Ecological responses to environmental variability in wet and dry chalk streams: towards better temporary stream monitoring and management

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Copyright statement

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Abstract

Temporary streams are those which stop flowing, and which typically dry, and form 52% of the global river network. Temporary streams are subjected to human impacts such as climate change, over-abstraction and channel modifications. Despite these threats, many studies do not fully characterise terrestrial species, or focus on aquatic macroinvertebrate responses to hydromorphology in perennial systems or responses to intermittence itself. Our lack of understanding means we cannot accurately assess the ecological health of temporary streams, and thus cannot effectively manage these ecosystems to protect, and potentially restore, their biodiversity. Therefore, this study aimed to analyse macroinvertebrate and dry-phase plant and invertebrate community responses to variability in habitat conditions, particularly those indicative of human impact.

The study sites were in temporary chalk streams in southern England, predominantly with agricultural and urban land use. An Environment Agency dataset was used to analyse macroinvertebrate community responses to hydromorphological conditions across a range of flow regimes (perennial to intermittent), characterised by a standardised habitat survey method. Dry-phase plant communities were surveyed using a modified version of a UK standard regulatory method to incorporate terrestrial species, and dry-phase invertebrate communities were sampled using pitfall traps, with environmental conditions characterised at each site.

Macroinvertebrates responded predominantly to flow and vegetation, with communities at intermittent sites particularly responding to the latter. These responses indicate that manging intermittent sites to restore flow and vegetation complexity could improve community resilience. Dry-phase invertebrates responded to vegetation (e.g. structural complexity), which was indicative of land use, in addition to sediment composition and moisture. Dry-phase plant communities responded to nutrient concentrations, despite a strong influence of sediment moisture, with metrics including plant dominance and grass richness increasing with increasing phosphorus concentrations. These results could inform biomonitoring methods and management practices to assess and protect ecosystem health regardless of in-channel flow conditions.

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Chapter One: Introduction and research context

1.1 General introduction

Temporary rivers and streams are watercourses which stop flowing, and typically dry completely or partial, leaving disconnected pools (Leigh et al., 2016). Flow cessation can occur at any point in a watercourse, with most streams having both perennial and temporary reaches (Costigan et al., 2017). The variations in the flow regime create a mosaic of aquatic, semi-aquatic and terrestrial habitats, and resultant biological communities, continually changing at various spatial scales (Arthington et al., 2014; Datry et al., 2014a). Temporary streams can be split broadly into two types: intermittent streams which stop flowing predictably, usually seasonally, or stop flowing in multiple year cycles, and ephemeral streams which flow due to rainfall (Belmonte & Beltran, 2001; Hansen, 2001; McDonough et al., 2011). They occur naturally in all biomes, representing around 51% of streams worldwide (Acuña et al., 2017; Messager et al., 2021) and can be considered more representative of global river systems than their perennial counterparts (Steward et al., 2012). Climate can have a strong influence on temporary stream flow regimes. Streams in arid regions are more likely to be dry for long periods of time, flowing during and after rainfall events, whilst streams in Mediterranean climates with hot, dry summers and mild, wet winters are likely to be seasonal, with flows associated with fluctuations in the water table (Gordon et al., 2004; Bonada & Resh, 2013).

Historically, temporary rivers have been overlooked, particularly in temperate climates, by both terrestrial and aquatic disciplines as they were not perceived to be within either science (Steward et al., 2012; Datry et al., 2017; Acuña et al., 2017). However, in the past thirty years the number of temporary river studies has increased (Leigh et al., 2016), providing an assortment of ecosystem services, supporting ecosystem processes and demonstrating their diverse and specialised aquatic and terrestrial biodiversity (Steward et al., 2012; Corti & Datry, 2016; Datry et al., 2017; Stubbington et al., 2020). The biodiversity found in temporary streams can be partially attributed to their physical diversity which influences the variability in environmental drivers (e.g. geology, flow regime), that determine the availability of differing habitats such as riffles, pools and the dry channel (Stubbington et al., 2017). For example, in the UK, there are a range of temporary stream types, each with different hydrogeomorphological characteristics and, consequently biodiversity, with some streams supporting specialists. There are predictably flowing, typically lowland, chalk streams, karstic limestone streams where drying relates to fissures in the bedrock and upland mountain streams which only flow in the snowmelt.

These systems, and other freshwater ecosystems, are under threat from numerous anthropogenic impacts such as climate change, land-use change, over-abstraction, and channel morphology alterations.

