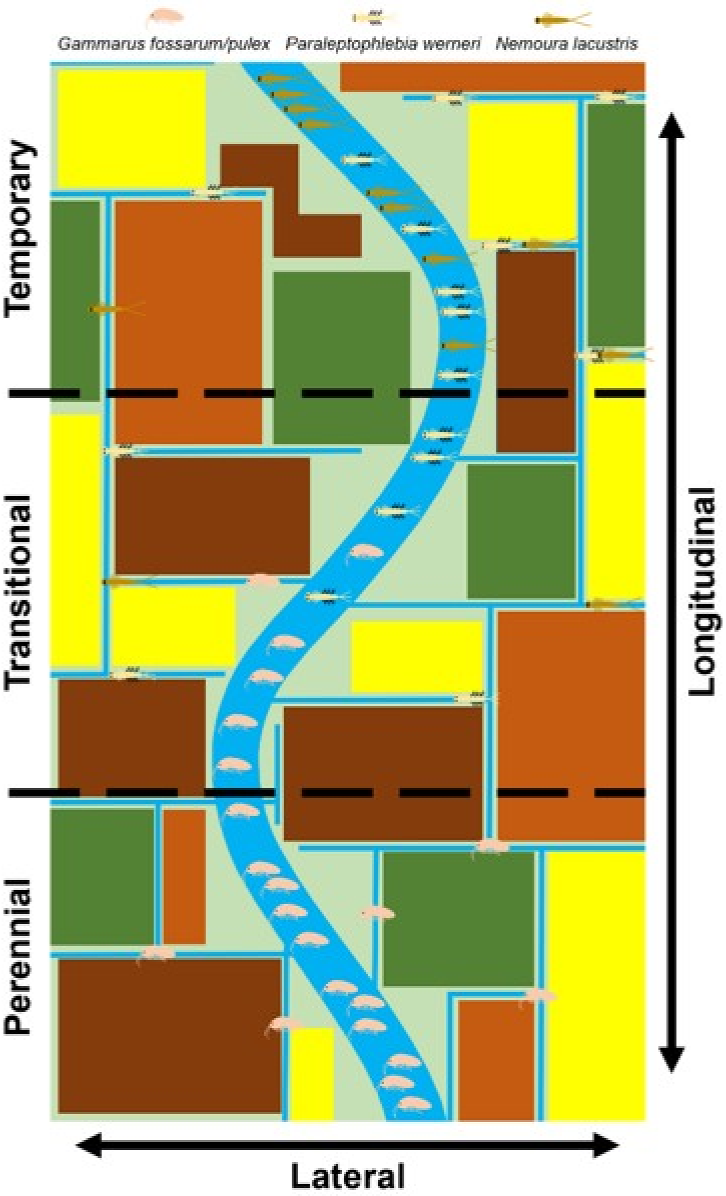


Figure 8.2: Plan view of perennial, transitional and temporary reaches, visualising lateral and longitudinal connectivity between populations of temporary stream specialist species (*Nemoura lacustris* and *Paraleptophlebia werneri*) and their aquatic competitors and predators (*Gammarus fossarum/pulex*) in networks which include a stream (thick, blue, central line) and ditches (narrow, blue, peripheral lines). Different coloured polygons represent differing land uses, which thus apply different stressors upon nearby waterbodies.

Limited connectivity between temporary and perennial habitats may also promote the survival of temporary stream specialists (Chapter 4). Where temporary reaches are closer to, and thus often have higher hydrological connectivity with, perennial reaches, temporary stream specialists are less common (i.e. transitional reaches in **Figure 8.2**: Aspin & House, 2022). Where temporary stream specialists are spatially isolated from competitors/predators, they can survive (i.e. at the temporary extreme of the longitudinal gradient in **Figure 8.2**). Thus, an understanding of the connectivity between natural and artificial waterbodies, which can both have temporary and perennial flow permanence regimes, is needed to accurately assess the risk to temporary stream species of conservation interest posed by natural and anthropogenic pressures.

Chapter 5 presents the first study to assess how drying influences connectivity between terrestrial cross-channel assemblages (i.e. assemblages in parallel riparian zones). My finding that cross-channel assemblage similarity was unaffected by flow permanence regime indicates that temporary and perennial reaches were comparable barriers (or not) to spatial connectivity (i.e. lateral connectivity was comparable in perennial, transitional and temporary reaches: **Figure 8.3**). Connectivity between cross-channel assemblages increased over time as flows declined in both temporary and perennial reaches, suggesting that stream channels do restrict cross-channel movement. Similar to the separation of temporary stream specialists from predators and competitors by drying (Chapter 3: Aspin & House, 2022), assemblages that were spatially isolated by higher flows earlier in the year contained more wetland specialists (Before flow recession in **Figure 8.3**). As flows declined in both perennial and temporary reaches, these wetland specialists were likely replaced by generalist competitors (During/after flow recession in **Figure 8.3**). Thus, whilst lateral connectivity between aquatic populations can support their catchment-wide population (e.g. Chapter 4), both longitudinal (Chapter 3) and lateral (Chapter 5) isolation may also promote the survival of aquatic and terrestrial specialists.

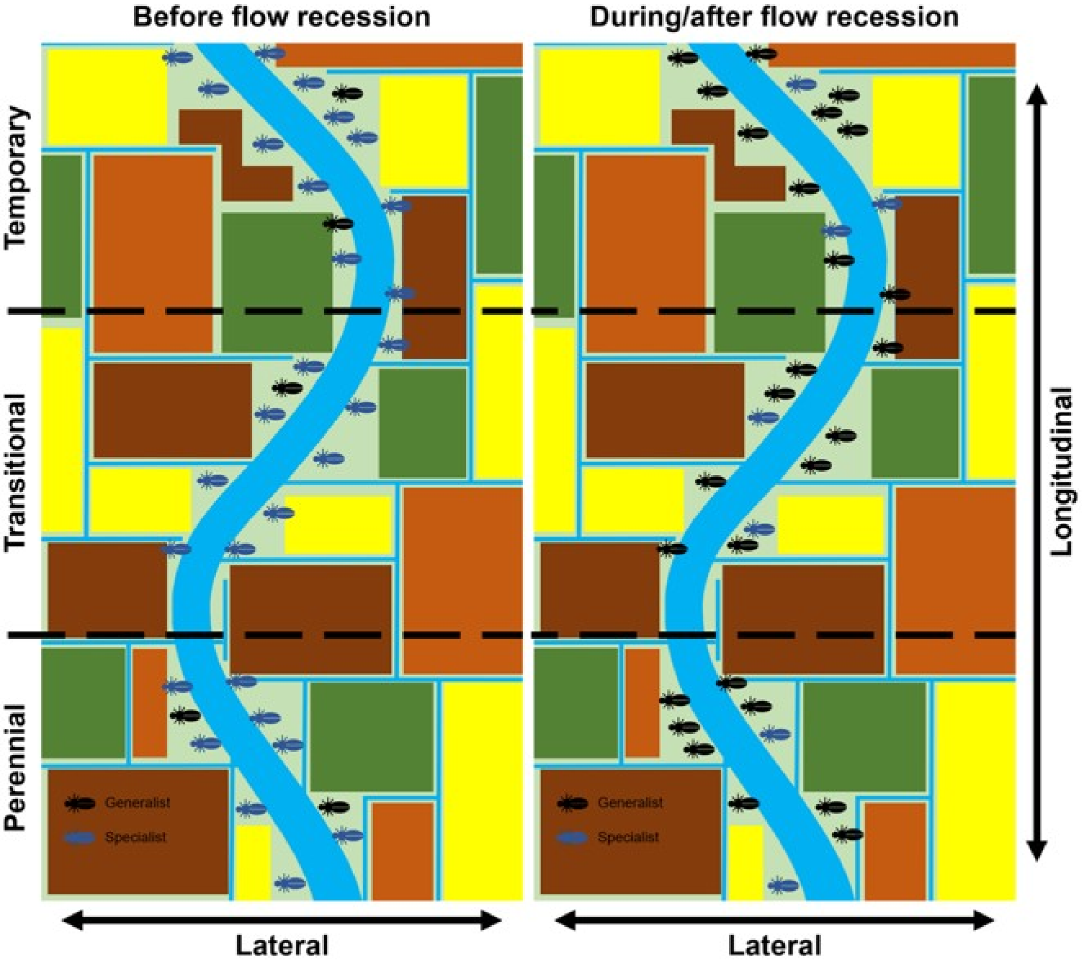


Figure 8.3: Plan view of perennial, transitional and temporary reaches, visualising lateral connectivity between cross-channel terrestrial assemblages, where black beetles represent generalists and blue beetles represent specialists.

8.3 Objective 3: Adapt and evaluate methods to characterise the biotic communities of temporary streams across their flowing and dry states

Consistent with previous research (e.g. Corti et al., 2013; Steward et al., 2018; Robinson, 2019; Bunting et al., 2021; Hayes, 2022), I found that pitfall trapping and hand searching methods may be applied to characterise dry-phase in-channel assemblages. These characterisations contribute to limited evidence that both methods have the potential to detect assemblage responses to flow permanence and environmental parameters indicative of human impacts (Chapter 6, also see Hayes, 2022). This research is the first to demonstrate that these methods could be sufficient to characterise in-channel responses to such environmental conditions even when applied for short periods (i.e. <12 hours), although longer sampling periods would provide more robust characterisations and thus better evidence to inform management actions (Bunting et al., 2021). I thus demonstrate that these methods have the potential to provide insights into in-channel assemblages and their responses to multiple pressures, which could enable more regular and holistic monitoring of aquatic–terrestrial temporary stream communities.

During flowing phases, in-channel terrestrial assemblages cannot be effectively sampled. I am the first to demonstrate that key characteristics of dry-phase assemblages (e.g. their richness and conservation value) can be predicted from habitat conditions (Chapter 7). The methods used to assess habitat conditions are simple, being used by citizen scientists nationally (Shuker et al., 2017), and thus have the potential to enable predictions of temporary stream assemblage characteristics over large areas—when biotic surveys are not possible. Collectively, Chapters 6 and 7 highlight opportunities for citizen scientists and regulators to characterise the terrestrial assemblages supported by temporary streams, enabling assessments of ecosystem health on the basis of their terrestrial as well as their more commonly sampled aquatic assemblages.

8.4 Objective 4: Make recommendations for management of temporary streams to maximise biodiversity

Biomonitoring of temporary streams has previously focused on aquatic assemblages, partly because temporary streams have been perceived as purely aquatic ecosystems and partly because methods for characterising their terrestrial assemblages are mostly untested. Here, like several authors (e.g. Steward et al., 2011; Robinson, 2019; Bunting et al., 2021; Hayes, 2022), I have demonstrated that the terrestrial assemblages in and around temporary streams are biodiverse, and are thus inherently worthy of study in a period of global biodiversity decline (Sánchez-Bayo & Wyckhuys, 2019). Their responsiveness to both flow permanence and anthropogenic pressures suggests that terrestrial assemblages have the potential to indicate dry-phase habitat quality and, in conjunction with aquatic assemblages, may enable ecosystem health assessments regardless of in-channel conditions. This inclusion of both aquatic and terrestrial fauna may be particularly important for maximising temporary stream biodiversity, because assessments based solely on aquatic biota assume that aquatic and terrestrial assemblages require the same habitat conditions. For example, regardless of physical habitat conditions, poor water quality resulting in low dissolved oxygen concentrations can decrease aquatic biodiversity (Croijmans et al., 2021), and an assessment based only on aquatic assemblages would reflect this degraded state. However, during a dry phase, physical habitat complexity can increase terrestrial richness (Lassau et al., 2005; Lengyel et al., 2016), implying a habitat in good condition. Thus, holistic characterisation of the aquatic–terrestrial communities supported by temporary streams and their responses to natural and anthropogenic pressures is needed to enable biomonitoring and subsequent management actions that maximise the diversity of their component assemblages.

Management of temporary streams for aquatic assemblages can be based on evidence from long-standardised methods, such as three-minute kick sampling (Murray-Bligh & Griffiths, 2022), but equivalent terrestrial invertebrate sampling methods are needed (Steward et al., 2022). In this thesis I characterised terrestrial assemblage responses to environmental conditions via pitfall trapping, hand searching and prediction from habitat surveys (Chapters 5 and 6, 6, and 7 respectively). The ability of these methods to detect assemblage responses highlights key environmental variables that could be the focus of terrestrial management activities, such as increasing habitat complexity (Chapter 7) and restoring natural flow regimes (Chapter 5). However, these methods require standardised application (similar to Webb et al., 2022) to provide consistent evidence for informing management actions in temporary streams. To balance the need for evidence with the finite sampling resources of regulators and citizen scientists, a sampling effort which is sufficient to robustly characterise terrestrial assemblages and their responses to environmental conditions should be determined.

Management of riverine ecosystems often focuses on increasing connectivity between habitats (e.g. by removing artificial barriers: Birnie-Gauvin et al., 2018; Thieme et al., 2023), which can be beneficial for many species (e.g. Atlantic salmon: Garcia de Leaniz, 2008; Newton et al., 2018). However, connectivity can jeopardise the survival of some rare specialist species (Chapters 3 and 5), because they are out-competed by more generalist competitors and predators (Aspin & House, 2022). Thus, management of temporary streams and in particular their flow regimes should not focus on increasing connectivity *per se*, but on restoring a natural flow regime which allows spatiotemporal variability in connectivity that promotes the survival of biodiverse assemblages which include a balance of generalist and specialist species.

Flow permanence is the key driver of both aquatic and terrestrial assemblages in and around temporary streams (Chapters 3 and 5: Leigh & Datry, 2017). So far, the response of temporary stream communities to all other tested pressures are controlled by this overarching drying pressure (Chapter 3), making the true effects of pressures such as agriculture on temporary stream communities difficult to assess. All communities have a finite ability to resist pressures and management actions should seek to minimise anthropogenic pressures on temporary stream ecosystems, thus maximising their communities' capacity to tolerate natural pressures.

8.5 Limitations and future research priorities

In characterising the responses of biotic communities to different types and intensities of human impacts in temporary streams (Objective 1), I identified opportunities for further study. The pre-existing dataset used in Chapter 3 offered limited opportunities to differentiate the human impacts associated with agriculture. Thus, given the site-specific variability in multiple stressors often caused by agricultural land uses, future studies should more finely quantify the associated impacts on temporary streams. Additionally, I infer that temporary stream assemblages resist the effects of agriculture because drying and agriculture act via similar stressors (e.g. reduced dissolved oxygen concentrations). Although experimental studies have considered the co-occurring effects of low flow and other stressors (e.g. Matthaei et al., 2010; Beermann et al., 2018), studies confirming how a combination of drying and other stressors interact to shape temporary stream assemblages in agricultural areas are needed to inform temporary stream management and restoration strategies. In particular, determining the types and intensities of co-occurring stressors tolerated by temporary stream specialists, such as the Nationally Rare *N. lacustris* and Nationally Scarce *Paraleptophlebia werneri*, may be key to supporting their populations, and may thus support community-level conservation value.

I characterised terrestrial in-stream assemblages in relation to factors affected by human activities, however, these characterisations were limited in their spatial extent and short impact gradients (Feld et al., 2016). Further research is thus needed to expand the spatial scale and impact gradients assessed to ensure robust characterisations of assemblage–environment relationships. Finally, these terrestrial studies were conducted in the field, and characterisations of assemblage–environment relationships were influenced by multiple, covarying biological and environmental stressors. Thus, similar to aquatic assemblages, research on the impact of differing types and intensities of human activities on terrestrial assemblages in temporary streams is needed.

To test the role of connectivity in shaping the biotic communities of temporary streams (Objective 2; Chapters 4 and 5), I used assemblage data and did not observe the actual movement of individuals between habitats. Thus, further studies are required to determine how and why individuals move between habitats, the role of land cover (e.g. hedgerows, natural vs anthropogenic land uses) and other nearby waterbodies (e.g. floodplain ponds) in shaping dispersal patterns (e.g. Elek et al., 2021). Specifically, it is unclear whether temporary stream specialists such as *N. lacustris* move from streams to ditches and/or from ditches to streams, and the extent to which they disperse between habitats via aquatic and/or aerial means. Because a combination of connectivity and isolation is key to maintaining high in-catchment biodiversity (Chapters 4 and 5: Newton et al., 2018; Aspin & House, 2022), further research is needed to understand the balance of connectivity and isolation (and factors affecting connectivity such as land use) which maximises biodiversity in temporary streams.

Although I was able to adapt and evaluate methods to characterise the biotic communities of temporary streams across their flowing and dry states (Objective 3), a standard method for sampling in-channel terrestrial assemblages (e.g. Webb et al., 2022) is needed to provide consistent and transferable evidence for informing management actions. To inform the development of a standardised method that can be used for ecosystem health assessments, studies on the minimum amount of sampling effort (e.g. the minimum number of hours/days pitfall trapping) required to gain a sufficiently robust characterisation of a the terrestrial assemblage are required (Stenzel et al., 2017; Hoffmann et al., 2019).

9 Concluding remarks

Temporary streams are the globe's dominant lotic ecosystem (Messager et al., 2021), but—like other freshwater ecosystems—are increasingly threatened by human activities (Dudgeon et al., 2006; Reid et al., 2019). In particular, winterbourne chalk streams are globally rare, but are threatened by humans via pollution and abstraction, and are often overlooked by aquatic and terrestrial ecologists.

My research demonstrates that, like aquatic assemblages (e.g. Leigh & Datry, 2017), it is likely that terrestrial temporary stream assemblages are primarily shaped by the flow regime. Although agriculture threatens aquatic ecosystems, temporary streams in agricultural landscapes can support diverse aquatic assemblages that include drying-tolerant specialists of conservation interest. Additionally, artificial waterbodies constructed for agriculture such as ditches may support aquatic assemblages in temporary streams. Inferences of habitat quality made via sampling of aquatic assemblages do not necessarily reflect habitat quality for terrestrial assemblages, and thus a holistic approach that includes monitoring of and management for both aquatic and terrestrial components of a temporary stream community are needed.

I demonstrate that terrestrial assemblages respond to both natural pressures and human impacts, and that habitat quality can be assessed during both wet and dry phases, potentially enabling the holistic monitoring and management temporary stream communities need. My research highlights that considerations of connectivity may be key to effectively managing aquatic–terrestrial communities in temporary streams, because exchanges between streams and artificial waterbodies in the catchment may support populations of rare, drying-tolerant specialists. However, this connectivity must be balanced by isolation which protects such specialists from highly competitive generalist taxa. Management should seek to create an appropriate balance of connectivity and isolation by promoting natural flow regimes and minimising stress imposed on temporary stream communities by anthropogenic pressures. This thesis contributes novel understanding of how aquatic–terrestrial communities are affected by natural and anthropogenic pressures, how managers and citizen scientists can monitor their responses to such pressures and how the effects of human activities may be mitigated in a time of unprecedented global change.

10 References

Acuña, V., T. Datry, J. Marshall, D. Barceló, C. N. Dahm, A. Ginebreda, G. McGregor, S. Sabater, K. Tockner, & M. A. Palmer, 2014. Why should we care about temporary waterways? Science 343: 1080–1081.

Acuña, V., M. Hunter, & A. Ruhí, 2017. Managing temporary streams and rivers as unique rather than second-class ecosystems. Biological Conservation 211: 12–19.

Adis, J., 1979. Problems of interpreting arthropod sampling with pitfall traps. Zoologischer Anzeiger (Jena) 202: 177–184.

Adis, J., & W. J. Junk, 2002. Terrestrial invertebrates inhabiting lowland river floodplains of central Amazonia and central Europe: A review. Freshwater Biology 47: 711–731.

Agency, U. E. P., 2017. National rivers and streams assessment 2018/19: Field operations manual – wadeable. US Environmental Protection Agency, Washington D.C.

Aldridge, D. W., B. S. Payne, & A. C. Miller, 1987. The effects of intermittent exposure to suspended solids and turbulence on three species of freshwater mussels. Environmental Pollution 45: 17–28.

Alexander, K. N. A., 2004. Revision of the index of ecological continuity as used for saproxylic beetles. English Nature, Peterborough, UK: 61.

Alexander, K. N. A., 2014. Natural England commissioned report NECR134: A review of the beetles of Great Britain: The soldier beetles and their allies. Natural England, Sheffield.

Allan, J. D., 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35: 257–284.

Allema, B., L. Hemerik, W. A. H. Rossing, J. C. J. Groot, J. C. van Lenteren, & W. van der Werf, 2019. Dispersal of a carabid beetle in farmland is driven by habitat-specific motility and preference at habitat interfaces. Entomologia Experimentalis et Applicata 167: 741–754.

Allen, D. J., P. J. Bloomfield, D. K. Buckley, J. E. Cunningham, P. M. Hopson, P. D. Merrin, A. J. Newell, P. Shand, E. L. Tribe, & A. G. Vivanco, 2019. Chalk aquifer of the Wessex Basin: Research report no. RR/11/02. British Geological Survey, Keyworth, Nottingham: 118.

Alvarado-Montero, S., A. L. Boesing, J. P. Metzger, & R. Jaffé, 2021. Higher forest cover and less contrasting matrices improve carrion removal service by scavenger insects in tropical landscapes. Journal of Applied Ecology 58: 2637–2649.

Andersen, J., 1968. The effect of inundation and choice of hibernation sites of Coleoptera living on river banks. Norsk Entomologisk Tidsskrift 15: 115–133.

Andersen, J., 1995. A comparison of pitfall trapping and quadrat sampling of Carabidae (Coleoptera) on river banks. Entomologica Fennica 6: 65–77.

Andersen, J., 2011. Hibernation sites of riparian ground beetles (Coleoptera, Carabidae) in central and northern Norway. Norwegian Journal of Entomology 58: 111–121.

Anderson, M. J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62: 245–253.

Anderson, M. J., 2017. Permutational multivariate analysis of variance (PERMANOVA). In Balakrishnan, N., T. Colton, B. Everitt, W. Piegorsch, R. F., & J. L. Teugels (eds), Wiley StatsRef: Statistics reference online. Wiley.

Andersson, P., A. Koffman, N. E. Sjödin, & V. Johansson, 2017. Roads may act as barriers to flying insects: Species composition of bees and wasps differs on two sides of a large highway. 18: 47–59.

Anthony, A., 2018. Feargal Sharkey's mission to save our chalk streams. The Guardian, https://www.theguardian.com/music/2018/dec/01/feargal-sharkey-mission-save-our-chalk-streams-water-environment.

Arias-Real, R., C. Gutiérrez-Cánovas, M. Menéndez, & I. Muñoz, 2022. Drying niches of aquatic macroinvertebrates identify potential biomonitoring indicators in intermittent and ephemeral streams. Ecological Indicators 142: 109263.

Armitage, P. D., & J. A. B. Bass, 2013. Long-term resilience and short-term vulnerability of South Winterbourne macroinvertebrates. Proceedings of the Dorset Natural History & Archaeological Society 134: 43–55.

Armitage, P. D., P. S. Cranston, & L. V. C. Pinder, 1995. The Chironomidae: The biology and ecology of non-biting midges. Chapman & Hall, Scarborough, UK.

Armitage, P. D., D. Moss, J. F. Wright, & M. T. Furse, 1983. The performance of a new biological water quality score system based on macroinvertebrates over a wide range of unpolluted running-water sites. Water Research 17: 333–347.

Armitage, P. D., K. Szoszkiewicz, J. H. Blackburn, & I. Nesbitt, 2003. Ditch communities: A major contributor to floodplain biodiversity. Aquatic Conservation: Marine and Freshwater Ecosystems 13: 165–185.

Arnell, N. W., S. J. Halliday, R. W. Battarbee, R. A. Skeffington, & A. J. Wade, 2015. The implications of climate change for the water environment in England. Progress in Physical Geography: Earth and Environment 39: 93–120.

Arnott, S., J. Hilton, & B. W. Webb, 2009. The impact of geological control on flow accretion in lowland permeable catchments. Hydrology Research 40: 533–543.

Arroita, M., L. Flores, A. Larrañaga, A. Martinez, M. Martinez-Santos, O. Pereda, E. Ruiz-Romera, L. Solagaistua, & A. Elosegi, 2017. Water abstraction impacts stream ecosystem functioning via wetted-channel contraction. Freshwater Biology 62: 243–257.

Arscott, D. B., S. Larned, M. R. Scarsbrook, & P. Lambert, 2010. Aquatic invertebrate community structure along an intermittence gradient: Selwyn River, New Zealand. Journal of the North American Benthological Society 29: 530–545.

Aspin, T. W. H., K. Khamis, T. J. Matthews, A. M. Milner, M. J. O’Callaghan, M. Trimmer, G. Woodward, & M. E. Ledger, 2019. Extreme drought pushes stream invertebrate communities over functional thresholds. Global Change Biology 25: 230–244.

Aspin, T., & A. House, 2022. Alpha and beta diversity and species co-occurrence patterns in headwaters supporting rare intermittent-stream specialists. Freshwater Biology 67: 1188–1202.

Baiocchi, S., S. Fattorini, P. Bonavita, & A. V. Taglianti, 2012. Patterns of beta diversity in riparian ground beetle assemblages (Coleoptera Carabidae): A case study in the River Aniene (Central Italy). Italian Journal of Zoology 79: 136–150.

Ballinger, A., & P. S. Lake, 2006. Energy and nutrient fluxes from rivers and streams into terrestrial food webs. Marine and Freshwater Research 57: 15–28.

Baniya, M. B., T. Asaeda, T. Fujino, S. M. D. H. Jayasanka, G. Muhetaer, & J. Li, 2020. Mechanism of riparian vegetation growth and sediment transport interaction in floodplain: A dynamic riparian vegetation model (DRIPVEM) approach. Water 12: 77.

Barko, J. W., & R. M. Smart, 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. Ecology 67: 1328–1340.

Barnett, T. P., D. W. Pierce, H. G. Hidalgo, C. Bonfils, B. D. Santer, T. Das, G. Bala, A. W. Wood, T. Nozawa, A. A. Mirin, D. R. Cayan, & M. D. Dettinger, 2008. Human-induced changes in the hydrology of the western United States. Science 319: 1080–1083.

Bartholomew, A., R. J. Diaz, & G. Cicchetti, 2000. New dimensionless indices of structural habitat complexity: Predicted and actual effects on a predator¹s foraging success. Marine Ecology Pprogress Series 206: 45–58.

Bartoń, K., 2020. MuMIn: Multi-model inference. R package version 1.43.17, https://CRAN.R-project.org/package=MuMIn.

Bartrons, M., J. Sardans, D. Hoekman, & J. Peñuelas, 2018. Trophic transfer from aquatic to terrestrial ecosystems: A test of the biogeochemical niche hypothesis. Ecosphere 9: e02338.

Baselga, A., D. Orme, S. Villeger, J. De Bortoli, F. Leprieur, & M. Logez, 2021. Betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.5.4, https://CRAN.R-project.org/package=betapart.

Basoren, O., & N. Kazanci, 2012. Simuliidae species and sampling sites were grouped according to their similarities, by using the UPGMA (unweighted pair group method with arithmetic average) clustering method. 5th international scientific conference on water, climate and environment. Ohrid, Macedonia: 1–7.

Başören, O., & N. Kazanci, 2016. The distributional data of Simuliidae (Insecta, Diptera) species in Yeşilirmak River (Turkey). Transylvanian Review of Systematical and Ecological Research 17: 29–38.

Bates, A. J., J. P. Sadler, & A. P. Fowles, 2006. Condition-dependent dispersal of a patchily distributed riparian ground beetle in response to disturbance. Oecologica 150: 50–60.

Bates, A. J., J. P. Sadler, J. N. Perry, & A. P. Fowles, 2007. The microspatial distribution of beetles (Coleoptera) on exposed riverine sediments (ERS). European Journal of Entomology 104: 479–487.

Bates, A., J. Sadler, A. Fowles, & C. Butcher, 2005. Spatial dynamics of beetles living on exposed riverine sediments in the upper River Severn: Method development and preliminary results. Aquatic Conservation: Marine and Freshwater Ecosystems 15: 159–174.

Bates, D., M. Mächler, B. Bolker, & S. Walker, 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.

Bauernfeind, E., & T. Soldán, 2012. The mayflies of Europe (Ephemeroptera). Apollo Books, Ollerup.

Baumgartner, S., & C. Robinson, 2017. Short-term colonization dynamics of macroinvertebrates in restored channelized streams. Hydrobiologia 784: 321–335.

Beermann, A. J., V. Elbrecht, S. Karnatz, L. Ma, C. D. Matthaei, J. J. Piggott, & F. Leese, 2018. Multiple-stressor effects on stream macroinvertebrate communities: A mesocosm experiment manipulating salinity, fine sediment and flow velocity. Science of The Total Environment 610–611: 961–971.

Beketov, M. A., K. Foit, R. B. Schäfer, C. A. Schriever, A. Sacchi, E. Capri, J. Biggs, C. Wells, & M. Liess, 2009. SPEAR indicates pesticide effects in streams – comparative use of species- and family-level biomonitoring data. Environmental Pollution 157: 1841–1848.

Bell, J. R., D. A. Bohan, E. M. Shaw, & G. S. Weyman, 2005. Ballooning dispersal using silk: World fauna, phylogenies, genetics and models. Bulletin of Entomological Research 95: 69–114.

Benkwitt, C. E., S. K. Wilson, & N. A. J. Graham, 2019. Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event. Global Change Biology 25: 2619–2632.

Bennett, A. F., 1999. Linkages in the landscape: The role of corridors and connectivity in wildlife conservation. IUCN, Cambridge, UK.

Bennewicz, J., & T. Barczak, 2020. Ground beetles (Carabidae) of field margin habitats. Biologia 75: 1631–1641.

Benson, M. G., 1953. The importance of ground water to trout populations in the Pigeon River, Michigan. Transactions of the eighteenth North American wildlife conference. Washington D.C.: 269–281.

Bernal, S., D. von Schiller, F. Sabater, & E. Martí, 2013. Hydrological extremes modulate nutrient dynamics in Mediterranean climate streams across different spatial scales. Hydrobiologia 719: 31–42.

Bernard, T., & N. Moetapele, 2005. Desiccation of the Gomoti river: Biophysical process and indigenous resource management in northern Botswana. Journal of Arid Environments 63: 256–283.

Berrie, A. D., 1992. The chalk-stream environment. Hydrobiologia 248: 3–9.

Bestgen, K. R., N. L. Poff, D. W. Baker, B. P. Bledsoe, D. M. Merritt, M. Lorie, G. T. Auble, J. S. Sanderson, & B. C. Kondratieff, 2019. Designing flows to enhance ecosystem functioning in heavily altered rivers. Ecological Applications 30: e02005.

Biemans, H., I. Haddeland, P. Kabat, F. Ludwig, R. W. A. Hutjes, J. Heinke, W. von Bloh, & D. Gerten, 2011. Impact of reservoirs on river discharge and irrigation water supply during the 20th century. Water Resources Research 47: W03509.

Biondi, G., K. J. Gething, J. Kabir, T. Sykes, & R. Stubbington, 2022. The invertebrate biodiversity in the hidden headwater springs and streams of the southern chalk. Freshwater Biological Association News 85: 8–11.

Birkett, A. J., G. A. Blackburn, & R. Menéndez, 2018. Linking species thermal tolerance to elevational range shifts in upland dung beetles. Ecography 41: 1510–1519.

Birnie-Gauvin, K., M. M. Candee, H. Baktoft, M. H. Larsen, A. Koed, & K. Aarestrup, 2018. River connectivity reestablished: Effects and implications of six weir removals on brown trout smolt migration. River Research and Applications 34: 548–554.

Blake, S., D. I. McCracken, M. D. Eyre, A. Garside, & G. N. Foster, 2003. The relationship between the classification of Scottish ground beetle assemblages (Coleoptera Carabidae) and the National Vegetation Classification of British plant communities. Ecography 26: 602–616.

Blandenier, G., 2009. Ballooning of spiders (Araneae) in Switzerland: General results from an eleven-year survey. Arachnology 14: 308–316.

Boersma, K. S., M. T. Bogan, B. A. Henrichs, & D. A. Lytle, 2014. Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. Freshwater Biology 59: 491–501.

Bogan, M. T., & K. S. Boersma, 2012. Aerial dispersal of aquatic invertebrates along and away from arid-land streams. Freshwater Science 31: 1131–1144.

Bogan, M. T., K. S. Boersma, & D. A. Lytle, 2015. Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams. Freshwater Biology 60: 2547–2558.

Bogan, M. T., E. T. Chester, T. Datry, A. L. Murphy, B. J. Robson, A. Ruhi, R. Stubbington, & J. E. Whitney, 2017. Chapter 4.8 - resistance, resilience, and community recovery in intermittent rivers and ephemeral streams. In

Datry, T., N. Bonada, & A. Boulton (eds), Intermittent rivers and ephemeral streams. Academic Press: 349–376.

Bogan, M. T., & D. A. Lytle, 2007. Seasonal flow variation allows ’time-sharing’ by disparate aquatic insect communities in montane desert streams. Freshwater Biology 52: 290–304.

Bonada, N., M. Rieradevall, & N. Prat, 2007. Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. Hydrobiologia 589: 91–106.

Bond, N., & P. Cottingham, 2008. Ecology and hydrology of temporary streams: Implications for sustainable water management. eWater Cooperative Research Centre, Canberra: 35.

Bonn, A., K. Hagen, & D. W. Reiche, 2002. The significance of flood regimes for carabid beetle and spider communities in riparian habitats—a comparison of three major rivers in Germany. River Research and Applications 18: 43–64.

Borges, F. L., M. Oliveira, T. Almeida, J. Majer, & L. Garcia, 2021. Terrestrial invertebrates as bioindicators in restoration ecology: A global bibliometric survey. Ecological Indicators 125: 107458.

Botwe, P. K., L. A. Barmuta, R. Magierowski, P. McEvoy, P. Goonan, & S. Carver, 2015. Temporal patterns and environmental correlates of macroinvertebrate communities in temporary streams. PLOS ONE 10: e0142370.

Boudot, J. P., 2020. *Coenagrion mercuriale*: The IUCN Red List of Threatened Species., https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T5081A83841084.en .

Boulton, A. J., 1993. Stream ecology and surface-hyporheic hydrologic exchange: Implications, techniques and limitations. Marine and Freshwater Research 44: 553–564.

Boulton, A. J., M. Brock, B. Robson, D. Ryder, J. Chambers, & J. Davis, 2014. Australian freshwater ecology: Processes and management. John Wiley & Sons, Chichester, UK.

Boulton, A. J., T. Datry, T. Kasahara, M. Mutz, & J. A. Stanford, 2010. Ecology and management of the hyporheic zone: Stream-groundwater interactions of running waters and their floodplains. Journal of the North American Benthological Society 29: 26–40.

Boulton, A. J., S. Findlay, P. Marmonier, E. H. Stanley, & H. M. Valett, 1998. The functional significance of the hyporheic zone in streams and rivers. Annual Review of Ecology and Systematics 29: 59–81.

Boulton, A. J., & P. S. Lake, 1992. The ecology of two intermittent streams in Victoria, Australia. Freshwater Biology 27: 99–121.

Bowes, M. J., D. V. Leach, & W. A. House, 2005. Seasonal nutrient dynamics in a chalk stream: The River Frome, Dorset, UK. Science of The Total Environment 336: 225–241.

Bowler, D. E., R. Mant, H. Orr, D. M. Hannah, & A. S. Pullin, 2012. What are the effects of wooded riparian zones on stream temperature? Environmental Evidence 1: 3.

Brand, A., L. Allen, M. Altman, M. Hlava, & J. Scott, 2015. Beyond authorship: Attribution, contribution, collaboration, and credit. Learned Publishing 28: 151–155.

Brintrup, K., C. Amigo, J. Fernández, A. Hernández, F. Pérez, J. Félez-Bernal, A. Butturini, K. Saez-Carrillo, M. A. Yevenes, & R. Figueroa, 2019. Comparison of organic matter in intermittent and perennial rivers of Mediterranean Chile with the support of citizen science. Revista Chilena de Historia Natural 92: 3.

British Geological Survey, 2021. Geology of Britain viewer (1:625 000 scale digital geological mapping)., http://www.bgs.ac.uk/discoveringGeology/geologyOfBritain/viewer.html.

Britton, J. R., M. Berry, S. Sewell, C. Lees, & P. Reading, 2017. Importance of small fishes and invasive crayfish in otter *Lutra lutra* diet in an English chalk stream. Knowledge and Management of Aquatic Ecosystems 13.

Brooks, K. N., P. F. Ffolliott, & J. A. Magner, 2012. Hydrology and the management of watersheds. Wiley-Blackwell, Ames, Iowa.

Brooks, S. J., B. Fitch, J. Davy-Bowker, & S. A. Codesal, 2019. Anglers' Riverfly Monitoring Initiative (ARMI): A UK-wide citizen science project for water quality assessment. Freshwater Science 38: 270–280.

Brose, U., 2002. Estimating species richness of pitfall catches by non-parametric estimators. Pedobiologia 46: 101–107.

Brose, U., 2003. Bottom-up control of carabid beetle communities in early successional wetlands: Mediated by vegetation structure or plant diversity? Oecologia 135: 407–413.

Brown, J. H., & A. Kodric-Brown, 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. Ecology 58: 445–449.

Brown, L. E., K. Khamis, M. Wilkes, P. Blaen, J. E. Brittain, J. L. Carrivick, S. Fell, N. Friberg, L. Füreder, G. M. Gislason, S. Hainie, D. M. Hannah, W. H. M. James, V. Lencioni, J. S. Olafsson, C. T. Robinson, S. J. Saltveit, C. Thompson, & A. M. Milner, 2018. Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover. Nature Ecology and Evolution 2: 325–333.

Buczkowski, G., & D. S. Richmond, 2012. The effect of urbanization on ant abundance and diversity: A temporal examination of factors affecting biodiversity. PLOS ONE 7: 1–9.

Buffagni, A., 2020. The lentic and lotic characteristics of habitats determine the distribution of benthic macroinvertebrates in Mediterranean rivers. Freshwater Biology.

Buffagni, A., D. G. Armanini, & S. Erba, 2009. Does the lentic-lotic character of rivers affect invertebrate metrics used in the assessment of ecological quality? Journal of Limnology 68: 92–105.

Buffagni, A., R. Tenchini, M. Cazzola, S. Erba, R. Balestrini, C. Belfiore, & R. Pagnotta, 2016. Detecting the impact of bank and channel modification on invertebrate communities in Mediterranean temporary streams. Science of The Total Environment 565: 1138–1150.

Bunn, S. E., & A. H. Arthington, 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30: 492–507.

Bunting, G., J. England, K. Gething, T. Sykes, J. Webb, & R. Stubbington, 2021. Aquatic and terrestrial invertebrate community responses to drying in chalk streams. Water and Environment Journal 35: 229–241.

Burgmer, T., H. Hillebrand, & M. Pfenninger, 2007. Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. Oecologia 151: 93–103.

Burnham, K. P., & D. R. Anderson (eds), 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer-Verlag, New York.

Burt, T. P., 1979. Diurnal variations in stream discharge and throughflow during a period of low flow. Journal of Hydrology 41: 291–301.

Burt, T. P., G. Pinay, F. E. Matheson, N. E. Haycock, A. Butturini, J. C. Clement, S. Danielescu, D. J. Dowrick, M. M. Hefting, A. Hillbricht-Ilkowska, & V. Maitre, 2002. Water table fluctuations in the riparian zone: Comparative results from a pan-European experiment. Journal of Hydrology 265: 129–148.

Busch, M. H., K. H. Costigan, K. M. Fritz, T. Datry, C. A. Krabbenhoft, J. C. Hammond, M. Zimmer, J. D. Olden, R. M. Burrows, W. K. Dodds, K. S. Boersma, M. Shanafield, S. K. Kampf, M. C. Mims, M. T. Bogan, A. S. Ward, M. Perez-Rocha, S. Godsey, G. H. Allen, J. R. Blaszczak, C. N. Jones, & D. C. Allen, 2020. What's in a name? Patterns, trends, and suggestions for defining non-perennial rivers and streams. Water 12: 1980.

Caissie, D., 2006. The thermal regime of rivers: A review. Freshwater Biology 51: 1389–1406.

Cajaiba, R. L., E. Périco, W. B. da Silva, T. B. Vieira, M. S. Dalzochio, R. Bastos, J. A. Cabral, & M. Santos, 2018. How informative is the response of ground beetles' (Coleoptera: Carabidae) assemblages to anthropogenic land use changes? Insights for ecological status assessments from a case study in the neotropics. Science of the Total Environment 636: 1219–1227.

Campbell, I. C. (ed), 1990. Mayflies and stoneflies: Life histories and biology. Kluwer Academic Publishers, London.

Cañedo-Argüelles, M., K. S. Boersma, M. T. Bogan, J. D. Olden, I. Phillipsen, T. A. Schriever, & D. A. Lytle, 2015. Dispersal strength determines meta-community structure in a dendritic riverine network. Journal of Biogeography 42: 778–790.

Cañedo-Argüelles, M., C. Gutiérrez-Cánovas, R. Acosta, D. Castro-López, N. Cid, P. Fortuño, A. Munné, C. Múrria, A. R. Pimentão, R. Sarremejane, M. Soria, P. Tarrats, I. Verkaik, N. Prat, & N. Bonada, 2020. As time goes by: 20 years of changes in the aquatic macroinvertebrate metacommunity of Mediterranean river networks. Journal of Biogeography 47: 1861–1874.

Chadd, R. P., J. England, D. Constable, M. J. Dunbar, C. Extence, D. J. Leeming, J. Murray-Bligh, & P. J. Wood, 2017. An index to track the ecological effects of drought development and recovery on riverine invertebrate communities. Ecological Indicators 82: 344–356.

Chalkley, A., 2006. *Paraleptophlebia werneri* (Ulmer) (Ephemeroptera: Leptophlebiidae), an unexpected addition to the Suffolk list. Transactions of the Suffolk Natural History Society 42: 62–64.

Charlton, R., 2008. Fundamentals of fluvial geomorphology. Routledge, London.

Chevenet, F., S. Dolédec, & D. Chessel, 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshwater Biology 31: 295–309.

Chiu, M-C, C. Leigh, R. Mazor, N. Cid, & V. Resh, 2017. Chapter 5.1 - Anthropogenic threats to intermittent rivers and ephemeral streams. In Datry, T., N. Bonada, & A. Boulton (eds), Intermittent rivers and ephemeral streams. Academic Press, London: 433–454.

Ciutti, F., C. Cappelletti, C. Monauni, & M. Siligardi, 2004. Influence of substrate composition and current velocity on macroinvertebrates in a semi-artificial system. Journal of Freshwater Ecology 19: 455–460.

Claret, C., & A. J. Boulton, 2003. Diel variation in surface and subsurface microbial activity along a gradient of drying in an Australian sand-bed stream. Freshwater Biology 48: 1739–1755.

Claret, C., P. Marmonier, M. J. Dole-Olivier, & E. Castella, 1999. Effects of management works on the interstitial fauna of floodplain aquatic systems (River Rhône, France). Biodiversity & Conservation 8: 1179–1204.

Clark, M. S., S. H. Gage, & J. R. Spence, 1997. Habitats and management associated with common ground beetles (Coleoptera: Carabidae) in a Michigan agricultural landscape. Environmental Entomology 26: 519–527.

Clarke, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117–143.

Clifford, N. J., A. Robert, & K. S. Richards, 1992. Estimation of flow resistance in gravel-bedded rivers: A physical explanation of the multiplier of roughness length. Earth Surface Processes and Landforms 17: 111–126.

Cole, L. J., R. Morton, W. Harrison, D. I. McCracken, & D. Robertson, 2008. The influence of riparian buffer strips on carabid beetle (Coleoptera Carabidae) assemblage structure and diversity in intensively managed grassland fields.

Biodiversity and Conservation 17: 2233–2245.

Colvin, R., G. R. Giannico, J. Li, K. L. Boyer, & W. J. Gerth, 2009. Fish use of intermittent watercourses draining agricultural lands in the Upper Willamette River Valley, Oregon. Transactions of the American Fisheries Society 138: 1302–1313.

Cook, S. C., L. Housley, J. A. Back, & R. S. King, 2018. Freshwater eutrophication drives sharp reductions in temporal beta diversity. Ecology 99: 47–56.

Corbet, P. S., 1999. Dragonflies: Behaviour and ecology of Odonata. Harley books, Colchester, UK.

Corbin, T. A., & P. M. Goonan, 2010. Habitat and water quality preferences of mayflies and stoneflies from south Australian streams. Transactions of the Royal Society of South Australia 134: 5–18.

Corti, R., & T. Datry, 2012. Invertebrates and sestonic matter in an advancing wetted front travelling down a dry river bed (Albarine, France). Freshwater Science 31: 1187–1201.

Corti, R., & T. Datry, 2014. Drying of a temperate, intermittent river has little effect on adjacent riparian arthropod communities. Freshwater Biology 59: 666–678.

Corti, R., & T. Datry, 2016. Terrestrial and aquatic invertebrates in the riverbed of an intermittent river: Parallels and contrasts in community organisation. Freshwater Biology 61: 1308–1320.

Corti, R., S. T. Larned, & T. Datry, 2013. A comparison of pitfall-trap and quadrat methods for sampling ground-dwelling invertebrates in dry riverbeds. Hydrobiologia 717: 13–26.

Costigan, K. H., M. J. Kennard, C. Leigh, E. Sauquet, T. Datry, & A. J. Boulton, 2017. Chapter 2.2 - Flow regimes in intermittent rivers and ephemeral streams. In Datry, T., N. Bonada, & A. J. Boulton (eds), Intermittent rivers and ephemeral streams. Academic Press, London: 51–78.

Côté, I. M., E. S. Darling, & C. J. Brown, 2016. Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B: Biological Sciences 283: 20152592.

Crabot, J., S. Dolédec, M. Forcellini, & T. Datry, 2021. Efficiency of invertebrate-based bioassessment for evaluating the ecological status of streams along a gradient of flow intermittence. Ecological Indicators 133: 108440.

Crisp, D. T., A. M. Matthews, & D. F. Westlake, 1982. The temperatures of nine flowing waters in southern England. Hydrobiologia 89: 193–204.

Croft-White, M. V., E. Budgell, C. Jacobs, S. E. Doka, D. T. Reddick, J. Gardner Costa, & J. D. Midwood, 2021. Fish composition, but not richness or abundance, differ among *Phragmites*, *Typha*, and *Schoenoplectus* zones during a high-water year. Hydrobiologia 848: 4945–4963.

Croijmans, L., J. F. De Jong, & H. H. T. Prins, 2021. Oxygen is a better predictor of macroinvertebrate richness than temperature—a systematic review. Environmental Research Letters 16: 023002.

CrowdWater App, 2023. CrowdWater app dashboard., https://crowdwater.ch/en/app-2/.

Cuffney, T. F., M. D. Bilger, & A. M. Haigler, 2007. Ambiguous taxa: Effects on the characterization and interpretation of invertebrate assemblages. Journal of the North American Benthological Society 26: 286–307.

Cummins, M. P., 1992. Amphibious behaviour of a tropical, adult tiger beetle, *Oxycheila polita* Bates (Coleoptera: Cicindelidae). The Coleopterists Bulletin 46: 145–151.

Cunillera-Montcusí, D., A. I. Borthagaray, D. Boix, S. Gascón, J. Sala, I. Tornero, X. D. Quintana, & M. Arim, 2021. Metacommunity resilience against simulated gradients of wildfire: Disturbance intensity and species dispersal ability determine landscape recover capacity. Ecography 44: 1022–1034.

Datry, T., N. Bonada, & A. J. Boulton (eds), 2017b. Intermittent rivers and ephemeral streams. Academic Press, London.

Datry, T., N. Bonada, & A. J. Boulton, 2017a. Chapter 1 - General introduction. In Datry, T., N. Bonada, & A. J. Boulton (eds), Intermittent rivers and ephemeral streams. Academic Press, London: 1–20.

Datry, T., N. Bonada, & J. Heino, 2016a. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. Oikos 125: 149–159.

Datry, T., A. Foulquier, R. Corti, D. von Schiller, K. Tockner, C. Mendoza-Lera, J. C. Clément, M. O. Gessner, M. Moleón, R. Stubbington, B. Gücker, R. Albariño, D. C. Allen, F. Altermatt, M. I. Arce, S. Arnon, D. Banas, A. Banegas-Medina, E. Beller, M. L. Blanchette, J. F. Blanco-Libreros, J. J. Blessing, I. G. Boëchat, K. S. Boersma, M. T. Bogan, N. Bonada, N. R. Bond, K. C. Brintrup Barría, A. Bruder, R. M. Burrows, T. Cancellario,

C. Canhoto, S. M. Carlson, S. Cauvy-Fraunié, N. Cid, M. Danger, B. de Freitas Terra, A. M. De Girolamo, E. de La Barra, R. del Campo, V. D. Diaz-Villanueva, F. Dyer, A. Elosegi, E. Faye, C. Febria, B. Four, S. Gafny, S. D. Ghate, R. Gómez, L. Gómez-Gener, M. A. S. Graça, S. Guareschi, F. Hoppeler, J. L. Hwan, J. I. Jones, S. Kubheka, A. Laini, S. D. Langhans, C. Leigh, C. J. Little, S. Lorenz, J. C. Marshall, E. Martín, A. R. McIntosh, E. I. Meyer, M. Miliša, M. C. Mlambo, M. Morais, N. Moya, P. M. Negus, D. K. Niyogi, A. Papatheodoulou, I. Pardo, P. Pařil, S. U. Pauls, V. Pešić, M. Polášek, C. T. Robinson, P. Rodríguez-Lozano, R. J. Rolls, M. M. Sánchez-Montoya, A. Savić, O. Shumilova, K. R. Sridhar, A. L. Steward, R. Storey, A. Taleb, A. Uzan, R. Vander Vorste, N. J. Waltham, C. Woelfle-Erskine, D. Zak, C. Zarfl, & A. Zoppini, 2018. A global analysis of terrestrial plant litter dynamics in non-perennial waterways. Nature Geoscience 11: 497–503.

Datry, T., K. Fritz, & C. Leigh, 2016b. Challenges, developments and perspectives in intermittent river ecology. Freshwater Biology 61: 1171–1180.

Datry, T., S. T. Larned, K. M. Fritz, M. T. Bogan, P. J. Wood, E. I. Meyer, & A. N. Santos, 2014a. Broad-scale patterns of invertebrate richness and community composition in temporary rivers: Effects of flow intermittence. Ecography 37: 94–104.

Datry, T., S. T. Larned, & K. Tockner, 2014b. Intermittent rivers: A challenge for freshwater ecology. BioScience 64: 229–235.

Datry, T., H. Pella, C. Leigh, N. Bonada, & B. Hugueny, 2016c. A landscape approach to advance intermittent river ecology. Freshwater Biology 61: 1200–1213.

Datry, T., G. Singer, E. Sauquet, D. Jorda-Capdevila, D. von Schiller, R. Stubbington, C. Magand, P. Paril, M. Miliša, V. Acuña, N. H. Alves, B. Augeard, M. Brunke, N. Cid, Z. Csabai, J. England, J. Froebrich, P. Koundouri, N. Lamouroux, E. Marti, M. Morais, A. Munné, M. Mutz, V. Pesic, A. Previšic, A. Reynaud, C. Robinson, J. Sadler, N. Skoulikidis, B. Terrier, K. Tockner, D. Vesely, & A. Zoppini, 2017c. Science and management of intermittent rivers and ephemeral streams (SMIRES). Research Ideas and Outcomes 3: e21774.

Datry, T., A. Truchy, J. D. Olden, M. H. Busch, R. Stubbington, W. K. Dodds, S. Zipper, S. Yu, M. L. Messager, J. D. Tonkin, K. E. Kaiser, J. C. Hammond, E. K. Moody, R. M. Burrows, R. Sarremejane, A. G. DelVecchia, M. L. Fork, C. J. Little, R. H. Walker, A. W. Walters, & D. Allen, 2022. Causes, responses, and implications of anthropogenic versus natural flow intermittence in river networks. BioScience 73: 9–22.

Datry, T., R. Vander Vorste, E. Goïtia, N. Moya, M. Campero, F. Rodriguez, J. Zubieta, & T. Oberdorff, 2017d. Context-dependent resistance of freshwater invertebrate communities to drying. Ecology and Evolution 7: 3201–3211.

Davies, B. R., J. Biggs, P. J. Williams, J. T. Lee, & S. Thompson, 2008a. A comparison of the catchment sizes of rivers, streams, ponds, ditches and lakes: Implications for protecting aquatic biodiversity in an agricultural landscape. Hydrobiologia 597: 7–17.

Davies, B., J. Biggs, P. Williams, M. Whitfield, P. Nicolet, D. Sear, S. Bray, & S. Maund, 2008b. Comparative biodiversity of aquatic habitats in the European agricultural landscape. Agriculture, Ecosystems & Environment 125: 1–8.

Davies, L., 1966. The taxonomy of British black-flies (Diptera: Simuliidae). Transactions of the Royal Entomological Society of London 118: 413–506.

Day, D. G., 1983. Drainage density variability and drainage density outputs. Journal of Hydrology (New Zealand) 22: 3–17.

Day, J. C., M. Mustapha, & R. J. Post, 2010. The subgenus *Eusimulium* (Diptera: Simuliidae: *Simulium*) in Britain. Aquatic Insects 32: 281–292.

De Caceres, M., & P. Legendre, 2009. Associations between species and groups of sites: Indices and statistical inference. Ecology 90: 3566–3574.

Décamps, H., R. J. Naiman, & M. E. McClain, 2009. Riparian Zones. In Likens, G. E. (ed), Encyclopedia of inland waters. Academic Press, Oxford: 396–403.