The lack of recognition of temporary streams, and their varying flowing, ponded and drying phases, has previously meant that dry-phase biomonitoring is either rare, or methods for all phases are based on those developed for perennial streams, which are inefficient, and likely inaccurate, for temporary streams (Stubbington et al., 2018; Crabot et al., 2021). Biomonitoring methods rarely incorporate the dry phase or terrestrial taxa, an important community within the ecosystem, and if they are included identification is to a coarse taxonomic resolution limiting inferences to ecological health (Stubbington et al., 2018). Without sufficient knowledge and biomonitoring methods, particularly for the dry phase, it is difficult to assess temporary stream ecological health, and thus to inform their restoration. Therefore, improving our knowledge of temporary streams including their aquatic and terrestrial species throughout all flowing, ponded and dry conditions, is crucial to monitor, restore and protect these ecosystems and their biological communities.

This chapter will present a review of the literature exploring temporary streams: their hydrology, geology, geomorphology, and biological communities, in addition to the ecosystem services they provide and the threats they face. Also, I will present an overview of biomonitoring and restoration, including the current methods and legislation. I will expand on the rationale for this thesis and outline its structure.

1.2 Temporary streams

1.2.1 Hydrology

Temporary streams are hydrologically dynamic and experience the cycling of three main environmental states: lotic (flowing), lentic (ponding), and terrestrial (dry) phases (Cid et al., 2017). The hydrological links between the channel and its catchment can occur longitudinally (e.g. from upstream to downstream), laterally (e.g. between the channel and the riparian zone) and vertically (e.g. between the channel and the hyporheic zone: an area between the groundwater and surficial sediments), and is particularly important in temporary streams, influencing the movement of sediment, organic matter, nutrients and organisms within the system (Ward, 1989; Freeman et al., 2007; Nadeau & Rains, 2007).

During the flowing phase, temporary streams resemble perennial streams with hydrological connectivity between the channel and riparian zone and differing flow velocities within the channel. Riffles and pools can form due to high and low energy flows respectively (Allan & Castillo, 2007; Bisson et al., 2017). As flow discharge begins to reduce between the lotic and lentic phases, the water levels begin to drop, isolating the water in the channel from the marginal habitats (Boulton, 2003). Pools may form in deeper areas of the channel as the water levels continue to drop, whereas raised sediment, such as riffle crests and bars become exposed (Corti et al., 2011; Hwan & Carlson, 2016; Datry, 2017). The presence and connectivity of these pools is highly variable: dependent on the geomorphology of the stream (the sediments and shape of the channel) and/or the time that has passed since flow recession/drying began (Gasith & Resh, 1999; McDonough et al., 2011; Hwan & Carlson, 2016). The dry phase begins when the streambed is largely dry, and most pools have receded, leading to increased fragmentation hydrologically, and therefore in aquatic habitat (Hwan & Carlson, 2016). However, water can still be present below the streambed in the hyporheic zone, allowing vertical connectivity to any remaining surface water (Argyroudi et al., 2009; Costigan et al., 2017). Once flow resumes and water levels increase, isolated pools are re-connected, and any organic matter and material accumulated during the dry phase is swept downstream (Nadeau & Rains, 2007; Obermann et al., 2007; Corti & Datry, 2012). Variations on this typical cycle are considerable because the duration and spatial occurrence of each state vary between streams or reaches (Stanley et al., 1997).

The flow regime of intermittent streams is influenced strongly by seasonal precipitation patterns and/or fluctuations in the water table (Gordon et al., 2004; McDonough et al., 2011), meaning that the flowing, ponded and dry phases occur predictably, often in a certain season. During the flowing phase the water table is above the channel bed, typically during winter when evaporation levels are low and precipitation is high (Williams, 2006; McDonough et al., 2011; Snelder et al., 2013; Figure 1.1a). Whilst the dry phase tends to occur during the late spring, summer and early autumn, when the water table is at its lowest (Berrie, 1992; McDonough et al., 2011; Snelder et al., 2013; Figure 1.1b). However, in alpine streams, flow stops during the winter when the streams freeze and flows during spring when the water stored in the ice is released as it melts (Robinson et al., 2016).