Delong, M. D., & M. A. Brusven, 1998. Macroinvertebrate community structure along the longitudinal gradient of an agriculturally impacted stream. Environmental Management 22: 445—457.

Demars, B. O. L., J. L. Kemp, N. Friberg, P. Usseglio-Polatera, & D. M. Harper, 2012. Linking biotopes to invertebrates in rivers: Biological traits, taxonomic composition and diversity. Ecological Indicators 23: 301–311.

Dennis, P., R. J. Aspinall, & I. J. Gordon, 2002. Spatial distribution of upland beetles in relation to landform, vegetation and grazing management. Basic and Applied Ecology 3: 183–193.

Department for Levelling Up, Housing & Communities, UK Government, 2022. Land use statistics: England 2022., https://www.gov.uk/government/statistics/land-use-in-england-2022/land-use-statistics-england-2022.

Desender, K., 2000. Flight muscle development and dispersal in the life cycle of carabid beetles patterns and processes. Bulletin van het Koninlijk Belgisch

Instituut voor Natuurwetenschappen - Entomologie 70: 13–31.

Desender, K., M. Dufrene, M. Loreau, M. L. Luff, & J. P. Maelfait, 1994. Carabid beetles: Ecology and evolution. Klu- wer Academic, Dordrecht.

Devictor, V., R. Julliard, & F. Jiguet, 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117: 507–514.

Díaz, A. M., M. L. S. Alonso, & M. R. V. A. Gutiérrez, 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: Patterns along complex environmental gradients. Freshwater Biology 53: 1–21.

Dick, J. T. A., M. E. Alexander, & C. MacNeil, 2013. Natural born killers: An invasive amphipod is predatory throughout its life-history. Biological Invasions 15: 309–313.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, & B. Collen, 2014. Defaunation in the anthropocene. Science 345: 401–406.

Dodds, W. K., 2007. Trophic state, eutrophication and nutrient criteria in streams. Trends in Ecology & Evolution 22: 669–676.

Dodemaide, D. T., T. G. Matthews, D. Iervasi, & R. E. Lester, 2018. Anthropogenic water bodies as drought refuge for aquatic macroinvertebrates and macrophytes. Science of The Total Environment 616–617: 543–553.

Döll, P., & H. M. Schmied, 2012. How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. Environmental Research Letters 7: 014037.

Donahue, D. L., L. J. MacDonnell, Austen, D. J., R. L. Beschta, T. A. Dillaha, M.

M. Brinson, S. V. Gregory, J. W. Harvey, M. C. Molles, E. I. Rogers, & J. A. Stanford, 2002. Riparian areas: Functions and strategies for management. National Academy Press, Washington D.C.

dos Reis Oliveira, P. C., H. G. van der Geest, M. H. S. Kraak, & P. M. F. Verdonschot, 2019. Land use affects lowland stream ecosystems through dissolved oxygen regimes. Scientific Reports 9: 19685.

Drake, C. M., D. A. Lott, K. N. A. Alexander, & J. Webb, 2007. Natural England research report NERR005: Surveying terrestrial and freshwater invertebrates for conservation evaluation. Natural England, Sheffield, UK: 139.

Dray, S., D. Bauman, G. Blanchet, D. Borcard, S. Clappe, G. Guénard, T. Jombart, G. Larocque, P. Legendre, N. Madi, & H. H. Wagner, 2023. adespatial: Multivariate multiscale spatial analysis., https://CRAN.R-project.org/package=adespatial.

DRYRivERS App, 2023. DRYRivERS app dashboard., https://www.dryver.eu/app.

Dubois, N., E. Saulnier-Talbot, K. Mills, P. Gell, R. Battarbee, H. Bennion, S. Chawchai, X. Dong, P. Francus, R. Flower, D. F. Gomes, I. Gregory-Eaves, S. Humane, G. Kattel, J. P. Jenny, P. Langdon, J. Massaferro, S. McGowan, A. Mikomägi, N. T. M. Ngoc, A. S. Ratnayake, M. Reid, N. Rose, J. Saros, D. Schillereff, M. Tolotti, & B. Valero-Garcés, 2018. First human impacts and responses of aquatic systems: A review of palaeolimnological records from around the world. The Anthropocene Review 5: 28–68.

Dudgeon, D., 2010. Prospects for sustaining freshwater biodiversity in the 21st century: Linking ecosystem structure and function. Current Opinion in Environmental Sustainability 2: 422–430.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny, & C. A. Sullivan, 2006. Freshwater biodiversity: Importance, threats, status and conservation challenges. Biological Reviews 81: 163–182.

Dufrêne, M., & P. Legendre, 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.

Durance, I., & S. J. Ormerod, 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. Global Change Biology 13: 942–957.

Edegbene, A. O., F. O. Arimoro, & O. N. Odume, 2020. Exploring the distribution patterns of macroinvertebrate signature traits and ecological preferences and their responses to urban and agricultural pollution in selected rivers in the Niger Delta ecoregion, Nigeria. Aquatic Ecology 54: 553–573.

Eisenhauer, N., & J. Hines, 2021. Invertebrate biodiversity and conservation. Current Biology 31: R1214–R1218.

Elek, Z., J. Růžičková, & P. Ódor, 2021. Individual decisions drive the changes in movement patterns of ground beetles between forestry management types. Biologia 76: 3287–3296.

Emmett, W. W., 1970. The hydraulics of overland flow on hillslopes. United States Government Printing Office, Washington.

Engel, J., L. Hertzog, J. Tiede, C. Wagg, A. Ebeling, H. Briesen, & W.

W. Weisser, 2017. Pitfall trap sampling bias depends on body mass, temperature, and trap number: Insights from an individual-based model. Ecosphere 8: e01790.

England, J., R. Chadd, M. J. Dunbar, R. Sarremejane, R. Stubbington, C. G. Westwood, & D. Leeming, 2019. An invertebrate-based index to characterize ecological responses to flow intermittence in rivers. Fundamental and Applied Limnology 193: 93–117.

England, J., C. Hayes, J. C. White, & T. Johns, 2021. Evidence of taxonomic and functional recovery of macroinvertebrate communities following river restoration. Water 13: 2239.

Errochdi, S., G. Vinçon, & M. El Alami, 2014. Contribution to the knowledge of the stoneflies (Plecoptera) of the Moroccan Rif. Bulletin Société Entomologique Suisse 87: 25–40.

Erwin, T. L., G. E. Ball, D. R. Whitehead, & A. L. Halpern (eds), 1979. Carabid beetles: Their evolution, natural history, and classification. Springer Netherlands, Hague, Netherlands.

European Commission, 2000. Water framework directive (2000/60/EC). The European Parliament, Brussels: OJL 327, 1–73.

Evans, M. E. G., 1994. The carabid body plan: A functional interpretation. In Desender, K., M. Dufrêne, M. Loreau, M. L. Luff, & J. P. Maelfait (eds), Carabid beetles: Ecology and evolution. Springer Netherlands, Dordrecht: 25–31.

Evans, M. E. G., & T. G. Forsythe, 1984. A comparison of adaptations to running, pushing and burrowing in some adult Coleoptera: Especially

Carabidae. Journal of Zoology 202: 513–534.

Extence, C. A., D. M. Balbi, & R. P. Chadd, 1999. River flow indexing using British benthic macroinvertebrates: A framework for setting hydroecological objectives. Regulated Rivers: Research and Management 15: 545–574.

Extence, C. A., R. P. Chadd, J. England, M. J. Dunbar, P. J. Wood, & E. D. Taylor, 2013. The assessment of fine sediment accumulation in rivers using macro-invertebrate community response. River Research and Applications 29: 17–55.

Eyre, M. D., D. A. Lott, & M. L. Luff, 2001a. The rove beetles (Coleoptera Staphylinidae) of exposed riverine sediments in Scotland and Northern England: Habitat classification and conservation aspects. Journal of Insect Conservation 5: 173–186.

Eyre, M. D., M. L. Luff, & D. A. Phillips, 2001b. The ground beetles (Coleoptera Carabidae) of exposed riverine sediments in Scotland and Northern England. Biodiversity & Conservation 10: 403–426.

Feld, C. K., 2013. Response of three lotic assemblages to riparian and catchment-scale land use: Implications for designing catchment monitoring programmes. Freshwater Biology 58: 715–729.

Feld, C. K., M. Rosário Fernandes, M. T. Ferreira, D. Hering, S. J. Ormerod, M. Venohr, & C. Gutiérrez-Cánovas, 2018. Evaluating riparian solutions to multiple stressor problems in river ecosystems—a conceptual study. Water Research 139: 381–394.

Feld, C. K., P. Segurado, & C. Gutiérrez-Cánovas, 2016. Analysing the impact of multiple stressors in aquatic biomonitoring data: A “cookbook” with applications in R. Science of The Total Environment 573: 1320–1339.

Fenster, M. S., C. B. Knisley, & C. T. Reed, 2006. Habitat preference and the effects of beach nourishment on the federally threatened northeastern beach tiger beetle, *Cicindela dorsalis dorsalis*: Western Shore, Chesapeake Bay, Virginia. Journal of Coastal Research 225: 1133–1144.

Ficklin, D. L., J. T. Abatzoglou, S. M. Robeson, S. E. Null, & J. H. Knouft, 2018. Natural and managed watersheds show similar responses to recent climate change. Proceedings of the National Academy of Sciences 115: 8553–8557.

Fleishman, E., R. F. Noss, & B. R. Noon, 2006. Utility and limitations of species richness metrics for conservation planning. Ecological Indicators 6: 543–553.

Fleming, K. J., J. A. Schaefer, K. F. Abraham, M. A. Smith, & D. V. Beresford, 2021. Evidence for passive dispersal of ground beetles (Coleoptera: Carabidae) in the nearctic boreal forest. Ecoscience 28: 93–105.

Food and Agriculture Organization of the United Nations, 2017. Water pollution from agriculture: A global review. United Nations, Rome: 35.

Foster, G. N., 2010. A review of the scarce and threatened Coleoptera of Great Britain. Part 3: Water beetles of Great Britain. Joint Nature Conservation Committee, Peterborough, UK: 143.

Fournier, R. J., G. de Mendoza, R. Sarremejane, & A. Ruhi, 2023. Isolation controls reestablishment mechanisms and post-drying community structure in an intermittent stream. Ecology 104: e3911.

Fowles, A. P., K. N. A. Alexander, & R. S. Key, 1999. The saproxylic quality index: Evaluating wooded habitats for the conservation of dead-wood coleoptera. The Coleopterist 8: 121–141.

Francis, B. A., L. K. Francis, & M. B. Cardenas, 2010. Water table dynamics and groundwater-surface water interaction during filling and draining of a large fluvial island due to dam-induced river stage fluctuations. Water Resources Research 46: W07513.

Franken, R. J. M., R. G. Storey, & D. Dudley Williams, 2001. Biological, chemical and physical characteristics of downwelling and upwelling zones in the hyporheic zone of a north-temperate stream. Hydrobiologia 444: 183–195.

French, B. W., N. C. Elliott, R. C. Berberet, & J. D. Burd, 2001. Effects of riparian and grassland habitats on ground beetle (Coleoptera Carabidae) assemblages in adjacent wheat fields. Environmental Entomology 30: 225–234.

Fricke, U., I. Steffan-Dewenter, J. Zhang, C. Tobisch, S. Rojas-Botero, C. S. Benjamin, J. Englmeier, C. Ganuza, M. Haensel, R. Riebl, J. Uhler, L. Uphus, J. Ewald, J. Kollmann, & S. Redlich, 2022. Landscape diversity and local temperature, but not climate, affect arthropod predation among habitat types. PLOS ONE 17: 1–15.

Fritz, K. M., & W. K. Dodds, 2005. Harshness: Characterisation of intermittent stream habitat over space and time. Marine and Freshwater Research 56: 13–23.

Fritz, K. M., E. Hagenbuch, E. D’Amico, M. Reif, P. J. Wigington, S. G. Leibowitz, R. L. Comeleo, J. L. Ebersole, & T. Nadeau, 2013. Comparing the extent and permanence of headwater streams from two field surveys to values from hydrographic databases and maps. Journal of the American Water Resources Association 49: 867–882.

Frouz, J., A. Ali, J. Frouzova, & R. J. Lobinske, 2004. Horizontal and vertical distribution of soil macroarthropods along a spatio-temporal moisture gradient in subtropical central Florida. Environmental Entomology 33: 1282–1295.

Fu, G., S. Chen, C. Liu, & D. Shepard, 2004. Hydro-climatic trends of the Yellow River basin for the last 50 years. Climatic Change 65: 149–178.

Gabarrón-Galeote, M. A., J. F. Martinez-Murillo, M. A. Quesada, & J. D. Ruiz-Sinoga, 2013. Seasonal changes in the soil hydrological and erosive response depending on aspect, vegetation type and soil water repellency in different Mediterranean microenvironments. Solid Earth 4: 497–509.

Gamvroudis, C., N. P. Nikolaidis, O. Tzoraki, V. Papadoulakis, & N. Karalemas, 2015. Water and sediment transport modelling of a large temporary river basin in Greece. Science of The Total Environment 508: 354–365.

Garcia, A. F., G. J. K. Griffiths, & C. F. G. Thomas, 2000. Density, distribution and dispersal of the carabid beetle nebria brevicollis in two adjacent cereal fields. Annals of Applied Biology 137: 89–97.

Garcia de Leaniz, C., 2008. Weir removal in salmonid streams: Implications, challenges and practicalities. Hydrobiologia 609: 83–96.

Garcia, X., & D. Pargament, 2015. Rehabilitating rivers and enhancing ecosystem services in a water-scarcity context: The Yarqon River. International Journal of Water Resources Development 31: 73–87.

Garrido, P., A. Mårell, E. Öckinger, A. Skarin, A. Jansson, & C. G. Thulin, 2019. Experimental rewilding enhances grassland functional composition and pollinator habitat use. Journal of Applied Ecology 56: 946–955.

Genito, D., W. J. Gburek, & A. N. Sharpley, 2002. Response of stream macroinvertebrates to agricultural land cover in a small watershed. Journal of Freshwater Ecology 17: 109–119.

Gerth, W. J., J. Li, & G. R. Giannico, 2017. Agricultural land use and macroinvertebrate assemblages in lowland temporary streams of the Willamette Valley, Oregon, USA. Agriculture, Ecosystems & Environment 236: 154–165.

Gething, K. J., 2021. Physicochemical drivers of managed river and agricultural drainage channel macroinvertebrate communities. River Research and Applications 37: 675–680.

Gething, K. J., C. Hayes, J. R. Webb, T. Sykes, J. England, & R. Stubbington, 2022. Living on the edge: Predicting invertebrate richness and rarity in disturbance-prone aquatic–terrestrial ecosystems. Ecological Solutions and Evidence 3: e12196.

Gething, K. J., & S. Little, 2020. The importance of artificial drains for macroinvertebrate biodiversity in reclaimed agricultural landscapes. Hydrobiologia 847: 3129–3138.

Gething, K. J., M. C. Ripley, K. L. Mathers, R. P. Chadd, & P. J. Wood, 2020. The influence of substrate type on macroinvertebrate assemblages within agricultural drainage ditches. Hydrobiologia 847: 4273–4284.

Gething, K. J., T. Sykes, G. Biondi, C. Macadam, & R. Stubbington, 2021.

Ditching misconceptions: Rare temporary stream specialists in artificial habitats. Freshwater Biological Association News 83: 14–18.

Ghannem, S., S. Touaylia, & M. Boumaiza, 2018. Beetles (Insecta: Coleoptera) as bioindicators of the assessment of environmental pollution. Human and Ecological Risk Assessment: An International Joural 24: 456–464.

Gill, B. A., A. Sanabria, M. Gonzales, S. M. Carlson, & M. T. Bogan, 2022. Effects of drying and orientation to perennial refuges on aquatic biodiversity across two basins differing in aridity. Ecosphere 13: e4071.

Giller, P., & B. Malmqvist, 1998. The biology of streams and rivers. Oxford University Press, Oxford.

Gilpin, M., & I. Hanski, 1991. Metapopulation dynamics: Empirical and theoretical investigations. Academic Press, London.

Gladstone-Gallagher, R. V., C. A. Pilditch, F. Stephenson, & S. F. Thrush, 2019. Linking traits across ecological scales determines functional resilience. Trends in Ecology & Evolution 34: 1080–1091.

Gobbi, M., A. Barragán, M. Brambilla, E. Moreno, W. Pruna, & P. Moret, 2018. Hand searching versus pitfall trapping: How to assess biodiversity of ground beetles (Coleoptera: Carabidae) in high altitude equatorial Andes. Journal of Insect Conservation 22: 533–543.

Godoy, B. S., L. L. Queiroz, S. Lodi, J. D. Nascimento de Jesus, & L. G. Oliveira, 2016. Successional colonization of temporary streams: An experimental approach using aquatic insects. Acta Oecologica 77: 43–49.

Gómez, R., M. S. Arce, D. S. Baldwin, & C. N. Dahm, 2017. Chapter 3.1 - Water physicochemistry in intermittent rivers and ephemeral streams. In Datry, T., N. Bonada, & A. J. Boulton (eds), Intermittent rivers and ephemeral streams. Academic Press, London: 109–134.

Gómez-Cifuentes, A., A. Munevar, V. C. Gimenez, M. G. Gatti, & G. A. Zurita, 2017. Influence of land use on the taxonomic and functional diversity of dung beetles (Coleoptera: Scarabaeinae) in the southern Atlantic forest of Argentina. Journal of Insect Conservation 21: 147–156.

Gomi, T., R. C. Sidle, & J. S. Richardson, 2002. Understanding processes and downstream linkages of headwater systems. BioScience 52: 905.

Gooderham, J. P. R., L. A. Barmuta, & P. E. Davies, 2007. Upstream heterogeneous zones: Small stream systems structured by a lack of competence? Journal of the North American Benthological Society 26: 365–374.

Google, 2021. Google maps., http://maps.google.com/.

Govers, G., I. Takken, & K. Helming, 2000. Soil roughness and overland flow. Agronomie 20: 131–146.

Greenwood, M. J., J. S. Harding, D. K. Niyogi, & A. R. McIntosh, 2012. Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: Stream size and land-use legacies. Journal of Applied Ecology 49: 213–222.

Greenwood, M. J., & A. R. McIntosh, 2010. Low river flow alters the biomass and population structure of a riparian predatory invertebrate. Freshwater Biology 55: 2062–2076.

Greenwood, M. T., M. A. Bickerton, & G. E. Petts, 1995. Floodplain Coleoptera distributions: River Trent, U.K. Fundamental and Applied Limnology 101: 427–437.

Gurnell, A. M., D. Corenblit, D. García de Jalón, M. González del Tánago, R. C. Grabowski, M. T. O'Hare, & M. Szewczyk, 2016. A conceptual model of vegetation–hydrogeomorphology interactions within river corridors. River Research and Applications 32: 142–163.

Gurnell, A., J. England, L. Shuker, G. Wharton, & D. Gurnell, 2020b. The MoRPh survey: MoRPh indicator calculations (revised January 2020). Queen Mary University; Environment Agency, London: 6, https://modularriversurvey.org/citizen-science-help/.

Gurnell, A., J. England, L. Shuker, G. Wharton, & D. Gurnell, 2020a. The MoRPh survey: Technical reference manual. Queen Mary University; Environment Agency, London: 43, https://modularriversurvey.org/citizen-science-help/.

Gutiérrez-Cánovas, C., D. Sánchez-Fernández, J. Velasco, A. Millán, & N. Bonada, 2015. Similarity in the difference: Changes in community functional features along natural and anthropogenic stress gradients. Ecology 96: 2458–2466.

Hadwen, W. L., C. S. Fellows, D. P. Westhorpe, G. N. Rees, S. M. Mitrovic, B. Taylor, D. S. Baldwin, E. Silvester, & R. Croome, 2010. Longitudinal trends in river functioning: Patterns of nutrient and carbon processing in three Australian rivers. River Research and Applications 26: 1129–1152.

Haidvogl, G., 2018. Historic milestones of human river uses and ecological impacts. In Schmutz, S., & J. Sendzimir (eds), Riverine ecosystem management: Science for governing towards a sustainable future. Springer International Publishing, Cham: 19–39.

Haklay, M., D. Dörler, F. Heigl, M. Manzoni, S. Hecker, & K. Vohland, 2021. What is citizen science? The challenges of definition. In Vohland, K., A. Land-Zandstra, L. Ceccaroni, R. Lemmens, J. Perelló, M. Ponti, R. Samson, & K. Wagenknecht (eds), The science of citizen science. Springer International Publishing: 13–33.

Hammett, M. J., 2012. *Nemoura lacustris* Pictet, 1865 (Plecoptera: Nemouridae) – an addition to the British list. Entomologist's Monthly Magazine 148: 43–45.

Hampshire and Isle of Wight Wildlife Trust, 2023. Watercress and Winterbournes., https://www.hiwwt.org.uk/watercress-and-winterbournes.

Hancock, P. J., 2002. Human impacts on the stream–groundwater exchange zone. Environmental Management 29: 763–781.

Hannaford, J., & G. Buys, 2012. Trends in seasonal river flow regimes in the UK. Journal of Hydrology 475: 158–174.

Hannam, J. J., J. K. Liebherr, & A. E. Hajek, 2008. Climbing behaviour and aphid predation by *Agonum muelleri* (Coleoptera: Carabidae). The Canadian Entomologist 140: 203–207.

Hao, X., Y. Chen, C. Xu, & W. Li, 2008. Impacts of climate change and human activities on the surface runoff in the Tarim River basin over the last fifty years. Water Resources Management 22: 1159–1171.

Harper, W. V., 2016. Reduced major axis regression. In Balakrishnan, N., T.

Colton, B. Everitt, W. Piegorsch, F. Ruggeri, & J. L. Teugels (eds), Wiley StatsRef: Statistics reference online. John Wiley & Sons, Ltd, Online: 1–6.

Hartig, F., 2020. DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.3.3.0, https://CRAN.R-project.org/package=DHARMa.

Hassan, M. A., & R. Egozi, 2001. Impact of wastewater discharge on the channel morphology of ephemeral streams. Earth Surface Processes and Landforms 26: 1285–1302.

Hauer, C., P. Leitner, G. Unfer, U. Pulg, H. Habersack, & W. Graf, 2018. The role of sediment and sediment dynamics in the aquatic environment. In Schmutz, S., & J. Sendzimir (eds), Riverine ecosystem management: Science for governing towards a sustainable future. Springer International Publishing, Cham: 151–169.

Hawkes, H. A., 1998. Origin and development of the biological monitoring working party score system. Water Research 32: 964–968.

Hayashi, M., M. Bakkali, A. Hyde, & S. L. Goodacre, 2015. Sail or sink: Novel behavioural adaptations on water in aerially dispersing species. BMC Evolutionary Biology 15: 118.

Hayes, C., 2022. Ecological responses to environmental variability in wet and dry chalk streams: Towards better temporary stream monitoring and management. PhD thesis, Nottingham Trent University.

Hayes, R., H. Austin, D. Cadman, D. Bradley, & N. Milner, 2017. Literature review of short-term flow reduction ecological impacts and recovery: R16115QQ. Scottish Environmental Protection Agency, Stirling.

Heino, J., 2013. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. Biological Reviews 88: 166–178.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, & L. M. Bini, 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. Freshwater Biology 60: 845–869.

Heino, J., H. Mykrä, J. Kotanen, & T. Muotka, 2007. Ecological filters and variability in stream macroinvertebrate communities: Do taxonomic and functional structure follow the same path? Ecography 30: 217–230.

Hendricks, S. P., & D. S. White, 2000. Stream and groundwater influences on phosphorus biogeochemistry. In Jones, J. B., & P. J. Mulholland (eds), Streams and ground waters. Academic Press, San Diego: 221–235.

Henshall, S. E., J. P. Sadler, D. M. Hannah, & A. J. Bates, 2011. The role of microhabitat and food availability in determining riparian invertebrate distributions on gravel bars: A habitat manipulation experiment. Ecohydrology 4: 512–519.

Hepp, L. U., S. V. Milesi, C. Biasi, & R. M. Restello, 2010. Effects of agricultural and urban impacts on macroinvertebrates assemblages in streams (Rio Grande do Sul, Brazil). Zoologia (Curitiba) 27: 106–113.

Hering, D., M. Gerhard, R. Manderbach, & M. Reich, 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.

Hering, D., & H. Plachter, 1997. Riparian ground beetles (Coeloptera, Carabidae) preying on aquatic invertebrates: A feeding strategy in Alpine floodplains. Oecologica 111: 261–270.

Hertzog, L. R., A. Ebeling, S. T. Meyer, N. Eisenhauer, C. Fischer, A. Hildebrandt, C. Wagg, & W. W. Weisser, 2016. High survival of *Lasius niger* during summer flooding in a European grassland. PLOS ONE 11: 1–12.

Herzon, I., & J. Helenius, 2008. Agricultural drainage ditches, their biological importance and functioning. Biological Conservation 141: 1171–1183.

Heydemann, B., 1957. Die biotopstruktur als raumwiderstand und raumfulle fur die tierwelt. Verhandlungen der Deutschen Zoologischen Gesellschaft 50: 332–347.

Heydemann, B., 1967. Der überflug von insekten tiber nord- und ostsee nach untersuchungen auf feuerschiffen. Deutsche Entomologische Zeitschrift 14: 185–215.

Hilbe, J. M., 2011. Negative binomial regression. Cambridge University Press, Cambridge.

Hildrew, A., & P. Giller, 2023. The biology and ecology of rivers and streams. Oxford University Press, Oxford, UK.

Hill, D., M. Fasham, G. Tucker, M. Shewry, & P. Shaw, 2005. Handbook of biodiversity methods: Survey, evaluation and monitoring. Cambridge University Press, Cambridge.

Hill, M. J., R. P. Chadd, N. Morris, J. D. Swaine, & P. J. Wood, 2016. Aquatic macroinvertebrate biodiversity associated with artificial agricultural drainage ditches. Hydrobiologia 776: 249–260.

Hill, M. J., K. L. Mathers, S. Little, T. Worrall, J. Gunn, & P. J. Wood, 2019. Ecological effects of a supra-seasonal drought on macroinvertebrate communities differ between near-perennial and ephemeral river reaches. Aquatic Sciences 81: 62.

Hill, M. J., & V. S. Milner, 2018. Ponding in intermittent streams: A refuge for lotic taxa and a habitat for newly colonising taxa? Science of the Total Environment 628–629: 1308–1316.

Hille, S., E. A. Kristensen, D. Graeber, T. Riis, N. K. Jørgensen, & A. Baattrup-Pedersen, 2014. Fast reaction of macroinvertebrate communities to stagnation and drought in streams with contrasting nutrient availability. Freshwater Science 33: 847–859.

Hisdal, H., K. Stahl, L. M. Tallaksen, & S. Demuth, 2001. Have streamflow droughts in Europe become more severe or frequent? International Journal of Climatology 21: 317–333.

Hoback, W. W., D. W. Stanley, L. G. Higley, & M. C. Barnhart, 1998. Survival of immersion and anoxia by larval tiger beetles, *Cicindela togata*. American Midland Naturalist 140: 27–33.

Hoffman, G. E., & E. E. Schadt, 2016. variancePartition: Interpreting drivers of variation in complex gene expression studies. BMC Bioinformatics 17: 483.

Hoffmann, S., L. Steiner, A. H. Schweiger, A. Chiarucci, & C. Beierkuhnlein, 2019. Optimizing sampling effort and information content of biodiversity surveys: A case study of alpine grassland. Ecological Informatics 51: 112–120.

Holman, I. P., 2006. Climate change impacts on groundwater recharge-uncertainty, shortcomings, and the way forward? Hydrogeology Journal 14: 637–647.

Hondzo, M., 1998. Dissolved oxygen transfer at the sediment-water interface in a turbulent flow. Water Resources Research 34: 3525–3533.

Horsák, M., J. Bojková, S. Zahrádková, M. Omesová, & J. Helešic, 2009. Impact of reservoirs and channelization on lowland river macroinvertebrates: A case study from central Europe. Limnologica 39: 140–151.

House, A., & G. Tapia, 2014. A new stonefly found in British winterbournes. Freshwater Biological Association News 64: 14.

House of Lords Library, 2021. In focus: Chalk stream restoration strategy., https://lordslibrary.parliament.uk/chalk-stream-restoration-strategy/.

Hu, D., L. Jiang, Z. Hou, J. Zhang, H. Wang, & G. Lv, 2022. Environmental filtration and dispersal limitation explain different aspects of beta diversity in desert plant communities. Global Ecology and Conservation 33: e01956.

Hubbell, S. P., 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton.

Hughes, S. J., J. M. Santos, M. T. Ferreira, R. Caraca, & A. M. Mendes, 2009. Ecological assessment of an intermittent Mediterranean river using community structure and function: Evaluating the role of different organism groups. Freshwater Biology 54: 2383–2400.

Hugman, R., T. Y. Stigter, J. P. Monteiro, & L. Nunes, 2012. Influence of aquifer properties and the spatial and temporal distribution of recharge and abstraction on sustainable yields in semi-arid regions. Hydrological Processes 26: 2791–2801.

Hynes, H. B. N., 1958. The effect of drought on the fauna of a small mountain stream in Wales. SIL Proceedings 1922-2010 13: 826–833.

Hynes, H. B. N., 1970. Ecology of running waters. Liverpool University Press, Liverpool, UK.

IUCN, 2021. The IUCN red list of threatened species., https://www.iucnredlist.org.

Iwamoto, H., D. Tahara, & T. Yoshida, 2022. Contrasting metacommunity patterns of fish and aquatic insects in drainage ditches of paddy fields. Ecological Research 37: 635–646.

Jackson, J. K., & V. H. Resh, 1989. Distribution and abundance of adult aquatic insects in the forest adjacent to a northern California stream. Environmental Entomology 18: 278–283.

Jacobsen, D., R. Schultz, & A. Encalada, 1997. Structure and diversity of stream invertebrate assemblages: The influence of temperature with altitude and latitude. Freshwater Biology 38: 247–261.

Jaeger, K. L., N. A. Sutfin, S. Tooth, K. Michaelides, & M. Singer, 2017. Chapter 2.1 - Geomorphology and sediment regimes of intermittent rivers and ephemeral streams. In Datry, T., N. Bonada, & A. Boulton (eds), Intermittent rivers and ephemeral streams. Academic Press, London: 21–49.

Jaeschke, A., T. Bittner, B. Reineking, & C. Beierkuhnlein, 2013. Can they keep up with climate change? – Integrating specific dispersal abilities of protected Odonata in species distribution modelling. Insect Conservation and Diversity 6: 93–103.

Januschke, K., & R. C. M. Verdonschot, 2016. Effects of river restoration on riparian ground beetles (Coleoptera: Carabidae) in Europe. Hydrobiologia 769: 93–104.

Jenkins, D. G., & P. F. Quintana-Ascencio, 2020. A solution to minimum sample size for regressions. PLoS One 15: e0229345.

Jenkins, M. F., 1960. On the method by which Stenus and Dianous (Coleoptera: Staphylinidae) return to the banks of a pool. Transactions of the Royal Entomological Society of London 112: 1–14.

Johns, T., J. I. Jones, L. Knight, P. Wood, L. Maurice, & A. Robertson, 2014. Regional scale drivers of groundwater faunal distributions. Freshwater science 33: 329–343.

Jones, J. I., C. E. M. Lloyd, J. F. Murphy, A. Arnold, C. P. Duerdoth, A. Hawczak, J. L. Pretty, P. J. Johnes, J. E. Freer, M. W. Stirling, C. Richmond, & A. L. Collins, 2023. What do macroinvertebrate indices measure? Stressor-specific stream macroinvertebrate indices can be confounded by other stressors. Freshwater Biology 68: 1330–1345.

Jopp, F., & H. Reuter, 2005. Dispersal of carabid beetles—emergence of distribution patterns. Journal of Ecological Modelling 186: 389–405.

Joy, N. H., 1910. The behaviour of Coleoptera in time of floods. Transactions of the Royal Entomological Society of London 58: 379–385.

Jung, J.-K., J.-C. Jeong, & J.-H. Lee, 2019. Effects of pitfall trap size and sampling duration on collection of ground beetles (Coleoptera: Carabidae) in temperate forests. Entomological Research 49: 229–236.

Kaller, M., K. Hartman, & T. Angradi, 2001. Experimental determination of benthic macro invertebrate metric sensitivity to fine sediment in Appalachian streams. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 55: 105–115.

Karaouzas, I., C. Theodoropoulos, L. Vardakas, E. Kalogianni, & N. Skoulikidis, 2018. A review of the effects of pollution and water scarcity on the stream biota of an intermittent Mediterranean basin. River Research and Applications 34: 291–299.

Kato, C., T. Iwata, & E. Wada, 2004. Prey use by web-building spiders: Stable isotope analyses of trophic flow at a forest-stream ecotone. Ecological Research 19: 633–643.

Kavanagh, J. A., & S. S. C. Harrison, 2014. The contribution of a drainage network to the spatial and temporal patterns of macroinvertebrate diversity across an agricultural headwater catchment. Biology and Environment: Proceedings of the Royal Irish Academy 114: 181–197.

Kazanci, N., & O. Başören, 2010. Use of Simuliidae (Insecta, Diptera) species as indicators of aquatic habitat quality of Yeşilırmak River Basin (Turkey). Review of Hydrobiology 3: 27–36.

Kelly, D. W., R. J. Bailey, C. MacNeil, J. T. A. Dick, & R. A. McDonald, 2006. Invasion by the amphipod *Gammarus pulex* alters community composition of native freshwater macroinvertebrates. Diversity and Distributions 12: 525–534.

Kelly, D. W., J. T. A. Dick, & W. I. Montgomery, 2002. The functional role of *Gammarus* (Crustacea, Amphipoda): Shredders, predators, or both? Hydrobiologia 485: 199–203.

Kendon, M., M. McCarthy, S. Jevrejeva, A. Matthews, J. Williams, T. Sparks, & F. West, 2023. State of the UK climate 2022. International Journal of Climatology 43: 1–82.

Kennedy, T. L., & T. F. Turner, 2011. River channelization reduces nutrient flow and macroinvertebrate diversity at the aquatic terrestrial transition zone. Ecosphere 2: art35.

Knapp, M., J. Knappová, P. Jakubec, P. Vonička, & P. Moravec, 2020. Incomplete species lists produced by pitfall trapping: How many carabid species and which functional traits are missing? Biological Conservation 245: 108545.

Koivula, M. J., 2011. Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. ZooKeys 100: 287–317.

Kolesnikov, F. N., A. N. Karamyan, & W. W. Hoback, 2012. Survival of ground beetles (Coleoptera: Carabidae) submerged during floods: Field and laboratory studies. European Journal of Entomology 109: 71–76.

Kopf, K., R, C. M. Finlayson, P. Humphries, N. C. Sims, & S. Hladyz, 2015. Anthropocene baselines: Assessing change and managing biodiversity in human-dominated aquatic ecosystems. BioScience 65: 798–881.

Korbel, K. L., S. Stephenson, & G. C. Hose, 2019. Sediment size influences habitat selection and use by groundwater macrofauna and meiofauna.

Aquatic Sciences 81: 39.

Korhonen, J. J., J. Soininen, & H. Hillebrand, 2010. A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. Ecology 91: 508–517.

Kosmala, M., A. Wiggins, A. Swanson, & B. Simmons, 2016. Assessing data quality in citizen science. Frontiers in Ecology and the Environment 14: 551–560.

Kottek, M., J. Grieser, C. Beck, B. Rudolf, & F. Rubel, 2006. World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15: 259–263.

Krogerus, H., 1948. Okologische untersuchungen fiber uferinsekten. Acta Zoologica Fennica 53: 1–153.

Kuznetsova, A., P. B. Brockhoff, & R. H. B. Christensen, 2017. lmerTest package: Tests in linear mixed effects models. Journal of Statistical Software 82: 1–26.

Lafage, D., E. Bergman, R. L. Eckstein, E. M. Österling, J. P. Sadler, & J. J. Piccolo, 2019. Local and landscape drivers of aquatic-to-terrestrial subsidies in riparian ecosystems: A worldwide meta-analysis. Ecosphere 10: e02697.

Lagisz, M., K. Wolff, R. A. Sanderson, & R. Laskowski, 2010. Genetic population structure of the ground beetle, *Pterostichus oblongopunctatus*, inhabiting a fragmented and polluted landscape: Evidence for sex-biased dispersal. Journal of Insect Science 10: 105.

Laini, A., S. Guareschi, R. Bolpagni, G. Burgazzi, D. Bruno, C. Gutiérrez-Cánovas, R. Miranda, C. Mondy, G. Várbíró, & T. Cancellario, 2022. biomonitoR: An r package for managing ecological data and calculating biomonitoring indices. PeerJ 10: e14183.

Lake, P. S., 2013. Resistance, resilience and restoration. Ecological Management and Restoration 14: 20–24.

Lake, P. S., N. Bond, & P. Reich, 2017. Chapter 5.4 - Restoration ecology of intermittent rivers and ephemeral streams. In Datry, T., N. Bonada, & A. Boulton (eds), Intermittent rivers and ephemeral streams. Academic Press: 509–533.

Lambeets, K., M. L. Vandegehuchte, J.-P. Maelfait, & D. Bonte, 2008. Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. Journal of Animal Ecology 77: 1162–1174.

Lambeets, K., M. L. Vandegehuchte, J.-P. Maelfait, & D. Bonte, 2009. Integrating environmental conditions and functional life-history traits for riparian arthropod conservation planning. Biodiversity Conservation 142: 625–637.

Lang, A., 2000. The pitfalls of pitfalls: A comparison of pitfall trap catches and absolute density estimates of epigeal invertebrate predators in arable land. Anzeiger für Schädlingskunde 73: 99–106.

Langhans, S. D., & K. Tockner, 2014. Is the unsaturated sediment a neglected habitat for riparian arthropods? Evidence from a large gravel-bed river. Global Ecology and Conservation 2: 129–137.

Langhans, S. D., & K. Tockner, 2015. Edge effects are important in supporting beetle biodiversity in a gravel-bed river floodplain. PLOS ONE 9: 1–19.

Langheinrich, U., S. Tischew, R. M. Gersberg, & V. Lüderitz, 2004. Ditches and canals in management of fens: Opportunity or risk? A case study in the Drömling Natural Park, Germany. Wetlands Ecology and Management 12: 429–445.

Larned, S. T., T. Datry, D. B. Arscott, & K. Tockner, 2010. Emerging concepts in temporary-river ecology. Freshwater Biology 55: 717–738.

Larned, S. T., J. Schmidt, T. Datry, C. P. Konrad, J. K. Dumas, & J. C. Diettrich, 2011. Longitudinal river ecohydrology: Flow variation down the lengths of alluvial rivers. Ecohydrology 4: 532–548.

Lassau, S. A., D. F. Hochuli, G. Cassis, & C. A. M. Reid, 2005. Effects of habitat complexity on forest beetle diversity: Do functional groups respond consistently? Diversity and Distributions 11: 73–82.

Legendre, P., 2018. lmodel2: Model II regression. R package version 1.7-3, https://CRAN.R-project.org/package=lmodel2.

Legendre, P., & M. De Cáceres, 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecology Letters 16: 951–963.

Legendre, P., & L. Legendre, 2012. Numerical ecology. Elsevier, Oxford, 1–990 pp.

Lehmann, H., 1965. Ökologische untersuchungen über die carabidenfauna des rheinufers in der umgebung von köln. Zeitschrift für Morphologie und

Ökologie der Tiere 55: 597–630.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, & A. Gonzalez, 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7: 601–613.

Leigh, C., A. J. Boulton, J. L. Courtwright, K. Fritz, C. L. May, R. H. Walker, & T. Datry, 2016. Ecological research and management of intermittent rivers: An historical review and future directions. Freshwater Biology 61: 1181–1199.

Leigh, C., & T. Datry, 2017. Drying as a primary hydrological determinant of biodiversity in river systems: A broad-scale analysis. Ecography 40: 487–499.

Lengyel, S., E. Déri, & T. Magura, 2016. Species richness responses to structural or compositional habitat diversity between and within grassland patches: A multi-taxon approach. PLOS ONE 11: e0149662.

Lenski, R. E., 1984. Food limitation and competition: A field experiment with two *Carabus* species. Journal of Animal Ecology 53: 203–216, 10.2307/4352.

Leslie, A. W., R. F. Smith, D. E. Ruppert, K. Bejleri, J. M. Mcgrath, B. A. Needelman, & W. O. Lamp, 2012. Environmental factors structuring benthic macroinvertebrate communities of agricultural ditches in Maryland. Environmental Entomology 41: 802–812.

Levick, L. R., D. C. Goodrich, M. Hernandez, J. Fonseca, D. J. Semmens, & J. C. Stromberg, 2008. The ecological and hydrological significance of ephemeral and intermittent streams in the arid and semi-arid American southwest. US Environmental Protection Agency, Washington D.C.

Liere, H., M. H. Egerer, & S. M. Philpott, 2019. Environmental and spatial filtering of ladybird beetle community composition and functional traits in urban landscapes. Journal of Urban Ecology 5: juz014.

Liess, M., & P. C. V. D. Ohe, 2005. Analyzing effects of pesticides on invertebrate communities in streams. Environmental Toxicology and Chemistry 24: 954–965.

Lillebø, I. A., M. Morais, P. Guilherme, R. Fonseca, A. Serafim, & R. Neves, 2007. Nutrient dynamics in Mediterranean temporary streams: A case study in Pardiela catchment (Degebe River, Portugal). Limnologica 37: 337–348.

Lindroth, C. H., 1992. Ground beetles (Carabidae) of Fennoscandia, a zoogeographie study part III: General analysis with a discussion on biogeographic principles. Smithsonian Institution Libraries; The National Science Foundation, Washington, D.C.

Lintern, A., J. A. Webb, D. Ryu, S. Liu, U. Bende-Michl, D. Waters, P. Leahy, P. Wilson, & A. W. Western, 2018. Key factors influencing differences in stream water quality across space. WIREs Water 5: e1260.

Lister, B. C., & A. Garcia, 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. Proceedings of the National Academy of Sciences 115: E10397–E10406.

Liu, X., H. Wang, D. He, X. Wang, & M. Bai, 2021. The modelling and forecasting of Carabid beetle distribution in northwestern China. Insects 12: 168.

Lock, K., T. Adriaens, & P. Goethals, 2014. Effect of water quality on blackflies (Diptera: Simuliidae) in Flanders (Belgium). Limnologica 44: 58–65.

Loke, L. H. L., & R. A. Chisholm, 2023. Unveiling the transition from niche to dispersal assembly in ecology. Nature.

Loreau, M., 1990. Competition in a beetle community: A field experiment. Oikos 58: 25–38.

Loskotová, B., M. Straka, B. Pernecker, A. Dostálová, Z. Csabai, M. Polášek, & P. Pařil, 2023. Combined effect of stream drying and nutrient enrichment on macroinvertebrate community: Experimental study from artificial stream mesocosms. Aquatic Sciences 85: 23.

Lott, D., 2001. Ground beetles and rove beetles be associated with temporary ponds in England. Freshwater Forum 17: 43–50.

Lott, D. A., 2003. An annotated list of wetland ground beetles (Carabidae) and rove beetles (Staphylinidae) fount in the British Isles including a literature review of their ecology. English Nature, Peterborough, UK: 85.

Lövei, G. L., A. Macleod, & J. M. Hickman, 1998. Dispersal and effects of barriers on the movement of the New Zealand hover fly *Melanostoma fasciatum* (Dipt., Syrphidae) on cultivated land. Journal of Applied Entomology 122: 115–120.

Lövei, G. L., & K. D. Sunderland, 1996. Ecology and behaviour of ground beetles (Coleoptera: Carabidae). Annual Review of Entomology 41: 231–256.

Lövei, G., & T. Magura, 2011. Can carabidologists spot a pitfall? The non-equivalence of two components of sampling effort in pitfall-trapped ground beetles (Carabidae). Community Ecology 12: 18–22.

Luff, M. L., 1978. Diel activity patterns of some field Carabidae. Ecological Entomology 3: 53–52.

Luff, M. L., 1998. Provisional atlas of the ground beetles (Coleoptera, Carabidae) of Britain. Biological Records Centre, Huntingdon.

Luff, M. L., 2007. The Carabidae (ground beetles) of Britain and Ireland. Royal Entomological Society, London.

Lupon, A., J. L. J. Ledesma, & S. Bernal, 2018. Riparian evapotranspiration is essential to simulate streamflow dynamics and water budgets in a Mediterranean catchment. Hydrology and Earth System Sciences 22: 4033–4045.

Maamri, A., H. Chergui, & E. Pattee, 1997. Leaf litter processing in a temporary northeastern Moroccan river. Fundamental and Applied Limnology 140: 513–531.

Macadam, C., R. Stubbington, & I. Wallace, 2021. The specialist insects that rely on the wet-dry habitats of temporary streams. Freshwater Biological Association News 81: 28–33.

MacNeil, C., J. T. A. Dick, & R. W. Elwood, 1997. The trophic ecology of the freshwater *Gammarus* spp. (Crustacea: Amphipoda): Problems and perspectives concerning the functional feeding group concept. Biological Reviews 72: 349–364.

Mader, H. J., 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation 29: 81–96.

Mader, H. J., C. Schell, & P. Kornacker, 1990. Linear barriers to arthropod movements in the landscape. Biological Conservation 54: 209–222.

Madsen, B. L., 2012. Submersion respiration in small diving beetles (Dytiscidae). Aquatic Insects 34: 57–76.

Maelfait, J.-P., & F. Hendrickx, 1998. Spiders as bio-indicators of anthropogenic stress in natural and semi-natural habitats in Flanders (Belgium): Some recent developments. Proceedings of the 17th European Colloquium of Arachnology. British Arachnological Society, Edinburgh: 293--300.

Magura, T., & G. L. Lövei, 2019. Environmental filtering is the main assembly rule of ground beetles in the forest and its edge but not in the adjacent grassland. Insect Science 154–163.

Magura, T., & G. L. Lövei, 2021. Consequences of urban living: Urbanization and ground beetles. Current Ecology Landscape Reports 6: 9–21.

Mainstone, C. P., 1999. Chalk rivers: Nature conservation and management. English Nature; Environment Agency, Medmenham, http://hdl.handle.net/1834/27247.

Malard, F., D. Ferreira, S. Dolédec, & J. V. Ward, 2003. Influence of groundwater upwelling on the distribution of the hyporheos in a headwater river flood plain. Fundamental and Applied Limnology 157: 89–116.

Malard, F., K. Tockner, M. Dole-Olivier, & J. V. Ward, 2002. A landscape perspective of surface-subsurface hydrological exchanges in river corridors. Freshwater Biology 47: 621–640.

Maltby, L., 1995. Sensitivity of the crustaceans *Gammarus pulex* (L.) And *Asellus aquaticus* (L.) To short-term exposure to hypoxia and unionized ammonia: Observations and possible mechanisms. Water Research 29: 781–787.

Marshall, J. C., J. J. Blessing, S. E. Clifford, P. M. Negus, & A. L. Steward, 2020. Epigeic invertebrates of pig-damaged, exposed wetland sediments are rooted: An ecological response to feral pigs (*Sus scrofa*). Aquatic Conservation: Marine and Freshwater Ecosystems 30: 2207–2220.

Martin, E. H., C. Kelleher, & T. Wagener, 2012. Has urbanization changed ecological streamflow characteristics in Maine (USA)? Hydrological Sciences Journal 57: 1337–1354.

Martinson, H. M., & M. J. Raupp, 2013. A meta-analysis of the effects of urbanization on ground beetle communities. Ecosphere 4: 60.

Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou, 2021. Climate change 2021: The physical science basis. Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, https://www.ipcc.ch/report/ar6/wg1/downloads/report/IPCC_AR6_WGI_SPM_final.pdf.

Masters, Z., I. Peteresen, A. G. Hildrew, & S. J. Ormerod, 2007. Insect dispersal does not limit the biological recovery of streams from acidification. Aquatic Conservation: Marine and Freshwater Ecosystems 17: 375–383.

Matalin, A. V., 1994. The strategy of dispersal behaviour in some Carabidae species of Southeastern Europe. In Desender, K., M. Dufrêne, M. Loreau, M. L. Luff, & J.-P. Maelfait (eds), Carabid beetles: Ecology and evolution.

Springer Netherlands, Dordrecht: 183–188.

Matalin, A. V., 2003. Variations in flight ability with sex and age in ground beetles (Coleoptera, Carabidae) of south-western Moldova. Pedobiologia 47: 311–319.

Mateo-Sagasta, J., S. M. Zadeh, & H. Turral, 2017. Water pollution from agriculture: A global review. Food; Agriculture Organization of the United Nations, Rome: 29, http://www.fao.org/3/i7754e/i7754e.pdf.

Matthaei, C. D., J. J. Piggott, & C. R. Townsend, 2010. Multiple stressors in agricultural streams: Interactions among sediment addition, nutrient enrichment and water abstraction. Journal of Applied Ecology 47: 639–649.

Mauremooto, J. R., S. D. Wratten, S. P. Worner, & G. L. A. Fry, 1995. Permeability of hedgerows to predatory carabid beetles. Agriculture, Ecosystems & Environment 52: 141–148.

Mazaheri, M. R., & M. Mahmoodabadi, 2012. Study on infiltration rate based on primary particle size distribution data in arid and semiarid region soils. Arabian Journal of Geosciences 5: 1039–1046.

McCluney, K. E., & J. L. Sabo, 2012. River drying lowers the diversity and alters the composition of an assemblage of desert riparian arthropods. Freshwater Biology 57: 91–103.

McDonough, O. T., J. D. Hosen, & M. A. Palmer, 2011. Temporary streams: The hydrology, geography, and ecology of non-perennially flowing waters. In Elliot, H. S., & L. E. Martin (eds), River ecosystems: Dynamics, management and conservation. NOVA Science Publishers Inc, Hauppauge, NY: 259–289.

McGrane, S. J., 2016. Impacts of urbanisation on hydrological and water quality dynamics, and urban water management: A review. Hydrological Sciences Journal 61: 2295–2311.

Melbourne, B. A., 1999. Bias in the effect of habitat structure on pitfall traps: An experimental evaluation. Australian Journal of Ecology 24: 228–239.

Menció, A., & D. Boix, 2018. Response of macroinvertebrate communities to hydrological and hydrochemical alterations in Mediterranean streams. Journal of Hydrology 566: 566–580.

Merchán, D., J. Causapé, & R. Abrahão, 2013. Impact of irrigation implementation on hydrology and water quality in a small agricultural basin in Spain. Hydrological Sciences Journal 58: 1400–1413.

Messager, M. L., B. Lehner, C. Cockburn, N. Lamouroux, H. Pella, T. Snelder, K. Tockner, T. Trautmann, C. Watt, & T. Datry, 2021. Global prevalence of non-perennial rivers and streams. Nature 594: 391–397.

Met Office, 2016. Southern england: climate. Met Office, https://www.metoffice.gov.uk/binaries/content/assets/metofficegovuk/pdf/weather/learn-about/uk-past-events/regional-climates/southern-england_-climate---met-office.pdf.

Met Office, 2022. UK climate averages: Martyr Worthy (Hampshire). Met Office, https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-climate-averages/gcp4eqcmh.

Meyer, A., E. I. Meyer, & C. Meyer, 2003. Lotic communities of two small temporary karstic stream systems (East Westphalia, Germany) along a longitudinal gradient of hydrological intermittency. Limnologica 33: 271–279.

Michaelides, K., R. Hollings, M. B. Singer, M. H. Nichols, & M. A. Nearing, 2018. Spatial and temporal analysis of hillslope-channel coupling and implications for the longitudinal profile in a dryland basin. Earth Surface Processes and Landforms 43: 1608–1621.

Miliša, M., S. Stubbington, T. Datry, N. Cid, N. Bonada, M. Šumanović, & D. Milošević, 2022. Taxon-specific sensitivities to flow intermittence reveal macroinvertebrates as potential bioindicators of intermittent rivers and streams. Science of The Total Environment 804: 150022.

Mirus, B. B., & K. Loague, 2013. How runoff begins (and ends): Characterizing hydrologic response at the catchment scale. Water Resources Research 49: 2987–3006.

Mojarrad, B. B., A. Betterle, T. Singh, C. Olid, & A. Wörman, 2019. The effect of stream discharge on hyporheic exchange. Water 11: 1436.

Mondon, B., D. A. Sear, A. L. Collins, P. J. Shaw, & T. Sykes, 2021. The scope for a system-based approach to determine fine sediment targets for chalk streams. CATENA 206: 105541.

Moody, E. K., & J. L. Sabo, 2017. Dissimilarity in the riparian arthropod communities along surface water permanence gradients in aridland streams. Ecohydrology 10: e1819.

Moorhead, L. C., & S. M. Philpott, 2013. Richness and composition of spiders in urban green spaces in Toledo, Ohio. The Journal of Arachnology American

Arachnological Society 41: 356–363.

Morhun, H., M. O. Son, T. Rewicz, E. Kazanavičiūtė, & D. Copilas-Ciocianu, 2022. The first records of *Niphargus hrabei* and *N. potamophilus* in Ukraine and Bulgaria significantly enlarge the ranges of these species. The European Zoological Journal 89: 1191–1200.

Morton, R. D., C. S. Rowland, C. M. Wood, L. Meek, C. G. Marston, & G. M. Smith, 2014. Land Cover Map 2007 (vector, GB) v1.2. NERC Environmental Information Data Centre.

Mukherjee, A., S. N. Bhanja, & Y. Wada, 2018. Groundwater depletion causing reduction of baseflow triggering Ganges river summer drying. Scientific Reports 8: 12049.

Mulieri, P. R., L. D. Patitucci, J. A. Schnack, & J. C. Mariluis, 2011. Diversity and seasonal dynamics of an assemblage of sarcophagid Diptera in a gradient of urbanization. Journal of Insect Science 11: 91.

Müller, J., H. Brustel, A. Brin, H. Bussler, C. Bouget, E. Obermaier, I. M. M. Heidinger, T. Lachat, B. Förster, J. Horak, J. Procházka, F. Köhler, L. Larrieu, U. Bense, G. Isacsson, L. Zapponi, & M. M. Gossner, 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography 38: 499–509.

Müller, P., D. Neuhoff, M. Nabel, K. Schiffers, & T. F. Döring, 2022. Tillage effects on ground beetles in temperate climates: A review. Agronomy for Sustainable Development 42: 65.

Mundy, C. A., L. J. Allen-Williams, N. Underwood, & S. Warrington, 2000. Prey selection and foraging behaviour by *Pterostichus cupreus* L. (Col., Carabidae) under laboratory conditions. Journal of Applied Entomology 124: 349–358.

Munné, A., N. Bonada, N. Cid, F. Gallart, C. Solà, M. Bardina, A. Rovira, C. Sierra, M. Soria, P. Fortuño, P. Llorens, J. Latron, T. Estrela, A. Fidalgo, I. Serrano, S. Jiménez, R. Vega, & N. Prat, 2021. A proposal to classify and assess ecological status in Mediterranean temporary rivers: Research insights to solve management needs. Water 13: 767.

Murray-Bligh, J. A. D., 1999. BT001: Procedure for collecting and analysing macro-invertebrate samples. Quality management systems for environmental monitoring: Biological techniques. Environment Agency, Bristol, UK.

Murray-Bligh, J., & M. Griffiths, 2022. Freshwater biology and ecology handbook. Foundation for Water Research; Freshwater Biological Association, Marlow, UK: 315.

Musthafa, M. M., F. Abdullah, A. P. Martínez-Falcón, & M. de Bruyn, 2021. How mountains and elevations shape the spatial distribution of beetles in Peninsular, Malaysia. Scientific Reports 11: 5791.

Nagy, H. B., Z. László, F. Szabó, L. Szőcs, G. Dévai, & B. Tóthmérész, 2019. Landscape-scale terrestrial factors are also vital in shaping Odonata assemblages of watercourses. Scientific Reports 9: 18196.

Naiman, R. J., J. S. Bechtold, D. C. Drake, J. J. Latterell, T. C. O’Keefe, & E. V. Balian, 2005a. Origins, patterns, and importance of heterogeneity in riparian systems. In Lovett, G. M., M. G. Turner, C. G. Jones, & K. C. Weathers (eds), Ecosystem function in heterogeneous landscapes. Springer, New York, NY: 279–309.

Naiman, R. J., H. Décamps, M. E. McClain, & G. E. Likens, 2005b. Catchments and the physical template. In Naiman, R. J., H. Décamps, M. E. McClain, & G. E. Likens (eds), Riparia. Academic Press, Burlington: 19–48.

Naimi, B., N. Hamm, T. A. Groen, A. K. Skidmore, & A. G. Toxopeus, 2014. Where is positional uncertainty a problem for species distribution modelling. Ecography 37: 191–203.

Nakamura, Y., & H. G. Stefan, 1994. Effect of flow velocity on sediment oxygen demand: theory. Journal of Environmental Engineering 120: 996–1016.

Nakano, S., & M. Murakami, 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences 98: 166–170.

Nassif, S. H., & E. M. Wilson, 1975. The influence of slope and rain intensity on runoff and infiltration. Hydrological Sciences Bulletin 20: 539–553.

National River Flow Archive, 2021. 43001 - Avon at Ringwood catchment information. Centre for Ecology and Hydrology, http://nrfa.ceh.ac.uk/data/station/spatial/43001.

National River Flow Archive, 2022a. 42024 - Test at Chilbolton catchment information. Centre for Ecology and Hydrology, https://nrfa.ceh.ac.uk/data/station/spatial/42024.

National River Flow Archive, 2022b. 42009 - Candover Stream at Borough Bridge catchment infofmation. Centre for Ecology and Hydrology, https://nrfa.ceh.ac.uk/data/station/spatial/42009.

National River Flow Archive, 2023a. 41015 - Ems at Westbourne. Centre for

Ecology and Hydrology, https://nrfa.ceh.ac.uk/data/station/spatial/41015.

National River Flow Archive, 2023b. 41023 - Lavant at Graylingwell. Centre for Ecology and Hydrology, https://nrfa.ceh.ac.uk/data/station/spatial/41023.

National River Flow Archive, 2023c. 42016 - Itchen at Easton. Centre for Ecology and Hydrology, https://nrfa.ceh.ac.uk/data/station/spatial/42016.

National River Flow Archive, 2023d. 42029 - Test at Timsbury. Centre for Ecology and Hydrology, https://nrfa.ceh.ac.uk/data/station/spatial/42029.

Natural England, 2021. Sites of Special Scientific Interest (England). Natural England, https://naturalengland-defra.opendata.arcgis.com/datasets/f10cbb4425154bfda349ccf493487a80_0?geometry=-13.155%2C50.522%2C8.796%2C55.161.

Natural England, 2023. Lathkill dale SSSI. Natural England, https://designatedsites.naturalengland.org.uk/SiteDetail.aspx?SiteCode=S1003711&SiteName=lathkill&countyCode=&responsiblePerson=&SeaArea=&IFCAArea=.

Newton, M., J. A. Dodd, J. Barry, P. Boylan, & C. E. Adams, 2018. The impact of a small-scale riverine obstacle on the upstream migration of Atlantic Salmon. Hydrobiologia 806: 251–264.

Niemelä, H., J., 1990. Balancing sampling effort in pitfall trapping of carabid beetles. Entomologica Fennica 1: 233–238.

Niemelä, J., & D. J. Kotze, 2009. Carabid beetle assemblages along urban to rural gradients: A review. Landscape and Urban Planning 92: 65–71.

O'Callaghan, M. J., D. M. Hannah, I. Boomer, M. Williams, & J. P. Sadler, 2013a.

Responses to river inundation pressures control prey selection of riparian beetles. PLOS ONE 8: e61866.

O'Callaghan, M. J., D. M. Hannah, M. Williams, & J. P. Sadler, 2013b. Exposed riverine sediments (ERS) in England and Wales: Distribution, controls and management. Aquatic Conservation: Marine and Freshwat Ecosystems 23: 924–938.

O'Connor, D. J., 1967. The temporal and spatial distribution of dissolved oxygen in streams. Water Resources Research 3: 65–79.

O'Driscoll, M., S. Clinton, A. Jefferson, A. Manda, & S. McMillan, 2010. Urbanization effects on watershed hydrology and in-stream processes in the southern United States. Water 2: 605–648.

O'Gorman, P. A., 2015. Precipitation extremes under climate change. Current Climate Change Reports 1: 49–59.

O'Hare, M. T., A. Baattrup-Pedersen, I. Baumgarte, A. Freeman, I. D. M. Gunn, A. N. Lázár, R. Sinclair, A. J. Wade, & M. J. Bowes, 2018. Responses of aquatic plants to eutrophication in rivers: A revised conceptual model. Frontiers in Plant Science 9: 451.

Obermann, M., J. Froebrich, J.-L. Perrin, & M.-G. Tournoud, 2007. Impact of significant floods on the annual load in an agricultural catchment in the Mediterranean. Journal of Hydrology 334: 99–108.

Ocon, C., M. V. L. Oosterom, M. I. Muñoz, & A. Rodrigues-Capítulo, 2013. Macroinvertebrate trophic responses to nutrient addition in a temperate stream in South America. Fundamental and Applied Limnology 182: 17–30.

Oksanen, J., F. G. Blanchet, M. Friendly, K. R., P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, & H. Wagner, 2019. Vegan: Community ecology package. R package version 2.5.7, https://CRAN.R-project.org/package=vegan.

Omoniyi, G. E., C. Piscart, L. Pellan, & B. Bergerot, 2022. Responses of macroinvertebrate communities to hydromorphological restoration of headwater streams in Brittany. Water 14: e553.

Owens, D. C., T. N. Heatherly, K. M. Eskridge, C. V. Baxter, & S. A. Thomas, 2022. Seasonal variation in terrestrial invertebrate subsidies to tropical streams and implications for the feeding ecology of Hart's Rivulus (*Anablepsoides hartii*). Frontiers in Ecology and Evolution 10:

Paetzold, A., C. J. Schubert, & K. Tockner, 2005. Aquatic terrestrial linkages along a braided-river: Riparian arthropods feeding on aquatic insects. Ecosystems 8: 748–759.

Paetzold, A., C. Yoshimura, & K. Tockner, 2008. Riparian arthropod responses to flow regulation and river channelization. Journal of Applied Ecology 45: 894–903.

Painter, D., 1999. Macroinvertebrate distributions and the conservation value of aquatic Coleoptera, Mollusca and Odonata in the ditches of traditionally managed and grazing fen at Wicken Fen, UK. Journal of Applied Ecology 36: 33–48.

Paisley, M. F., D. J. Trigg, & W. J. Walley, 2014. Revision of the biological monitoring working party (BMWP) score system: Derivation of present-only and abundance-related scores from field data. River Research and Applications 30: 887–904.

Palmer, M. A., A. P. Covich, S. Lake, P. Biro, J. J. Brooks, J. Cole, C. Dahm, J. Gibert, W. Goedkoop, K. Martens, J. Verhoeven, & W. J. Van De Bund, 2000. Linkages between aquatic sediment biota and life above sediments as potential drivers of biodiversity and ecological processes. BioScience 50: 1062–1075.

Palmer-Felgate, E. J., H. P. Jarvie, R. J. Williams, R. J. G. Mortimer, M. Loewenthal, & C. Neal, 2008. Phosphorus dynamics and productivity in a sewage-impacted lowland chalk stream. Journal of Hydrology 351: 87–97.

Pardo, M. T., M. A. Esteve, A. Giménez, J. Martínez-Fernández, M. F. Carreño, J. Serrano, & Miñano. J., 2008. Assessment of hydrological alterations on wandering beetle assemblages (Coleoptera: Carabidae and Tenebrionidae) in coastal wetlands of arid Mediterranean systems. Journal of Arid Environments 70: 1803–1810.

Paredes, I., N. Otero, A. Soler, A. J. Green, & D. X. Soto, 2020. Agricultural and urban delivered nitrate pollution input to Mediterranean temporary freshwaters. Agriculture, Ecosystems & Environment 294: 106859.

Partnership, T. R., 2021. The Riverfly Partnership: Anglers' Riverfly Monitoring Initiative., https://www.royensoc.co.uk/facts-and-figures.

Patrick, C. J., K. E. Anderson, B. L. Brown, C. P. Hawkins, A. Metcalfe, P. Saffarinia, T. Siqueira, C. M. Swan, J. D. Tonkin, & L. L. Yuan, 2021. The application of metacommunity theory to the management of riverine ecosystems. WIREs Water 8: e1557.

Peckarsky, B. L., 1983. Biotic interactions or abiotic limitations? A model of lotic community structure. In Fontaine, T. D., & S. M. Bartell (eds), Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, MI: 303–323.

Pelletier, M. C., J. Ebersole, K. Mulvaney, B. Rashleigh, M. N. Gutierrez, M. Chintala, A. Kuhn, M. Molina, M. Bagley, & C. Lane, 2020. Resilience of aquatic systems: Review and management implications. Aquatic Sciences 82: 44.

Petersen, I., J. H. Winterbottom, S. Orton, N. Friberg, A. G. Hildrew, D. C. Spiers, & W. S. C. Gurney, 1999. Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, U.K. Freshwater Biology 42: 401–416.

Pettit, N. E., J. J. Latterell, & R. J. Naiman, 2006. Formation, distribution and ecological consequences of flood-related wood debris piles in a bedrock confined river in semi-arid South Africa. River Research and Applications 22: 1097–1110.

Petts, G. E., A. M. Gurnell, A. J. Gerrard, D. M. Hannah, B. Hansford, I. P. Morrissey, P. J. Edwards, J. Kollmann, J. V. Ward, K. Tockner, & B. P. G. Smith, 2000. Longitudinal variations in exposed riverine sediments: A context for the ecology of the Fiume Tagliamento, Italy. Aquatic Conservation: Marine and Freshwater Ecosystems 10: 249–266.

Phillips, I. D., & T. P. Cobb, 2005. Effects of habitat structure and lid transparency on pitfall catches. Environmental Entomology 34: 875–882.

Pickwell, A., D. Constable, R. Chadd, C. Extence, & S. Little, 2022. The development of a novel macroinvertebrate indexing tool for the determination of salinity effects in freshwater habitats. River Research and Applications 38: 522–538.

Pik, A. J., I. Oliver, & A. J. Beattie, 1999. Taxonomic sufficiency in ecological studies of terrestrial invertebrates. Australian Journal of Ecology 24:

555–562.

Pineda-Morante, D., J. M. Fernández-Calero, S. Pölsterl, D. Cunillera-Montcusí, N. Bonada, & M. Cañedo-Argüelles, 2022. Local hydrological conditions and spatial connectivity shape invertebrate communities after rewetting in temporary rivers. Hydrobiologia 849: 1511–1530.

Pipan, T., & D. C. Culver, 2019. Shallow subterranean habitats. In White, W. B., D. C. Culver, & T. Pipan (eds), Encyclopedia of caves. Academic Press, London: 896–908.

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., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, & J. C. Stromberg, 1997. The natural flow regime: A paradigm for river conservation and restoration. BioScience 47: 769–784.

Power, M. E., & W. E. Rainey, 2000. Food webs and resource sheds: Towards spatially delimiting trophic interactions. In Hutchings, M. J., E. A. John, & A. J. A. Stewart (eds), Ecological consequences of habitat heterogeneity. Blackwell, Oxford: 291–314.

Prenda, J., & A. Gallardo-Mayenco, 1999. Distribution patterns, species assemblages and habitat selection of the stoneflies (Plecoptera) from two Mediterranean river basins in southern Spain. International Review of Hydrobiology 84: 595–608.

Privet, K., V. Vedel, C. Fortunel, J. Orivel, Q. Martinez, A. Cerdan, C. Baraloto, & J. Pétillon, 2020. Relative efficiency of pitfall trapping vs nocturnal hand collecting in assessing soil-dwelling spider diversity along a structural gradient of neotropical habitats. Diversity 12: 81.

Punchard, N., & A. House, 2009. The water and wildlife of the Hampshire Avon winterbournes. British Wildlife 21: 11–19.

Purse, B. V., G. W. Hopkins, K. J. Day, & D. J. Thompson, 2003. Dispersal characteristics and management of a rare damselfly. Journal of Applied Ecology 40: 716–728.

QGIS Development Team, 2021. QGIS geographic information system. Open Source Geospatial Foundation, Oregon, USA, http://qgis.osgeo.org.

Quinn, J. M., G. L. Steele, C. W. Hickey, & M. L. Vickers, 1994. Upper thermal tolerances of twelve New Zealand stream invertebrate species. New Zealand Journal of Marine and Freshwater Research 28: 391–397.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/.

Rainio, J., & J. Niemelä, 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodiversity Conservation 12: 487–506.

Ramey, T. L., & J. S. Richardson, 2017. Terrestrial invertebrates in the riparian zone: Mechanisms underlying their unique diversity. BioScience 67: 808–819.

Ramírez-Hernández, A., F. Escobar, E. Montes de Oca, & L. Arellano, 2018. Assessing three sampling methods to survey and monitor ground beetles (Coleoptera: Carabidae) in riparian cloud forests. Environmental

Entomology 47: 1565–1572.

Ramos, T. B., M. C. Gonçalves, M. A. Branco, D. Brito, S. Rodrigues, J. M. Sánchez-Pérez, S. Sauvage, Â. Prazeres, J. C. Martins, M. L. Fernandes, & F. P. Pires, 2015. Sediment and nutrient dynamics during storm events in the Enxoé temporary river, southern Portugal. Catena 127: 177–190.

Rangeley-Wilson, C., 2021. Catchment based approach: Chalk stream restoration strategy 2021 main report. River Restoration Centre: 138.

Räpple, B., H. Piégay, Stella J. C., & D. Mercier, 2017. What drives riparian vegetation encroachment in braided river channels at patch to reach scales? Insights from annual airborne surveys (Drôme River, SE France, 2005–2011). Ecohydrology 10: e1886.

Ratnieks, F. L. W., F. Schrell, R. C. Sheppard, E. Brown, O. E. Bristow, & M. Garbuzov, 2016. Data reliability in citizen science: Learning curve and the effects of training method, volunteer background and experience on identification accuracy of insects visiting ivy flowers. Methods in Ecology and Evolution 7: 1226–1235.

Refaeilzadeh, P., L. Tang, & H. Liu, 2009. Cross-validation. In Liu, L., & M. T. Özsu (eds), Encyclopedia of database systems. Springer, Boston: 532–538.

Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd, T. J. MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C. Vermaire, D. Dudgeon, & S. J. Cooke, 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 94: 849–873.

Reznikova, Z., & H. Dorosheva, 2004. Impacts of red wood ants *Formica polyctena* on the spatial distribution and behavioural patterns of ground beetles (Carabidae). Pedobiologia 48: 15–21.

Richter, B. D., J. V. Baumgartner, J. Powell, & D. P. Braun, 1996. A method for assessing hydrologic alteration within ecosystems. Conservation Biology 10: 1163–1174.

Riddick, E. W., 2008. Ground beetle (Coleoptera: Carabidae) feeding ecology. In Capinera, J. L. (ed), Encyclopedia of entomology. Springer Netherlands, Dordrecht: 1742–1747.

Rijnsdorp, A. D., 1980. Pattern of movement in and dispersal from a Dutch forest of *Carabus problematicus* Hbst. (Coleoptera, Carabidae). Oecologia 45: 274–281.

River Restoration Centre, 2020. Manual of river restoration techniques. River Restoration Centre, Cranfield, UK, https://www.therrc.co.uk/manual-river-restoration-techniques.

Roberts, D. W., 2019. Labdsv: Ordination and multivariate analysis for ecology. R package version 2.0-1, https://CRAN.R-project.org/package=labdsv.

Robinson, M. D., 2019. Development of biological indicators for the dry phase of non-perennial rivers and streams. PhD thesis, California State University.

Robinson, R. F. A., G. A. Mills, A. Gravell, M. Schumacher, & G. R. Fones, 2023. Occurrence of organic pollutants in the River Itchen and River Test—two chalk streams in southern England, UK. Environmental Science and Pollution Research 30: 17965–17983.

Rodrigues, S., J.-G. Bréhéret, J.-J. Macaire, F. Moatar, D. Nistoran, & P. Jugé, 2006. Flow and sediment dynamics in the vegetated secondary channels of an anabranching river: The Loire River (France). Sedimentary Geology 186: 89–109.

Rolke, D., B. Jaenicke, J. Pfaender, & U. Rothe, 2018. Drainage ditches as important habitat for species diversity and rare species of aquatic beetles in agricultural landscapes (Insecta: Coleoptera). Journal of Limnology 77: 466–482.

Rosado, J., M. Morais, & K. Tockner, 2015. Mass dispersal of terrestrial organisms during first flush events in a temporary stream. River Research and Applications 31: 912–917.

Rosburg, T. T., P. A. Nelson, & B. P. Bledsoe, 2017. Effects of urbanization on flow duration and stream flashiness: A case study of Puget Sound streams, western Washington, USA. Journal of the American Water Resources Association 53: 493–507.

Rosgen, D. L., 1985. A stream classification system. Riparian ecosystems and their management: Reconciling conflicting uses. Tucson, AZ: 5.

Rouabah, A., J. Villerd, B. Amiaud, S. Plantureux, & F. Lasserre-Joulin, 2015. Response of carabid beetles diversity and size distribution to the vegetation structure within differently managed field margins. Agriculture, Ecosystems and Environment 200: 21–32.

Rounds, S. A., F. D. Wilde, & G. F. Ritz, 2013. U.S. Geological Survey techniques of water-resources investigations: Dissolved oxygen. United States Geological Survey, Reston, Virginia: 55.

Ruhí, A., T. Datry, & J. L. Sabo, 2017. Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. Conservation Biology 31: 1459–1468.

Rutt, G. P., N. S. Weatherley, & S. J. Ormerod, 1990. Relationships between the physicochemistry and macroinvertebrates of British upland streams: The development of modelling and indicator systems for predicting fauna and detecting acidity. Freshwater Biology 24: 463–480.

Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, & J. Welter, 2005. Riparian zones increase regional species richness by harbouring different, not more, species. Ecology 86: 56–62.

Sadler, J., & D. Bell, 2002. Invertebrates of exposed riverine sediments: Phase 3 - baseline faunas. Environment Agency, Bristol.

Sadler, J., D. Bell, & A. Fowles, 2004. The hydroecological controls and conservation value of beetles on exposed riverine sediments in England and Wales. Biological Conservation 118: 41–56.

Salmela, S., J. and, 2013. New records of *Paraleptophlebia werneri* Ulmer, 1920 and *P. strandii* (Eaton, 1901) from Finland (Ephemeroptera, Leptophlebiidae). Biodiversity Data Journal 1: e969.

Salter, M., & S. Singleton-White, 2019. Chalk streams in crisis. The Rivers Trust, Callington: 49.

Sánchez, I. A., & D. McCollin, 2015. A comparison of microclimate and environmental modification produced by hedgerows and dehesa in the Mediterranean region: A study in the Guadarrama region, Spain.

Landscape and Urban Planning 143: 230–237.

Sánchez-Bayo, F., K. Goka, & D. Hayasaka, 2016. Contamination of the aquatic environment with neonicotinoids and its implication for ecosystems. Frontiers in Environmental Science 4: 1–12.

Sánchez-Bayo, F., & K. A. G. Wyckhuys, 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232: 8–27.

Sánchez-Montoya, M. M., R. Gómez, J. F. Calvo, T. Bartonička, T. Datry, & P. Paril, 2022. Ecological values of intermittent rivers for terrestrial vertebrate fauna. Science of The Total Environment 806: 151308.

Sánchez-Montoya, M. M., T. K., D. von Schiller, J. Miñano, C. C., J. L. Lencina, G. G. Barberá, & A. Ruhi, 2020. Dynamics of ground-dwelling arthropod metacommunities in intermittent streams: The key role of dry riverbeds. Biological Conservation 241: 108328.

Sánchez-Montoya, M. M., D. von Schiller, A. Rhui, G. Sting-Pechar, L. Proia, J. Minano, M. R. Vidal-Abarca, M. L. Suarez, & K. Tockner, 2016. Responses of ground-dwelling arthropods to surface flow drying in channels and adjacent habitats along Mediterranean streams. Ecohydrology 9: 1376–1387.

Sand-Jensen, K., T. Riis, O. Vestergaard, & S. E. Larsen, 2000. Macrophyte decline in Danish lakes and streams over the past 100 years. Journal of Ecology 88: 1030–1040.

Santos, A. N., & R. D. Stevenson, 2011. Comparison of macroinvertebrate diversity and community structure among perennial and non-perennial headwater streams. Northeastern Naturalist 18: 7–26.

Sarneel, J. M., M. M. Hefting, G. A. Kowalchuk, C. Nilsson, M. Van der Velden, E. J. W. Visser, L. A. C. J. Voesenek, & R. Jansson, 2019. Alternative transient states and slow plant community responses after changed flooding regimes. Global Change Biology 25: 1358–1367.

Sarremejane, R., M. Cañedo-Argüelles, N. Prat, H. Mykrä, T. Muotka, & N. Bonada, 2017a. Do metacommunities vary through time? Intermittent rivers as model systems. Journal of Biogeography 44: 2752–2763.

Sarremejane, R., N. Cid, R. Stubbington, T. Datry, M. Alp, M. Cañedo-Argüelles, A. Cordero-Rivera, Z. Csabai, C. Gutiérrez-Cánovas, J. Heino, M. Forcellini, A. Millán, A. Paillex, P. Pařil, M. Polášek, J. M. Tierno de Figueroa, P. Usseglio-Polatera, C. Zamora-Muñoz, & N. Bonada, 2020. DISPERSE, a trait database to assess the dispersal potential of European aquatic macroinvertebrates. Scientific Data 7: 386.

Sarremejane, R., H. Mykrä, N. Bonada, J. Aroviita, & T. Muotka, 2017b. Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. Freshwater Biology 62: 1073–1082.

Sarremejane, R., H. Mykrä, K. L. Huttunen, K. R. Mustonen, H. Marttila, R. Paavola, K. Sippel, N. Veijalainen, & T. Muotka, 2018. Climate-driven hydrological variability determines inter-annual changes in stream invertebrate community assembly. Oikos 127: 1586–1595.

Sarremejane, R., R. Stubbington, M. J. Dunbar, C. G. Westwood, & J. England, 2019. Biological indices to characterize community responses to drying in streams with contrasting flow permanence regimes. Ecological Indicators 107: 105620.

Sarremejane, R., R. Stubbington, J. England, C. E. M. Sefton, M. Eastman, S. Parry, & A. Ruhi, 2021. Drought effects on invertebrate metapopulation dynamics and quasi-extinction risk in an intermittent river network. Global Change Biology 27: 4024–4039.

Saska, P., W. van der Werf, L. Hemerik, M. L. Luff, T. D. Hatten, & A. Honek, 2013. Temperature effects on pitfall catches of epigeal arthropods: A model and method for bias correction. Journal of Applied Ecology 50: 181–189.

Sauquet, E., M. Shanafield, J. C. Hammond, C. Sefton, C. Leigh, & T. Datry, 2021. Classification and trends in intermittent river flow regimes in Australia, northwestern Europe and USA: A global perspective. Journal of Hydrology 597: 126170.

Schaffers, A., I. Raemakers, K. Sýkora, & C. Braak, 2008. Arthropod assemblages are best predicted by plant species composition. Ecology 89: 782–794.

Schindler, D. E., & A. P. Smits, 2017. Subsidies of aquatic resources in terrestrial ecosystems. Ecosystems 20: 78–93.

Schmidt-Kloiber, A., & D. Hering, 2015. Www.freshwaterecology.info - an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. Ecological Indicators 53: 271–282.

Schoelynck, J., T. de Groote, K. Bal, W. Vandenbruwaene, P. Meire, & S. Temmerman, 2012. Self-organised patchiness and scale-dependent bio-geomorphic feedbacks in aquatic river vegetation. Ecography 35: 760–768.

Schuch, S., K. Wesche, & M. Schaefer, 2012. Long-term decline in the abundance of leafhoppers and planthoppers (Auchenorrhyncha) in central European protected dry grasslands. Biological Conservation 149: 75–83.

Scrine, J., M. Jochum, J. S. Olafsson, & E. J. O'Gorman, 2017. Interactive effects of temperature and habitat complexity on freshwater communities. Ecology and Evolution 7: 9333–9346.

Sear, D. A., P. D. Armitage, & F. H. Dawson, 1999. Groundwater dominated rivers. Hydrological Processes 13: 255–276.

Sefton, C. E. M., S. Parry, J. England, & G. Angell, 2019. Visualising and quantifying the variability of hydrological state in intermittent rivers. Fundamental and Applied Limnology 193: 21–38.

Sefton, C., S. Parry, J. England, & G. Angell, 2017. Visualising and quantifying flow intermittence patterns in chalk streams. Centre for Ecology; Hydrology, Wallingford: 66.

Seibold, S., C. Bässler, R. Brandl, B. Büche, A. Szallies, S. Thorn, M. D. Ulyshen, & J. Müller, 2016. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. Journal of Applied Ecology 53: 934–943.

Shama, L. N., K. B. Kubow, J. Jokela, & C. T. Robinson, 2011. Bottlenecks drive temporal and spatial genetic changes in alpine caddisfly metapopulations. BMC Evolutionary Biology 11: 278.

Shand, P., R. Tyler-Whittle, T. Besien, D. W. Peach, A. R. Lawrence, H. O. Lewis, R. Hargreaves, & M. Barron, 2003. Baseline report series: 6. The chalk of the Colne and Lee River catchments. British Geological Survey;

Environment Agency, Keyworth, Nottingham: 65.

Shaw, R. F., P. J. Johnson, D. W. Macdonald, & R. E. Feber, 2015. Enhancing the biodiversity of ditches in intensively managed UK farmland. PLOS ONE 10: 1–19.

Shepherd, V., 2013. Beetle diversity of chalk river floodplains. PhD thesis, University College London.

Shivoga, W. A., 2001. The influence of hydrology on the structure of invertebrate communities in two streams flowing into Lake Nakuru, Kenya. Hydrobiologia 458: 121–130.

Shuker, L. J., A. M. Gurnell, G. Wharton, D. J. Gurnell, J. England, B. F. Finn Leeming, & E. Beach, 2017. MoRPh: A citizen science tool for monitoring and appraising physical habitat changes in rivers. Water and Environment Journal 31: 418–424.

Shumilova, O., D. Zak, T. Datry, D. von Schiller, R. Corti, A. Foulquier, B. Obrador, K. Tockner, D. C. Allan, F. Altermatt, M. I. Arce, S. Arnon, D. Banas, A. Banegas-Medina, E. Beller, M. L. Blanchette, J. F. Blanco-Libreros, J. Blessing, I. Gonçalves Boëchat, K. Boersma, M. T. Bogan, N. Bonada, N. R. Bond, K. Brintrup, A. Bruder, R. Burrows, T. Cancellario, S. M. Carlson, S. Cauvy-Fraunié, N. Cid, M. Danger, B. de Freitas Terra, A. M. De Girolamo, R. del Campo, F. Dyer, A. Elosegi, E. Faye, C. Febria, R. Figueroa, B. Four, M. O. Gessner, P. Gnohossou, R. Gómez Cerezo, L. Gomez-Gener, M. A. S. Graça, S. Guareschi, B. Gücker, J. L. Hwan, S. Kubheka, S. D. Langhans, C. Leigh, C. J. Little, S. Lorenz, J. Marshall, A. McIntosh, C. Mendoza-Lera, E. Irmgard Meyer, M. Miliša, M. C. Mlambo, M. Moleón, P. Negus, D. Niyogi, A. Papatheodoulou, I. Pardo, P. Paril, V. Pešić, P. Rodriguez-Lozano, R. J. Rolls, M. M. Sanchez-Montoya, A. Savić,

A. Steward, R. Stubbington, A. Taleb, R. Vander Vorste, N. Waltham, A. Zoppini, & C. Zarfl, 2019. Simulating rewetting events in intermittent rivers and ephemeral streams: A global analysis of leached nutrients and organic matter. Global Change Biology 25: 1591–1611.

Shurin, J. B., K. Cottenie, & H. Hillebrand, 2009. Spatial autocorrelation and dispersal limitation in freshwater organisms. Oecologia 159: 151–159.

Siewers, J., J. Schirmel, & S. Buchholz, 2014. The efficiency of pitfall traps as a method of sampling epigeal arthropods in litter rich forest habitats. European Journal of Entomology 111: 69–74.

Skoulikidis, N. T., S. Sabater, T. Datry, M. M. Morais, A. Buffagni, G. Dörflinger, S. Zogaris, M. M. Sánchez-Montoya, N. Bonada, E. Kalogianni, J. Rosado, L. Vardakas, A. M. De Girolamo, & K. Tockner, 2017. Non-perennial Mediterranean rivers in Europe: Status, pressures, and challenges for research and management. Science of The Total Environment 577: 1–18.

Skoulikidis, N., & Y. Amaxidis, 2009. Origin and dynamics of dissolved and particulate nutrients in a minimally disturbed Mediterranean river with intermittent flow. Journal of Hydrology 373: 218–229.

Skvarla, M. J., & A. P. Dowling, 2017. A comparison of trapping techniques (Coleoptera: Carabidae, Buprestidae, Cerambycidae, and Curculionoidea excluding Scolytinae). Journal of Insect Science 17: 7.

Smedley, P. L., K. Griffiths, R. Tyler-Whittle, R. Hargreaves, A. R. Lawrence, & T. Besien, 2003. Baseline report series: 5. The chalk of the North Downs, Kent and East Surrey. British Geological Survey; Environment Agency: 57.

Snelder, T. H., T. Datry, N. Lamouroux, S. T. Larned, E. Sauquet, H. Pella,

& C. Catalogne, 2013. Regionalization of patterns of flow intermittence from gauging station records. Hydrology and Earth System Sciences 17: 2685–2699.

Soininen, J., P. Bartels, J. Heino, M. Luoto, & H. Hillebrand, 2015. Toward more integrated ecosystem research in aquatic and terrestrial environments. BioScience 65: 174–182.

Solascasas, P., F. M. Azcárate, & V. Hevia, 2022. Edaphic arthropods as indicators of the ecological condition of temperate grassland ecosystems: A systematic review. Ecological Indicators 142: 109277.

Soria, M., C. Gutiérrez-Cánovas, N. Bonada, R. Acosta, P. Rodríguez-Lozano, P. Fortuño, G. Burgazzi, D. Vinyoles, F. Gallart, J. Latron, P. Llorens, N. Prat, & N. Cid, 2020. Natural disturbances can produce misleading bioassessment results: Identifying metrics to detect anthropogenic impacts in intermittent rivers. Journal of Applied Ecology 57: 283–295.

Soria, M., C. Leigh, T. Datry, L. M. Bini, & N. Bonada, 2017. Biodiversity in perennial and intermittent rivers: A meta-analysis. Oikos 126: 1078–1089.

Sosiak, C. E., & P. Barden, 2021. Multidimensional trait morphology predicts ecology across ant lineages. Functional Ecology 35: 139–152.

Sponseller, R. A., E. F. Benfield, & H. M. Valett, 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. Freshwater Biology 46: 1409–1424.

Sponseller, R. A., J. B. Heffernan, & S. G. Fisher, 2013. On the multiple ecological roles of water in river networks. Ecosphere 4: art17.

Spooner, P., I. Lunt, & W. Robinson, 2002. Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. Ecological Management and Restoration 3: 117–126.

Sprague, L. A., 2005. Drought effects on water quality in the south platte river basin, colorado. Journal of the American Water Resources Association 41: 11–24.

Sprößig, C., S. Buchholz, & F. Dziock, 2020. Defining the baseline for river restoration: Comparing carabid beetle diversity of natural and human-impacted riparian habitats. Journal of Insect Conservation 24: 805–820.

Stanford, J. A., & J. V. Ward, 1993. An ecosystem perspective of alluvial rivers: Connectivity and the hyporheic corridor. Journal of the North American Benthological Society 12: 48–60.

Stanley, E. H., S. G. Fisher, & N. B. Grimm, 1997. Ecosystem expansion and contraction in streams. BioScience 47: 427–435.

Staudacher, K., O. Rennstam Rubbmark, K. Birkhofer, G. Malsher, D. Sint, M. Jonsson, & M. Traugott, 2018. Habitat heterogeneity induces rapid changes in the feeding behaviour of generalist arthropod predators. Functional Ecology 32: 809–819.

Stenzel, S., F. E. Fassnacht, B. Mack, & S. Schmidtlein, 2017. Identification of high nature value grassland with remote sensing and minimal field data. Ecological Indicators 74: 28–38.

Stetler, C., M. Reich, V. Grimm, & C. Wissel, 1997. Modelling persistence in dynamic landscapes: Lessons from a metapopulation of the grasshopper

Bryodema tuberculata. Journal of Animal Ecology 66: 508–518.

Steward, A. L., 2012. When the river runs dry: The ecology of dry river beds. PhD thesis, Griffith University.

Steward, A. L., T. Datry, & S. D. Langhans, 2022. The terrestrial and semi-aquatic invertebrates of intermittent rivers and ephemeral streams. Biological Reviews 97: 1408–1425.

Steward, A. L., J. C. Marshall, F. Sheldon, B. Harch, S. Choy, S. E. Bunn, & K. Tockner, 2011. Terrestrial invertebrates of dry river beds are not simply subsets of riparian assemblages. Aquatic Sciences 73: 511.

Steward, A. L., P. Negus, J. C. Marshall, S. E. Clifford, & C. Dent, 2018. Assessing the ecological health of rivers when they are dry. Ecological Indicators 85: 537–547.

Stewart, B. A., P. G. Close, P. A. Cook, & P. M. Davies, 2013. Upper thermal tolerances of key taxonomic groups of stream invertebrates. Hydrobiologia 718: 131–140.

Storey, R., 2016. Macroinvertebrate community responses to duration, intensity and timing of annual dry events in intermittent forested and pasture streams. Aquatic Sciences 78: 395–414.

Storey, R. G., & J. M. Quinn, 2008. Composition and temporal changes in macroinvertebrate communities of intermittent streams in Hawke's Bay, New Zealand. New Zealand Journal of Marine and Freshwater Research 42: 109–125.

Strachan, S. R., E. T. Chester, & B. J. Robson, 2015. Freshwater invertebrate life history strategies for surviving desiccation. Springer Science Reviews 3: 57–75.

Straka, M., M. Polášek, V. Syrovátka, R. Stubbington, S. Zahrádková, D. Němejcová, L. Šikulová, P. Řezníčková, L. Opatřilová, T. Datry, & P. Pařil, 2019. Recognition of stream drying based on benthic macroinvertebrates: A new tool in Central Europe. Ecological Indicators 106: 105486.

Strayer, D. L., & D. Dudgeon, 2010. Freshwater biodiversity conservation: Recent progress and future challenges. Journal of the North American Benthological Society 29: 344–358.

Stuart, M. E., K. Manamsa, J. C. Talbot, & E. J. Crane, 2011. Open report 11/013: Emerging contaminants in groundwater. British Geological Survey, Keyworth: 123.

Stubbington, R., M. T. Bogan, N. Bonada, A. J. Boulton, T. Datry, C. Leigh, & R. Vander Vorste, 2017a. Chapter 4.3 - The biota of intermittent rivers and ephemeral streams: Aquatic invertebrates. In Datry, T., N. Bonada, & A. Boulton (eds), Intermittent rivers and ephemeral streams. Academic Press: 217–243.

Stubbington, R., R. P. Chadd, N. Cid, Z. Csabai, M. Miliša, M. Morais, A. Munné, P. Paril, V. Pešic, I. Tziortzis, R. C. M. Verdonschot, & T. Datry, 2018a. Biomonitoring of intermittent rivers and ephemeral streams in Europe: Current practice and priorities to enhance ecological status assessments. Science of The Total Environment 618: 1096–1113.

Stubbington, R., J. Dimon, J. England, & G. and Watts, 2022a. Chalk streams of the future: The effects of climate change on biodiversity in England's iconic river ecosystems. Nottingham Trent University; Environment Agency.

Stubbington, R., J. England, M. Acreman, P. J. Wood, C. Westwood, P. Boon, C. Mainstone, C. Macadam, A. Bates, A. House, & D. Jorda-Capdevila, 2018b. The natural capital of temporary rivers: Characterising the value of dynamic aquatic–terrestrial habitats. Valuing Nature Programme: 52.

Stubbington, R., J. England, P. J. Wood, & C. E. M. Sefton, 2017b. Temporary streams in temperate zones: Recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems. WIREs Water 4: e1223.

Stubbington, R., K. J. Gething, & T. Sykes, 2022b. Chalk streams: Why “England’s rainforests” are so rare and precious. The Conversation, https://theconversation.com/chalk-streams-why-englands-rainforests-are-so-rare-and-precious-172827.

Stubbington, R., J. Gunn, S. Little, T. P. Worrall, & P. J. Wood, 2016. Macroinvertebrate seedbank composition in relation to antecedent duration of drying and multiple wet-dry cycles in a temporary stream. Freshwater Biology 61: 1293–1307.

Stubbington, R., A. Paillex, J. England, A. Barthès, A. Bouchez, F. Rimet, M. Mar Sánchez-Montoya, C. G. Westwood, & T. Datry, 2019. A comparison of biotic groups as dry-phase indicators of ecological quality in intermittent rivers and ephemeral streams. Ecological Indicators 97: 165–174.

Stubbington, R., R. Sarremejane, A. Laini, N. Cid, Z. Csabai, J. England, A. Munné, T. Aspin, N. Bonada, D. Bruno, S. Cauvy-Fraunie, R. Chadd, C. Dienstl, P. Fortuño Estrada, W. Graf, C. Gutiérrez-Cánovas, A. House, I. Karaouzas, E. Kazila, A. Millán, M. Morais, P. Pařil, A. Pickwell, M. Polášek, D. Sánchez-Fernández, I. Tziortzis, G. Várbíró, C. Voreadou, E. Walker-Holden, J. White, & T. Datry, 2022c. Disentangling responses to natural stressor and human impact gradients in river ecosystems across

Europe. Journal of Applied Ecology 59: 537–548.

Stubbington, R., P. J. Wood, I. Reid, & J. Gunn, 2011. Benthic and hyporheic invertebrate community responses to seasonal flow recession in a groundwater-dominated stream. Ecohydrology 4: 500–511.

Sutanto, S. J., C. Vitolo, C. Di Napoli, M. D'Andrea, & H. A. J. Van Lanen, 2020. Heatwaves, droughts, and fires: Exploring compound and cascading dry hazards at the pan-European scale. Environment International 134: 105276.

Svec, J. R., R. K. Kolka, & J. W. Stringer, 2005. Defining perennial, intermittent, and ephemeral channels in eastern kentucky: Application to forestry best management practices. Forest Ecology and Management 214: 170–182.

Swan, C. M., & B. L. Brown, 2017.Ecological Applications 27: 2209–2219.

Tachet, H., P. Richoux, M. Bournaud, & P. Usseglio-Polatera, 2010. Invertébrés d'eau douce: Systématique, biologie, écologie. CNRS éditions Paris.

Tapia, G., J. A. B. Bass, & A. House, 2018. Further occurrence records for the Winterbourne Stonefly *Nemoura lacustris* Pictet, 1865 (Plecoptera: Nemouridae). Entomologist's Monthly Magazine 154: 60–64.

Thiele, H.-U. (ed), 1977c. Carabid beetles in their environments: A study on habitat selection by adaptations in physiology and behaviour, zoophysiology and ecology. Springer, Berlin.

Thiele, H.-U., 1977a. Quantitative investigations on the distribution of Carabids. In Thiele, H.-U. (ed), Carabid beetles in their environments: A study on habitat selection by adaptations in physiology and behaviour, zoophysiology and ecology. Springer, Berlin: 13–48.

Thiele, H.-U., 1977b. Dispersal and dispersal power of Carabid beetles. In Thiele, H.-U. (ed), Carabid beetles in their environments: A study on habitat selection by adaptations in physiology and behaviour, zoophysiology and ecology. Springer, Berlin: 284–297.

Thieme, M., K. Birnie-Gauvin, J. J. Opperman, P. A. Franklin, H. Richter, L. Baumgartner, N. Ning, A. V. Vu, K. Brink, M. Sakala, G. C. O'Brien, R. Petersen, P. Tongchai, & S. J. Cooke, 2023. Measures to safeguard and restore river connectivity. Environmental Reviews.

Thomas, C. F. G., N. J. Brown, & D. A. Kendall, 2006. Carabid movement and vegetation density: Implications for interpreting pitfall trap data from split-field trials. Agriculture Ecosystems and Environment 113: 51–61.

Thomas, C. F. G., L. Parkinson, & E. J. P. Marshall, 1998. Isolating the components of activity-density for the carabid beetle *Pterostichus melanarius* in farmland. Oecologia 116: 103–112.

Thorp, J. H., 2009. Models of ecological processes in riverine ecosystems. In Likens, G. E. (ed), Encyclopedia of inland waters. Academic Press, Oxford: 448–445.

Tierno de Figueroa, J. M., & M. J. López-Rodríguez, 2005. Ciclo de vida y composición de la dieta de *Nemoura lacustris* Pictet, 1865 (Plecoptera, Nemouridae). Boletín de la Asociación Española de Entomología 29: 87–97.

Timms, L. L., J. J. Bowden, K. S. Summerville, & C. M. Buddle, 2013. Does species-level resolution matter? Taxonomic sufficiency in terrestrial arthropod biodiversity studies. Insect Conservation and Diversity 6: 453–462.

Tooth, S., 2000. Process, form and change in dryland rivers: A review of recent research. Earth-Science Reviews 51: 67–107.

Tramblay, Y., A. Rutkowska, E. Sauquet, C. Sefton, G. Laaha, M. Osuch, T. Albuquerque, M. H. Alves, K. Banasik, A. Beaufort, L. Brocca, S. Camici, Z. Csabai, H. Dakhlaoui, A. M. DeGirolamo, G. Dörflinger, F. Gallart, T. Gauster, L. Hanich, S. Kohnová, L. Mediero, N. Plamen, S. Parry, P. Quintana-Seguí, O. Tzoraki, & T. Datry, 2021. Trends in flow intermittence for European rivers. Hydrological Sciences Journal 66: 37–49.

Truchy, A., Z. Csabai, L. Mimeau, A. Künne, B. Pernecker, W. Bertin, F. Pellizzaro, & T. Datry, 2023. Citizen scientists can help advance the science and management of intermittent rivers and ephemeral streams. BioScience biad045.

Tsafack, N., F. Rebaudo, H. Wang, D. D. Nagy, Y. Xie, X. Wang, & S. Fattorini, 2019. Carabid community structure in northern China grassland ecosystems: Effects of local habitat on species richness, species composition and functional diversity. PeerJ 6: e6197.

Tuf, I. H., P. Dedek, & M. Veselý, 2012. Does the diurnal activity pattern of Carabid beetles depend on season, ground temperature and habitat? Archives of Biological Sciences 64: 721–732.

Turley, M. D., G. S. Bilotta, T. Krueger, R. E. Brazier, & C. A. Extence, 2015. Developing an improved biomonitoring tool for fine sediment: Combining expert knowledge and empirical data. Ecological Indicators 54: 82–86.

Uetz, G. W., 1979. The influence of variation in litter habitats on spider communities. Oecologia 40: 29–41.

Upland Waters Monitoring Network, 2023. Upland Waters Monitoring Network: Invertebrates., https://uwmn.uk/invertebrate-sampling-methodology.

US Environmental Protection Agency, 2006. Estimation and application of macroinvertebrate tolerance values. US Environmental Protection Agency, Washington, D.C.: 80.

US Environmental Protection Agency, 2023. Revising the definition of ”Waters of the United States”. US Environmental Protection Agency, https://www.epa.gov/wotus/revising-definition-waters-united-states.

Uys, M. C., & J. H. O'Keeffe, 1997. Simple words and fuzzy zones: Early directions for temporary river research in South Africa. Environmental Management 21: 517–531.

Vadher, A. N., R. Stubbington, & P. J. Wood, 2015. Fine sediment reduces vertical migrations of *Gammarus pulex* (Crustacea: Amphipoda) in response to surface water loss. Hydrobiologia 753: 61–71.

Vadher, A. N., S. Watson, R. Copeland-Phillips, L. J. Durrant, & P. J. Wood, 2022. The effect of increasing fine sediment load and drying duration on the re-emergence of *Gammarus pulex* (Amphipoda: Gammaridae) from the subsurface following flow resumption. Freshwater Biology 67: 1984–1993.

van Huizen, T. H. P., 1990. Gone with the wind: Flight activities of carabid beetles in relation to wind directions and to reproductive state of females in flight. The role of ground beetles in ecological and environmental studies. Andover, Hampshire: 289–294.

Van Loon, A. F., T. Gleeson, J. Clark, A. I. J. M. Van Dijk, K. Stahl, J. Hannaford, G. Di Baldassarre, A. J. Teuling, L. M. Tallaksen, R. Uijlenhoet, D. M. Hannah, J. Sheffield, M. Svoboda, B. Verbeiren, T. Wagener, S. Rangecroft, N. Wanders, & H. A. J. Van Lanen, 2016. Drought in the anthropocene. Nature Geoscience 9: 89–91.

Van Looy, K., J. D. Tonkin, M. Floury, C. Leigh, J. Soininen, S. Larsen, J. Heino, N. LeRoy P., M. Delong, S. C. Jähnig, T. Datry, N. Bonada, J. Rosebery, A. Jamoneau, S. J. Ormerod, K. J. Collier, & C. Wolter, 2019. The three Rs of river ecosystem resilience: Resources, recruitment, and refugia. River Research and Applications 35: 107–120.

Vanbergen, A. J., B. A. Woodcock, A. D. Watt, & J. Niemelä, 2005. Effect of land-use heterogeneity on carabid communities at the landscape scale. Ecography 28: 3–16.

Vander Vorste, R., F. Malard, & T. Datry, 2016. Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. Freshwater Biology 61: 1276–1292.

Vangansbeke, D., J. Audenaert, D. T. Nguyen, R. Verhoeven, B. Gobin, L. Tirry, & P. De Clercq, 2015. Diurnal temperature variations affect development of a herbivorous arthropod pest and its predators. PLOS ONE 10: 1–19.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

Vaughan, D. M., 2002. Potential impact of road-stream crossings (culverts) on the upstream passage of aquatic macroinvertebrates. US Forest Service, San Dimas, California: 15.

Verdonschot, P., 1990. Ecological characterization of surface waters in the province of Overijssel. The Netherlands (Doctoral dissertation, Verdonschot).

Verdonschot, P. F. M., D. Hering, J. Murphy, S. C. Jähnig, N. L. Rose, W. Graf, K. Brabec, & L. Sandin, 2010. Climate change and the hydrology and morphology of freshwater ecosystems. In Kernan, M., R. W. Battarbee, & B. R. Moss (eds), Climate change impacts on freshwater ecosystems. Blackwell Publishing, Oxford: 65–83.

Verdonschot, R. C. M., D. K., & P. F. M. Verdonschot, 2012. Importance of habitat structure as a determinant of the taxonomic and functional composition of lentic macroinvertebrate assemblages. Limnologica 42: 31–42.

Verdonschot, R. C. M., H. E. Keizer-Vlek, & P. F. M. Verdonschot, 2011. Biodiversity value of agricultural drainage ditches: A comparative analysis of the aquatic invertebrate fauna of ditches and small lakes. Aquatic Conservation: Marine and Freshwater Ecosystems 21: 715–727.

Verdonschot, R. C. M., A. M. van Oosten-Siedlecka, C. J. F. ter Braak, & P. F. M. Verdonschot, 2015. Macroinvertebrate survival during cessation of flow and streambed drying in a lowland stream. Freshwater Biology 60: 282–296.

Vilenica, M., M. Rumišek, F. Rebrina, R. Matoničkin Kepčija, K. Medak, V. Gulin, & A. Brigić, 2021. Dinaric karst intermittent rivers harbour some rare mayflies (Insecta, Ephemeroptera). Natura Croatica 30: 377–387.

Villeneuve, B., J. Piffady, L. Valette, Y. Souchon, & P. Usseglio-Polatera, 2018.

Direct and indirect effects of multiple stressors on stream invertebrates across watershed, reach and site scales: A structural equation modelling better informing on hydromorphological impacts. Science of The Total Environment 612: 660–671.

Vinebrooke, R. D., K. L. Cottingham, M. Norberg, J. Scheffer, S. I. Dodson, S. C. Maberly, & U. Sommer, 2004. Impacts of multiple stressors on biodiversity and ecosystem functioning: The role of species co-tolerance. Oikos 104: 451–457.

Viza, A., R. Arias-Real, M. Menéndez, & I. Muñoz, 2023. Resistance to drying: The role of seedbanks and hyporheic refuges in invertebrate communities (preprint). Research Square.

von Schiller, D., V. Acuña, D. Graeber, E. Marti, M. Ribot, S. Sabater, X. Timoner, & K. Tockner, 2011. Contraction, fragmentation and expansion dynamics determine nutrient availability in a Mediterranean forest stream. Aquatic Sciences 73: 485.

von Schiller, D., S. Bernal, C. N. Dahm, & E. Martí, 2017. Chapter 3.2 - Nutrient and organic matter dynamics in intermittent rivers and ephemeral streams. In Datry, T., N. Bonada, & A. J. Boulton (eds), Intermittent rivers and ephemeral streams. Academic Press, London: 135–160.

Wallace, A. R., 1854. On the monkeys of the Amazon. Annals and Magazine of Natural History 14: 451–454.

Wallace, I. D., 2016. A review of the status of the caddis flies (Trichoptera) of Great Britain - species status no.27. Natural England, Peterborough, UK: 132.

Wallin, H., & B. Ekbom, 1994. Influence of hunger level and prey densities on movement patterns in three species of *Pterostichus* beetles (Coleoptera: Carabidae). Environmental Entomology 23: 1171–1181.

Wang, L., Y. Gao, B.-P. Han, H. Fan, & H. Yang, 2019. The impacts of agriculture on macroinvertebrate communities: From structural changes to functional changes in Asia's cold region streams. Science of The Total Environment 676: 155–164.

Warwick, R. M., & K. R. Clarke, 1993. Increased variability as a symptom of stress in marine communities. Journal of Experimental Marine Biology and Ecology 172: 215–226.

Watson, A. M., & S. J. Ormerod, 2004. The distribution of three uncommon freshwater gastropods in the drainage ditches of British grazing marshes. Biological Conservation 118: 455–466.

Watts, G., R. W. Battarbee, J. P. Bloomfield, J. Crossman, A. Daccache, I. Durance, J. A. Elliott, G. Garner, J. Hannaford, D. M. Hannah, T. Hess, C. R. Jackson, A. L. Kay, M. Kernan, J. Knox, J. Mackay, D. T. Monteith, S. J. Ormerod, J. Rance, M. E. Stuart, A. J. Wade, S. D. Wade, K. Weatherhead, P. G. Whitehead, & R. L. Wilby, 2015. Climate change and water in the UK – past changes and future prospects. Progress in Physical Geography: Earth and Environment 39: 6–28.

Webb, J. R., K. J. Gething, C. C. Kratz, J. England, A. L. Drewitt, & R. Stubbington, 2022. A standardized multi-method survey to enhance characterization of riparian invertebrate communities. Water and Environment Journal 36: 425–432.

Webb, J., A. L. Drewitt, & N. Mott, 2017. Guidelines for riparian beetle surveys incorporating site quality assessment via pantheon. Natural England, Peterborough, UK: 8.

Webb, J., D. Heaver, D. Lott, H. J. Dean, J. van Breda, J. Curson, M. C. Harvey, M. Gurney, D. B. Roy, A. van Breda, M. Drake, K. N. A. Alexander, & G. Foster, 2018. Pantheon - database version 3.7.6., http://www.brc.ac.uk/pantheon/.

Wessex Water Ltd, 2008. Low flow investigations on the River Avon SAC. Final Report for Steering Group Consultation, Wessex Water Ltd: 125.

Westlake, D. F., H. Casey, F. H. Dawson, M. Ladle, R. H. K. Mann, & A. F. H. Marker, 1972. The chalk stream ecosystem. Productivity problems of freshwaters 615–635.

Westwood, C. G., J. England, M. J. Dunbar, N. T. H. Holmes, D. J. Leeming, & D. Hammond, 2017. An approach to setting ecological flow thresholds for southern English chalk streams. Water and Environment Journal 31: 528–536.

Whatley, M. H., E. E. van Loon, J. A. Vonk, H. G. van der Geest, & W. Admiraal, 2014. The role of emergent vegetation in structuring aquatic insect communities in peatland drainage ditches. Aquatic Ecology 48: 267–283.

Whelan, M. J., C. Linstead, F. Worrall, S. J. Ormerod, I. Durance, A. C. Johnson, D. Johnson, M. Owen, E. Wiik, N. J. K. Howden, T. P. Burt, A. Boxall, C. D. Brown, & D. Oliver D. M.and Tickner, 2022. Is water quality in British rivers “better than at any time since the end of the industrial revolution”? Science of The Total Environment 843: 157014.

White, J. C., A. House, N. Punchard, D. M. Hannah, N. A. Wilding, & P. J. Wood, 2018. Macroinvertebrate community responses to hydrological controls and groundwater abstraction effects across intermittent and perennial headwater streams. Science of the Total Environment 610-611: 1514–1526.

Whittaker, R. H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30: 407–407.

Wild, T. C., J. F. Bernet, E. L. Westling, & D. N. Lerner, 2011. Deculverting: Reviewing the evidence on the “daylighting” and restoration of culverted rivers. Water and Environment Journal 25: 412–421.

Wilding, N. A., J. C. White, R. P. Chadd, A. House, & P. J. Wood, 2018. The influence of flow permanence and drying pattern on macroinvertebrate biomonitoring tools used in the assessment of riverine ecosystems. Ecological Indicators 85: 548–555.

Williams, D. D., 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. Journal of the North American Benthological Society 15: 634–650.

Williams, D. D., 2006. The biology of temporary waters. Oxford University Press, Oxford.

Williams, D. D., & H. B. N. Hynes, 1976. The ecology of temporary streams i. The faunas of two canadian streams. Internationale Revue der gesamten Hydrobiologie und Hydrographie 61: 761–787.

Williams, D. D., & H. B. N. Hynes, 1977. The ecology of temporary streams ii. General remarks on temporary streams. Internationale Revue der gesamten Hydrobiologie und Hydrographie 62: 53–61.

Williams, P., M. Whitfield, J. Biggs, S. Bray, G. Fox, P. Nicolet, & D. Sear, 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in southern England. Biological Conservation 115: 329–341.

Williams, R. S., B. S. Marbert, M. C. Fisk, & P. J. Hanson, 2014a. Ground-dwelling beetle responses to long-term precipitation alterations in a hardwood forest. Southeastern Naturalist 13: 138–155.

Williams, R. S., B. S. Marbert, M. C. Fisk, & P. J. Hanson, 2014b. Ground-dwelling beetle responses to long-term precipitation alterations in a hardwood forest. Southeastern Naturalist 13: 138–155.

Winter, T. C., 2007. The role of ground water in generating streamflow in headwater areas and in maintaining base flow. Journal of the American Water Resources Association 43: 15–25.

Withers, P. J. A., C. Neal, H. P. Jarvie, & D. G. Doody, 2014. Agriculture and eutrophication: Where do we go from here? Sustainability 6: 5853–5875.

Wondzell, S. M., 2011. The role of the hyporheic zone across stream networks. Hydrological Processes 25: 3525–3532.

Wood, P. J., & P. D. Armitage, 1997. Biological effects of fine sediment in the lotic environment. Environmental Management 21: 203–217.

Wright, J. F., J. H. Blackburn, R. J. M. Gunn, K. L. Symes, & J. Davy-Bowker, 1998. A scoping study on the Ephemeroptera of southern chalk streams. Institute of Freshwater Ecology; Environment Agency, Wareham, UK: 48.

Wright, J. F., P. D. Hiley, D. A. Cooling, A. C. and W. M. E. Cameron, & A. D.

Berrie, 1984. The invertebrate fauna of a small chalk stream in Berkshire, England, and the effect of intermittent flow. Archiv für Hydrobiologie 99: 176–199.

WWF, 2016. Living planet report: Risk and resilience in a new era. WWF International, Gland, Switzerland: 74.

Yilmaz, H., S. Toy, M. A. Irmak, S. Yilmaz, & Y. Bulut, 2008. Determination of temperature differences between asphalt concrete, soil and grass surfaces of the city of Erzurum, Turkey. Atmósfera 21: 135–146.

Yuan, L. L., 2010. Estimating the effects of excess nutrients on stream invertebrates from observational data. Ecological Applications 20: 110–125.

Zanetti, N. I., R. Camina, E. C. Visciarelli, & N. D. Centeno, 2016. Active search on carcasses versus pitfall traps: A comparison of sampling methods. Neotropical Entomology 45: 221–226.

Zeiringer, B., C. Seliger, F. Greimel, & S. Schmutz, 2018. River hydrology, flow alteration, and environmental flow. In Schmutz, S., & J. Sendzimir (eds), Riverine ecosystem management: Science for governing towards a sustainable future. Springer International Publishing, Cham: 67–89.

Zhang, J., F. A. Drummond, M. Liebman, & A. Hartke, 1997. Phenology and dispersal of *Harpalus rufipes* DeGeer (Coleoptera: Carabidae) in agroecosystems in Maine. Journal of Agricultural Entomology 14: 171–186.

Zhang, S., J. Zhang, Y. Liu, Y. Liu, & Z. Wang, 2018. The effects of vegetation distribution pattern on overland flow. Water and Environment Journal 32:

392–403.

Zhang, Y., H. Zheng, X. Zhang, L. R. Leung, C. Liu, C. Zheng, Y. Guo, F. H. S. Chiew, D. Post, D. Kong, H. Beck, C. Li, & G. Blöschl, 2023. Future global streamflow declines are probably more severe than previously estimated. Nature Water 1: 261–271.

Zipper, S. C., J. C. Hammond, M. Shanafield, M. Zimmer, T. Datry, C. N. Jones, K. E. Kaiser, S. E. Godsey, R. M. Burrows, J. R. Blaszczak, M. H. Busch, A. N. Price, K. S. Boersma, A. S. Ward, K. Costigan, G. H. Allen, C. A. Krabbenhoft, W. K. Dodds, M. C. Mims, J. O. Olden, S. K. Kampf, A. J. Burgin, & D. C. Allen, 2021. Pervasive changes in stream intermittency across the United States. Environmental Research Letters 16: 084033.

Zuur, A. F., E. N. Ieno, & C. S. Elphick, 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1: 3–14.

11 Appendix – Under pressure: aquatic macroinvertebrate responses to agriculture in temporary streams

11.1 Compositional differences between FlowCats and AgriCats

11.1.1 Method

To characterise the assemblages, we produced a Sørensen distance taxa-by-sample matrix and a Bray-Curtis distance trait-by-sample matrix to represent taxonomic and functional composition, respectively. To contextualise our testing of differences in variability (i.e. H1 and H2), we tested for differences in composition (represented either by the Sørensen or Bray-Curtis distance matrix) between FlowCats, AgriCats and the interaction of FlowCat and AgriCat using permutational analysis of variance (PERMANOVA: Anderson, 2017). Each PERMANOVA was run over 999 permutations with a permutation scheme restricted by Season.

11.1.2 Results

Taxonomic composition varied between temporary and perennial reaches (F (1) = 33.393, P = 0.001, R^2 = 0.252, **Figure 3.3A** and **B**), between high and low AgriCat reaches(F (1) = 2.956, P = 0.003, R^2 = 0.022, **Figure 3.2A** and **B**) and due to the interaction of FlowCat and AgriCat (F (1) = 2.058, P = 0.030, R^2 = 0.016).

Functional composition differed among temporary and perennial reaches (F (1) = 26.842, P = 0.001, R^2 = 0.217, **Figure 3.3C** and **D**), but high and low AgriCat reaches were functionally comparable (F (1) = 1.475, P = 0.152, R^2 = 0.012, **3.2C** and **D**). No interaction between FlowCat and AgriCat was detected (F (1) = 1.349, P = 0.206, R^2 = 0.010).

11.2 H1. Assemblage responses to agriculture in temporary and perennial reaches

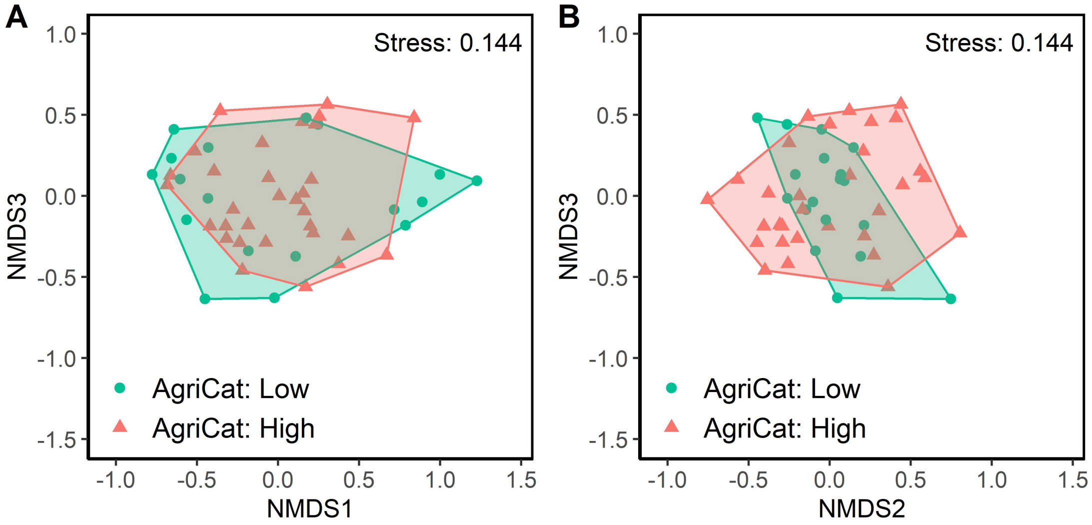


Figure 11.1: Non-metric multidimensional scaling of taxonomic variability in response to agricultural land use categories (AgriCat) in temporary reaches. Note: A and B represent NMDS3 of a three-dimensional ordination plotted against NMDS1 and NMDS2, see main text for plot of NMDS1 against NMDS2.

12 Appendix – Ditching misconceptions: the role of artificial habitats in supporting aquatic temporary stream assemblages

Figure 12.1: A selection of stream sites demonstrating the range of channel characteristics.

Figure 12.2: A selection of ditch sites demonstrating the range of channel characteristics.

Table 12.1: Taxa occuring in ≥25 samples that may be predators and/or competitors of *Nemoura lacustris* and *Paraleptophlebia werneri*, with their affinity to detritus (<1 mm), dead plant matter (≤1 mm), living microphytes and living macroinvertebrates as food sources. Affinity values range between 0 and 1, with 0 indicating no affinity and 1 indicating a taxa uses that food source exclusively.

Taxa	Detritus	Dead plants	Microphytes	Macroinvertebrates
Ampullaceana balthica	0.00	0.19	0.31	0.06
Asellus aquaticus	0.17	0.50	0.17	0.00
Baetis atlanticus/rhodani	0.18	0.18	0.45	0.00
Baetis vernus group	0.18	0.18	0.45	0.00
Dytiscidae	0.00	0.00	0.00	0.59
Gammarus fossarum/pulex	0.07	0.36	0.14	0.07
Glossiphoniidae	0.00	0.00	0.00	0.54
Gyraulus laevis	0.00	0.14	0.57	0.00
Limnephilus lunatus	0.01	0.36	0.22	0.07
Niphargus	0.63	0.13	0.00	0.13
Serratella ignita	0.08	0.25	0.33	0.00
Sphaeriidae	0.28	0.00	0.47	0.00

Note: *Baetis vernus group* includes *Baetis buceratus*, *Baetis fuscatus*, *Baetis scambus* and *Baetis vernus*.

Table 12.2: Taxa that were exclusively sampled from ditches, with their abundance (samples) at sites with perennial, temporary and unknown flow permanence regimes.

Taxon	Perennial	Temporary	Unknown
Agapetus	0	0	1
Anacaena limbata	0	2 (1)	0
Baetidae	1	0	0
Beraea pullata	0	0	4 (3)
Brachycentrus subnubilus	1	0	0
Calopteryx splendens	39 (7)	0	0
Cloeon	13 (2)	0	0
Coelostoma orbiculare	0	1	0
Coenagrion mercuriale	18 (4)	0	0
Coleoptera	1	1	1
Corixa	1	0	0
Crambidae	0	1	0
Ephemera	1	0	0
Hydraena rufipes	1	0	0
Hydrophilidae	1	1	0
Laccobius bipunctatus	0	1	0
Leptophlebia	1	0	0
Libellula depressa	1	0	0
Limnebius truncatellus	0	0	1
Limnephilus flavicornis group	13 (1)	0	0
Molanna angustata	1	0	0
Nemoura / Nemurella	0	0	2 (1)
Nemurella pictetii	0	0	1
Ochthebius	2 (1)	0	0
Ochthebius minimus	0	1	0
Odonata (Zygoptera)	1	0	0
Oreodytes sanmarkii	47 (3)	0	0
Plectrocnemia brevis / geniculata	0	0	3 (2)
Psychomyiidae	1	0	0
Scirtidae	2 (1)	0	0
Sialis lutaria	26 (6)	0	0
Valvata piscinalis	5 (2)	0	0

Note: *Limnephilus flavicornis group* includes *Limnephilus flavicornis*, *Limnephilus marmoratus*, *Limnephilus politus* and *Limnephilus stigma*.

Table 12.3: Taxa with an affinity for perennial streams, as identifed using indicator species analysis (IndVal).

Taxon	IndVal	P
Agapetus fuscipes	0.719	0.002
Ancylus fluviatilis	0.538	0.002
Caenis pusilla/rivulorum	0.507	0.014
Elmis aenea	0.335	0.027
Gammarus fossarum/pulex	0.570	0.014
Gyrinidae	0.444	0.002
Hydropsyche siltalai	0.454	0.012
Hydroptila	0.772	0.002
Lepidostoma hirtum	0.556	0.007
Leuctra nigra	0.281	0.026
Oecetis testacea	0.556	0.005
Paraleptoplebia submarginata	0.312	0.012
Potamopyrgus antipodarum	0.511	0.012
Rhyacophila dorsalis	0.298	0.026
Serratella ignita	0.716	0.003
Silo nigricornis	0.755	0.001
Sphaeriidae	0.405	0.037

13 Appendix – Why did the arthropod cross the river channel - to get to the other side?

Figure 13.1: Site B:P1 on the Bourne Rivulet during the first (A) and last (B) sampling visit.

Figure 13.2: Site B:T2 on the Bourne Rivulet during the first (A) and last (B) sampling visit.

Figure 13.3: Site B:T4 on the Bourne Rivulet during the first (A) and last (B) sampling visit.

Figure 13.4: Site C:T4 on the Candover Brook during the first (A) and last (B) sampling visit.

Table 13.1: Summary of left and right bank land use and bank angle for sampling sites in the Bourne Rivulet and Candover Brook catchments.

Site	Land use: left	Land use: right	Bank angle (°): left	Bank angle (°): right
B:P1	Wetland	Wetland	20	20
B:P2	Mown grassland	Woodland	40	40
B:T1	Mown grassland	Mown grassland	40	40
B:T2	Mown grassland	Mown grassland	20	20
B:T3	Mown grassland	Mown grassland	30	30/90
B:T4	Pasture	Pasture	30	30
C:P1	Pasture	Pasture	20	20
C:P2	Wetland	Wetland	20	20
C:T1	Pasture	Mown grassland	20	20
C:T2	Pasture	Pasture	40	40
C:T3	Wet woodland	Mown grass verge	20	35
C:T4	Mown grassland	Pasture	40	40

Table 13.2: The number of species captured per sample in the Bourne Rivulet and Candover Brook catchments, in temporary and perennial reaches and during visits one (V1) to 4 (V4).

	Minimum	Mean ± SD	Maximum
Bourne Rivulet	0	9.8 ± 6.0	22
Candover Brook	3	10.9 ± 4.4	20
Perennial	1	7.4 ± 4.4	18
Temporary	0	11.8 ± 5.0	22
V1	4	11.7 ± 5.9	20
V2	1	10.8 ± 5.4	22
V3	2	10.3 ± 5.5	20
V4	0	8.5 ± 5.1	21

Table 13.3: Summary statistics of the turnover and nestedness-resultant dissimilarity components of Sørensen beta (β) diversity for the Bourne Rivulet and Candover Brook catchments in the all species, flight capable and limited flight datasets.

Datset	Catchment	Partition	Minimum	Mean ± SD	Maximum
All species	Bourne Rivulet	Turnover	0.000	0.455 ± 0.264	1.000
		Nestedness	0.000	0.140 ± 0.171	0.714
	Candover Brook	Turnover	0.000	0.368 ± 0.206	0.833
		Nestedness	0.017	0.138 ± 0.119	0.455
Flight capable	Bourne Rivulet	Turnover	0.000	0.426 ± 0.335	1.000
		Nestedness	0.000	0.149 ± 0.210	0.667
	Candover Brook	Turnover	0.000	0.413 ± 0.322	1.000
		Nestedness	0.136	0.141 ± 0.136	0.429
Limited flight	Bourne Rivulet	Turnover	0.000	0.485 ± 0.293	1.000
		Nestedness	0.000	0.127 ± 0.187	0.600
	Candover Brook	Turnover	0.000	0.300 ± 0.258	0.833
		Nestedness	0.000	0.181 ± 0.155	0.500

Table 13.4: Summary statistics for models testing hypotheses 1–3 for the all species dataset while partitoning beta diversity into its nestedness resultant dissimilarity and turnover components.

Hypothesis	Partition	Estimate	SE	P	R^2
H1	Nestedness	-0.070	0.044	0.118	0.053
	Turnover	0.164	0.070	0.024	0.108
H2	Nestedness	-0.086–0.060	0.072–0.075	0.242–0.935	0.096
	Turnover	0.014–0.240	0.117–0.121	0.056–0.903	0.119
H3	Nestedness	0.004–0.100	0.058–0.061	0.095–0.945	0.085
	Turnover	-0.102–0.036	0.097–0.102	0.324–0.715	0.057

Table 13.5: Summary statistics for models testing hypotheses 1–3 for the flight capable dataset while partitoning beta diversity into its nestedness resultant dissimilarity and turnover components.

Hypothesis	Partition	Estimate	SE	P	R^2
H1	Nestedness	0.213	0.053	0.113	0.056
	Turnover	0.173	0.088	0.056	0.081
H2	Nestedness	-0.209–-0.101	0.084–0.087	0.017–0.250	0.138
	Turnover	0.165–0.346	0.141–0.146	0.023–0.266	0.129
H3	Nestedness	0.039–0.106	0.070–0.076	0.139–0.585	0.052
	Turnover	-0.108–-0.027	0.120–0.130	0.372–0.824	0.020

Table 13.6: Summary statistics for models testing hypotheses 1–3 for the limited flight dataset while partitoning beta diversity into its nestedness resultant dissimilarity and turnover components.

Hypothesis	Partition	Estimate	SE	P	R^2
H1	Nestedness	-0.051	0.055	0.352	0.020
	Turnover	0.164	0.101	0.113	0.056
H2	Nestedness	-0.064–0.032	0.090–0.093	0.493–0.821	0.027
	Turnover	-0.048–0.250	0.163–0.176	0.147–0.938	0.096
H3	Nestedness	-0.074–0.075	0.070–0.072	0.298–0.450	0.107
	Turnover	-0.294–0.009	0.130–0.133	0.034–0.948	0.129

Table 13.7: The abundance of species gained and lost between sampling visits one (V1) and four (V4), their habitat association and flight ability.

Species	Habitat association	Flight ability	V1	V2	V3	V4
Acupalpus parvulus	Wetlands	Macropterous	1	0	1	0
Agonum fuliginosum/gracile	Wetlands	Polymorphic	12	0	0	0
Agonum piceum	Wetlands	Polymorphic	3	0	0	0
Amara aenea	Open areas	Macropterous	8	1	0	0
Amara familiaris	Open areas	Macropterous	2	1	0	0
Anisodactylus binotatus	Wetlands	Macropterous	1	1	2	0
Asaphidion stierlini	Open areas	Macropterous	1	0	0	0
Badister peltatus	Wetlands	Macropterous	1	1	0	0
Bembidion assimile	Wetlands	Polymorphic	11	1	2	0
Bembidion varium	Wetlands	Macropterous	1	0	0	0
Bembidion biguttatum	Wetlands	Macropterous	3	3	0	0
Bembidion guttula	Wetlands	Polymorphic	8	4	5	0
Bembidium obtusum	Open areas	Polymorphic	6	0	1	0
Curtonotus aulicus	Open areas	Macropterous	3	0	0	0
Harpalus rubripes	Open areas	Macropterous	1	1	5	0
Leistus fulvibarbis	Tree-associated	Macropterous	16	6	2	0
Leistus terminatus	Open areas	Brachypterous	2	0	0	0
Microlestes minutulus	Open areas	Macropterous	1	0	0	0
Notiophilus rufipes	Tree-associated	Macropterous	2	0	0	0
Oxypselaphus obscurus	Tree-associated	Brachypterous	8	3	2	0
Paradromius linearis	Open areas	Polymorphic	2	0	0	0
Pterostichus vernalis	Open areas	Polymorphic	1	0	0	0
Stenolophus mixtus	Wetlands	Macropterous	5	1	1	0
Syntomus foveatus	Open areas	Brachypterous	12	2	12	0
Abax parallelepipedus	Woodland floor	Brachypterous	0	0	3	1
Amara plebeja	Open areas	Macropterous	0	0	1	2
Bembidion quadrimaculatum	Open areas	Macropterous	0	0	1	1
Bembidion dendellum	Wetlands	Macropterous	0	2	0	1
Calathus rotundicollis	Tree-associated	Polymorphic	0	1	1	1
Carabus violaceus	Open areas	Brachypterous	0	0	8	4
Harpalus rufipes	Open areas	Macropterous	0	13	9	14
Harpalus tardus	Open areas	Macropterous	0	0	0	1
Pterostichus niger	Open areas	Macropterous	0	0	2	2
Pterostichus oblongopunctatus	Tree-associated	Macropterous	0	2	0	1

14 Appendix – Working 9 to 5: diurnal variability in invertebrate activity does not prevent ecosystem health assessments in dry stream channels

14.1 H1. Diurnal variability of rapid bioassessment methods at family and order level

Method had no influence on family (P = 0.433: **Figure 14.1A**) or order (P = 0.789: **Figure 14.1A**) richness. Similarly, no difference in family (P = 0.192–0.807, R^2M = 0.090, R^2C = 0.093: **Figure 14.1C**) or order (P = 0.152–0.646, R^2M = 0.131, R^2C = 0.131: **Figure 14.1D**) richness was detected between sampling periods.

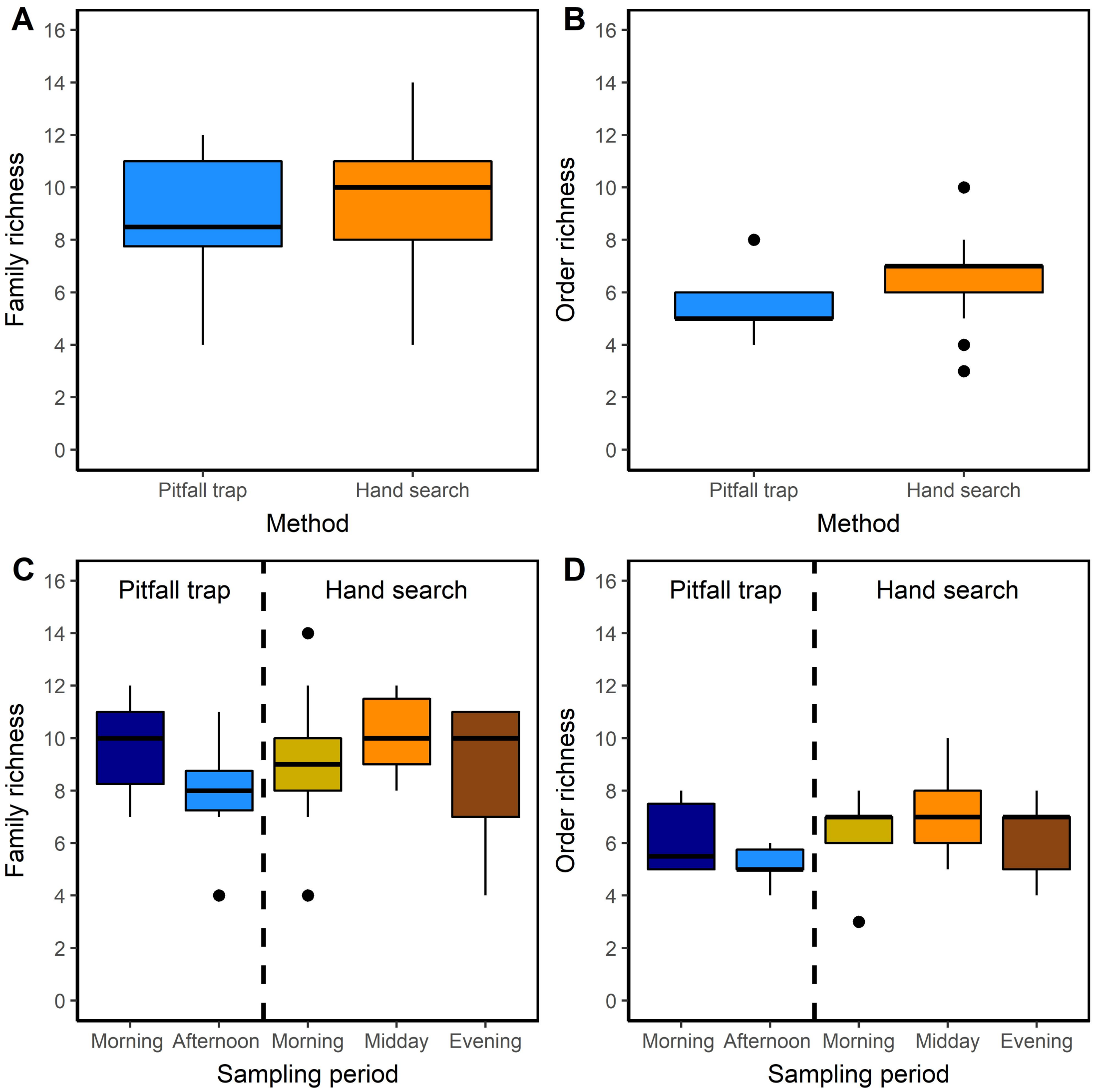


Figure 14.1: The family (A and C) and order (B and D) richness of assemblages sampled by hand searching and pitfall trapping methods (A and B) and sampled by pitfall trapping in the morning and afternoon, and by hand searching in the morning, midday and evening sampling periods (C and D). The centre line represents the median; boxes represent the interquartile range; whiskers represent the minimum/maximum values which are within 1.5× the interquartile range of the first and third quartiles; filled circles represent outliers.

Family (PERMANOVA: F (1) = 5.061, P <0.001, R^2 = 0.130: **Figure 14.2A**) and order (F (1) = 6.053, P <0.001, R^2 = 0.153: **Figure 14.2B**) composition were influenced by method, with pitfall traps more consistently characterising assemblages at both resolutions (PERMDISP2: family F (1) = 11.521, P = 0.002 and order F (1) = 15.627, P <0.001). Similar to taxa composition, family (F (3)

= 0.608, P = 0.874, R^2 = 0.047: **Figure 14.2C**) and order (F (3) = 0.542, P = 0.854, R^2 = 0.041: **Figure 14.2D**) composition were not influenced by sampling period. Dispersion differed among sampling periods at order (F (4) = 4.268, P = 0.007), but not family (F (4) = 2.605, P = 0.054) level. However, pairwise tests highlighted that all significant differences in dispersion at order level were between methods. Differences in both family and order composition between methods were driven by Diptera (SIMPER: 12.9% of dissimilarity, P <0.001), with pitfall trap samples containing 11.8 ± 6.5 (mean ± SD) individuals and hand search samples containing 2.1 ± 2.3 individuals.

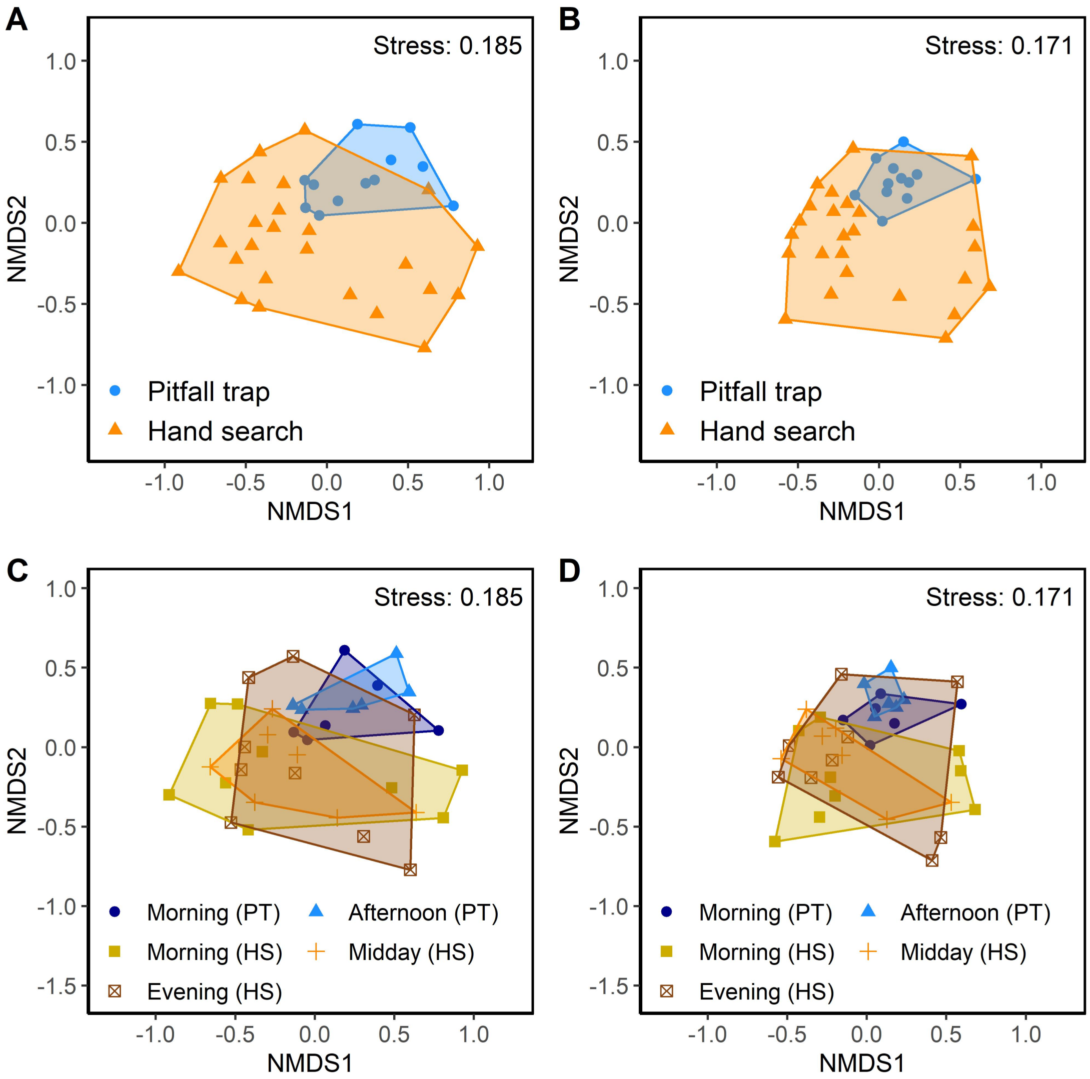


Figure 14.2: Non-metric multidimensional scaling of terrestrial invertebrate family (A and C) and order (B and D) composition sampled (A and B) by hand searching and pitfall trapping, and (C and D) by pitfall trapping (PT) in the morning and afternoon, and by hand searching (HS) in the morning, midday and evening sampling periods.

14.2 H2. Detecting responses to anthropogenic stressors at family and order level

Longitudinal position, silt, sand and temperature had no influence on family (P = 0.423–1.000, R^2M = 0.247, R^2C = 0.274: **Figure 14.3**) or order (P = 0.338–0.943, R^2M = 0.168, R^2C = 0.168: **Figure 14.4**) richness.

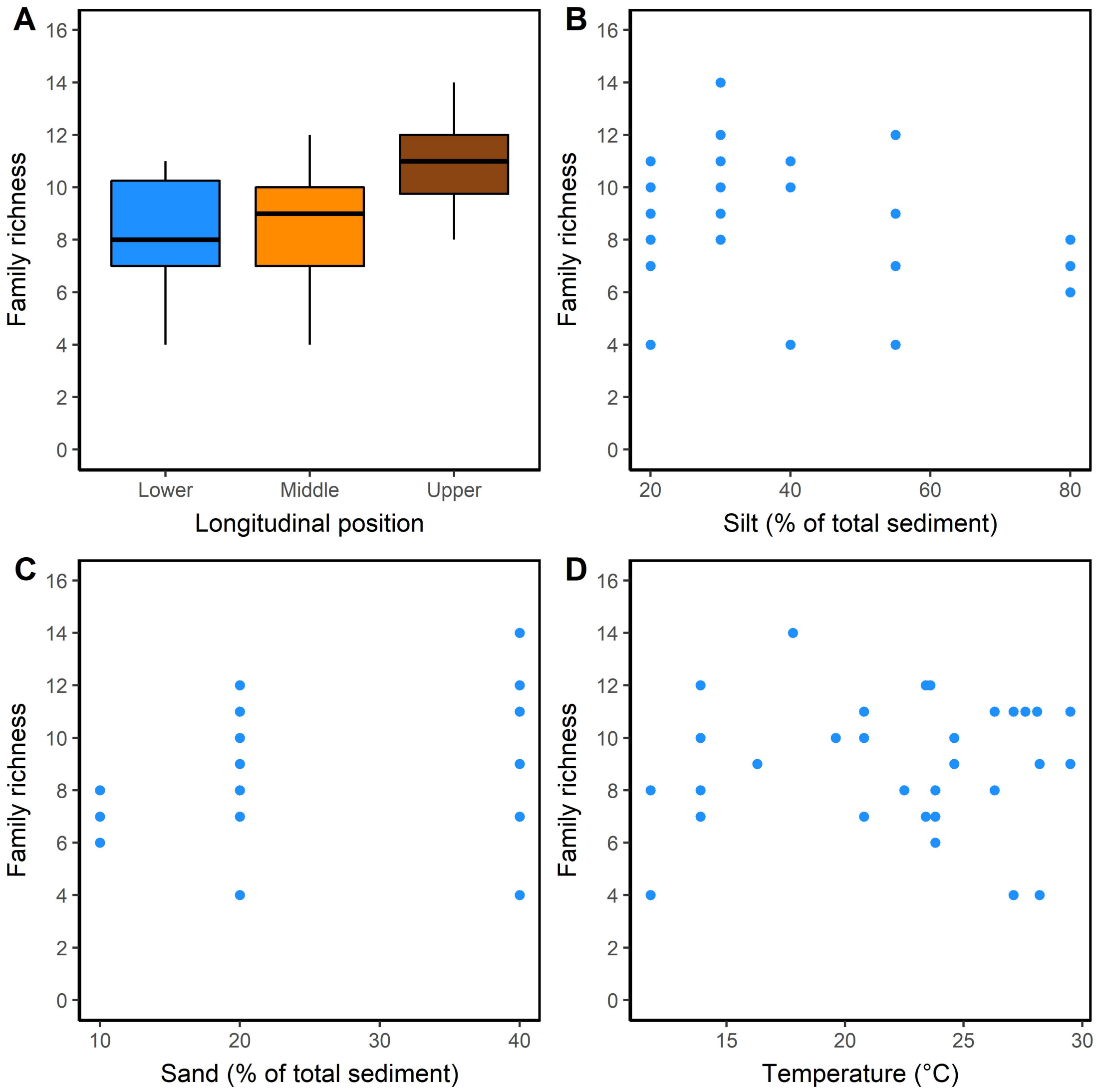


Figure 14.3: The family richness sampled at differing longitudinal positions (A) and the relationships between family richness and silt as a proportion of total sediment (B), sand as a proportion of total sediment (C) and air temperature at the channel bed (D). For A, the centre line represents the median; boxes represent the interquartile range; whiskers represent the minimum/maximum values which are within 1.5× the interquartile range of the first and third quartiles; filled circles represent outliers.

Family composition responded to longitudinal position (PERMANOVA: F (2) = 5.092, P <0.001, R^2 = 0.175: **Figure 14.5A**), silt (F (1) = 9.186, P <0.001, R^2 = 0.158) and temperature (F (1) = 3.376, P = 0.004, R^2 = 0.058), but not sand (F (1) = 2.201, P = 0.123, R^2 = 0.038: **Figure 14.5C**). Assemblages sampled from upper sites were more consistent than those sampled at lower

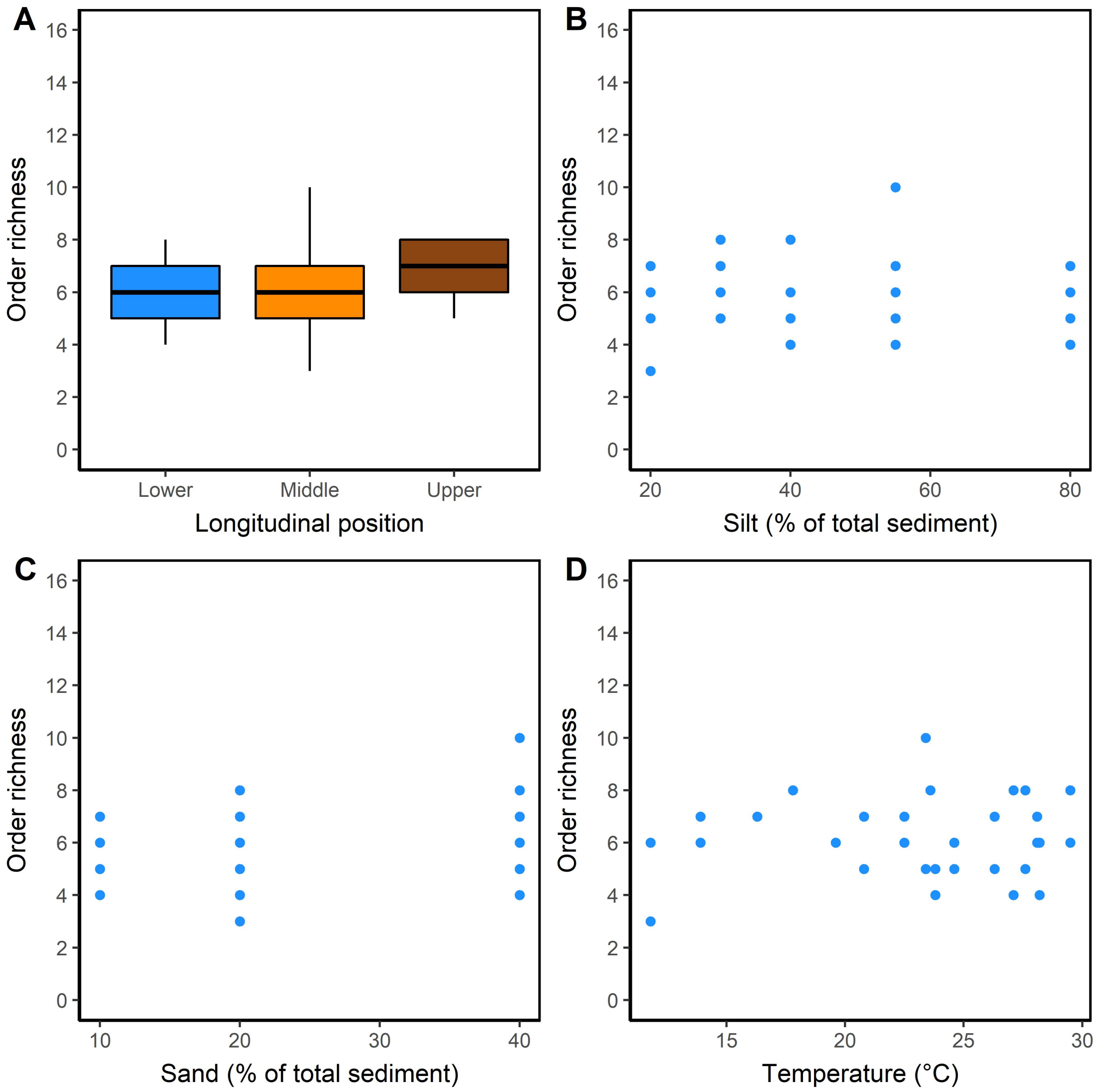


Figure 14.4: The order richness sampled at differing longitudinal positions (A) and the relationships between family and order richness and silt as a proportion of total sediment (B), sand as a proportion of total sediment (C) and air temperature at the channel bed (D). For, the centre line represents the median; boxes represent the interquartile range; whiskers represent the minimum/maximum values which are within 1.5× the interquartile range of the first and third quartiles; filled circles represent outliers.

sites (PERMDISP2: F (2) = 4.458, P = 0.019). Compositional differences between lower and middle sites were driven by Linyphiidae (SIMPER: 8.1% of dissimilarity, P = 0.026), Staphylinidae (7.0%, P = 0.002) and adult Diptera (10.1%, P = 0.029). Samples from lower sites contained 7.8 ± 7.0 (mean ± SD) Linyphiidae, whereas middle samples supported 4.8 ± 5.0 individuals.

Middle sites supported 7.8 ± 12.7 Staphylinidae and 7.2 ± 7.2 adult Diptera per sample, with lower sites supporting 1.9 ± 2.1 and 4.8 ± 6.2 individuals per sample, respectively. Dissimilarity between middle and upper sites was caused by Lycosidae (8.3%, $P < 0.001$), with 2.2 ± 4.6 individuals per sample at middle sites and 9.4 ± 5.6 individuals per sample at upper sites. Differences between lower and upper sites were caused by Linyphiidae (8.0%, $P = 0.046$), Lycosidae (9.8%, $P < 0.001$) and Craspedosomatidae (6.2%, $P = 0.008$). Lycosidae and Craspedosomatidae averaged 9.4 ± 5.6 and 8.6 ± 23.2 individual per sample at upper sites relative to 0.6 ± 1.0 and 0.7 ± 0.9 at lower sites. Linyphiidae was captured more frequently at lower (7.8 ± 7.0) than upper (1.8 ± 3.1) sites. Lycosidae (Pearson: $r = -0.453$, $P = 0.005$), Collembola ($r = 0.520$, $P = 0.001$), Carabidae ($r = -0.454$, $P = 0.005$) and Formicidae ($r = -0.436$, $P = 0.007$) abundance correlated with silt. Sand correlated with Lycosidae ($r = 0.403$, $P = 0.013$) and Porcellionidae ($r = 0.421$, $P = 0.010$) abundance, whereas no family correlated with temperature (all $P > 0.05$).

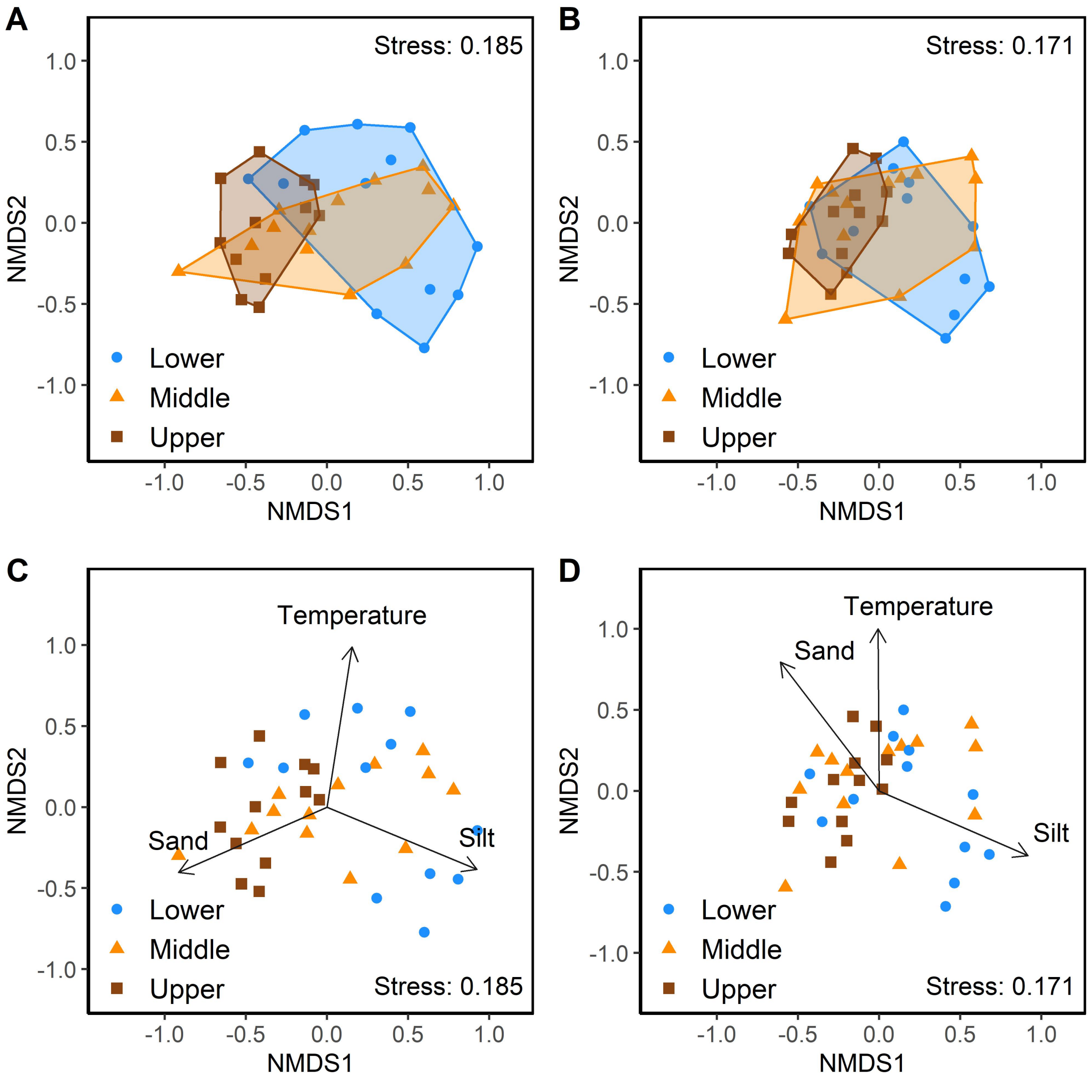


Figure 14.5: Non-metric multidimensional scaling of terrestrial invertebrate family (A and C) and order (B and D) composition sampled at lower, middle and upper sites (i.e. longitudinal position: A and B), and in relation to longitudinal position, silt, sand and temperature gradients (C and D).

Similar to taxa and family composition, order composition responded to longitudinal position (PERMANOVA: F (2) = 2.997, P = 0.005, R^2 = 0.111: **Figure 14.5B**), silt (F (1) = 11.054, P <0.001, R^2 = 0.205) and temperature (F (1) = 3.492, P = 0.005, R^2 = 0.065), but not sand (F (1) = 1.366, P = 0.555, R^2 = 0.025: **Figure 14.5D**). Samples collected from lower, middle and upper sites were comparably variable (PERMDISP2: F (2) = 2.107, P = 0.137). Differences between lower and middle sites were driven by Diptera (SIMPER: 10.4% of dissimilarity, P = 0.022), where middle samples contained 7.9 ± 7.4 (mean ± SD) individuals and lower samples contained 4.8 ± 6.2 individuals. Differences between lower and upper sites were caused by Chordeumatida (6.2%, P = 0.008) and Isopoda (8.5%, P = 0.018). Lower sites supported 0.7 ± 0.9 Chordeumatida individuals per sample, relative to 8.6 ± 23.4 at upper sites. Isopoda were represented by 2.1 ± 4.0 and 8.8 ± 9.5 individuals per sample at lower and upper sites, respectively. No order drove differences between middle and upper sites (all <5% and/or P >0.05). Silt correlated with Araneae (Pearson: *r* = -0.354, P = 0.031), Collembola (*r* = 0.520, P <0.001), Coleoptera (*r* = -0.424, P = 0.009), Hymenoptera (*r* = -0.420, P = 0.010) and Isopoda (*r* = -0.403, P = 0.013). No order correlated with temperature or sand (all P >0.05).

15 Appendix – Living on the edge: predicting invertebrate richness and rarity in disturbance-prone aquatic–terrestrial habitats

Figure 15.1: Examples of channel characteristics and surrounding land use at exposed riverine sediment sampling sites, photographs courtesy of Natural England, Buglife and Staffordshire Wildlife Trust.

Figure 15.2: Channel characteristics and surrounding land use at Candover Brook, the temporary stream surveyed by Bunting et al. (2021).

Figure 15.3: Examples of channel characteristics and surrounding land use at sites in the north London temporary stream dataset.

Table 15.1: Number of species, percent of total species and frequency of occurrence in samples per family.

	No. of species	% of total species	No. of samples
Anobiidae	2	0.6	2
Anthicidae	2	0.6	4
Apionidae	3	0.9	6
Cantharidae	1	0.3	1
Carabidae	97	28.2	79
Chrysomelidae	28	8.1	59
Clambidae	1	0.3	1
Coccinellidae	5	1.5	13
Cryptophagidae	4	1.2	3
Curculionidae	17	4.9	16
Elateridae	10	2.9	50
Heteroceridae	2	0.6	10
Latridiidae	3	0.9	3
Leiodidae	3	0.9	3
Lucanidae	1	0.3	2
Nitidulidae	2	0.6	6
Ptiliidae	3	0.9	4
Rhizophagidae	1	0.3	1
Scarabaeidae	5	1.5	16
Scolytidae	1	0.3	2
Silphidae	2	0.6	4
Staphylinidae	151	43.9	88

Table 15.2: Literature supporting the inclusion of habitat complexity (HabComplex), no. of vegetation morphotypes (VegMorph) and anthropogenic land cover (AnthroCover) in models predicting beetle richness and sum of species quality scores.

Predictor	Literature
Habitat complexity	Increased habitat complexity is associated with increased beetle richness (Lassau et al., 2005; Lengyel et al., 2016)
No. of vegetation morphotypes	Vegetation influences the movement of (Heydemann, 1957; Thomas et al., 2006; Allema et al., 2019), and microhabitat availability for beetles (Sadler and Bell, 2002)
Anthropogenic land cover	Anthropogenic land cover typically influences species specific beetle distributions (Eyre and Luff, 2004; Martinson and Raupp, 2013)

Table 15.3: Quality scores attributed to species of differing conservation status, adapted from Webb et al. 2018.

Quality score	Conservation status
1	Common native species
4	Nationally scarce native species
8	Nationally rare or scarce and IUCN vulnerable
16	Nationally rare or scarce and IUCN endangered
32	Nationally rare or scarce and IUCN critically endangered

Table 15.4: Descriptive statistics of non-significant reduced major axis regressions (RMA) between predicted and observed richness and the sum of species quality scores (sSQS) for terrestrial beetle assemblages sampled from exposed riverine sediments.

		Minimum	Mean ± SE	Maximum	SD
Richness	RMA slope	0.386	0.632 ± 0.006	0.962	0.137
	Pearson’s p	0.051	0.103 ± 0.003	0.379	0.068
sSQS	RMA slope	0.360	0.672 ± 0.008	1.114	0.175
	Pearson’s p	0.051	0.097 ± 0.002	0.296	0.052

Note: RMA cannot robustly summarise non-significant relationships (as tested using a Pearson correlation). Thus, the RMA summaries for subsets with non-significant Pearson correlations presented above are for comparison with significantly correlated subsets in **Table 7.1** only, and should not be considered as evidence for assessing correlation strength.

Table 15.5: Descriptive statistics of Pearson product-moment correlations between predicted and observed richness and the sum of species quality scores (sSQS) for terrestrial beetle assemblages sampled from exposed riverine sediments.

		Minimum	Mean ± SE	Maximum	SD
Richness	*r*	0.038	0.354 ± 0.006	0.801	0.134
	p	0.001	0.019 ± 0.002	0.379	0.037
sSQS	*r*	0.081	0.348 ± 0.005	0.711	0.119
	p	0.001	0.019 ± 0.002	0.296	0.034