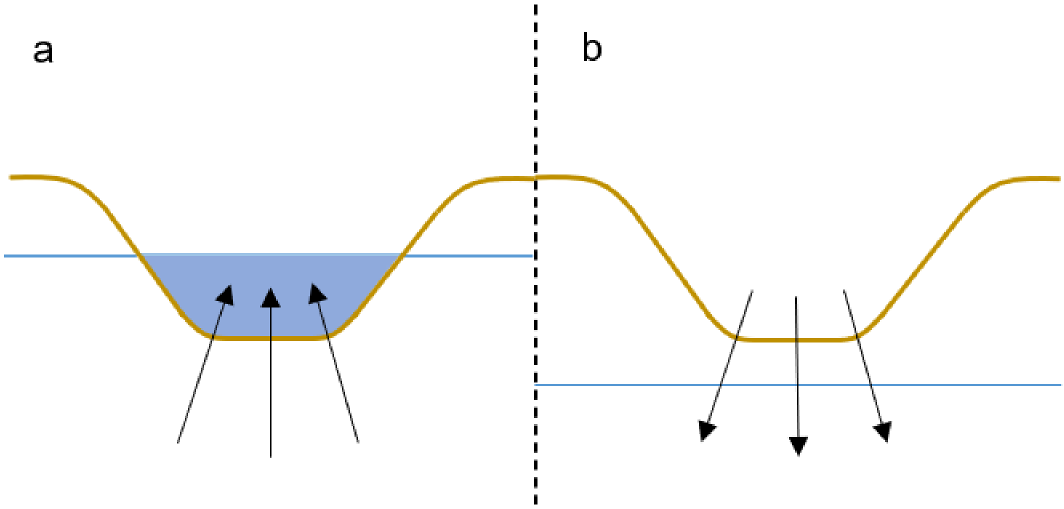

Figure 1.1. A cross section of intermittent streams with a) high and b) low groundwater tables, the groundwater tables represented by the blue line and the arrows representing the movement of water (adapted from McDonough et al., 2011, CC BY-NC-ND 4.0, https://creativecommons.org/licenses/by-nc-nd/4.0/).

In contrast to intermittent streams, ephemeral streams flow aseasonally, having typically longer dry and non-flowing states that last months or years, with flow only occurring in response to low frequency, high magnitude rainfall events (Belmonte & Beltran, 2001; Hansen, 2001; McDonough et al., 2011). The groundwater table in ephemeral streams is constantly below the channel bed, meaning there is no baseflow from groundwater (Gordon et al., 2004; McDonough et al., 2011; Figure 1.1).

Temperature can also influence temporary streams and their flow regimes. Higher temperatures promote greater evapotranspiration, allowing streams to dry more readily and often meaning watercourses are more likely to follow rainfall patterns, resulting in an ephemeral flow regime (Dieterich & Anderson, 1998; Gasith and Resh, 1999). In contrast, in northern Canada and other areas with subarctic climates, where temperatures are low (Köppen climate classification Dsc), flow can cease when precipitation is stored in the permafrost during the cold winter months (Buttle et al., 2012). Temperatures above zero in these climates can also impede the accumulation of snow, which can be an important water input into stream systems (Robinson et al., 2016; Costigan et al., 2017). Although cooler temperature climates, such as that in the UK, experience warm summers and cold winters, there are no extreme fluctuations in temperature, meaning flowing and drying phases are more predictable, relying more on the water table fluctuations (Stubbington et al., 2017).

1.2.2 Geology and sediments

The underlying geology or bedrock of a stream has strong influence on its flow regime and chemical properties (Sear et al., 1999). In temporary streams, the bedrock strongly influences patterns of flow cessation. Streams with porous bedrock, such as chalk, are likely to have increased natural intermittence because water can travel through the bedrock into groundwater storage, which then provides a steady source of water for streams (Mainstone 1999; Smith & Wood, 2002; Costigan et al., 2017. Similarly, karstic limestone streams lose water through fractures in the bedrock and have strong groundwater linkages, leading to a seasonal flow regime (Buttle et al., 2012). Impermeable bedrocks can lead to ephemeral flows with insufficient groundwater linkages to supply the stream with sufficient flows (Costigan et al., 2017).

Sediment composition is influenced by flow and vegetation, with flow transporting sediment particles from upstream to downstream and differing vegetation structures trapping sediments (Bull, 1997; Jaeger et al., 2017). The size, presence and transport of sediment in a given location is also influenced by the balance between the ability of the flow carry certain sediment sizes (i.e. flow competence) and the availability and size of sediment for potential transport within the channel. In temporary streams, the transport of larger sediments typically only occurs during flowing phases when flow competence is higher, with smaller sediment sizes (e.g. silts) potentially still transported during lower-energy flowing phases. When flow declines as the stream dries, sediment is then deposited, as flow competency drops, and then builds up on the streambed (Reid & Frostick, 2011).

1.2.3 Geomorphology

Fluvial geomorphology refers to the landforms, and associated sediments and processes of a streams, and how they interact with the landscape (Brierley & Fryirs, 2013). Rivers and streams are formed by a series of erosional and depositional processes, variations in which create the considerable differences in stream geomorphology and associated features (Williams, 2006; Jaeger et al., 2017). Stream geomorphic characteristics include channel morphology, geology and sediments, which form the basis of the physiochemical processes that occur in stream and influence habitat availability (Jaeger et al., 2017).

Stream geomorphology is closely tied to hydrology, with the discharge of a watercourse influencing geomorphological diversity and the distribution of geomorphic features (Rolls et al., 2012). High energy flows create erosional features such as pools, whilst low energy flows create more depositional features, such as riffles (Charlton, 2007; Rolls et al., 2012). Temporary streams are more geomorphologically variable than perennial watercourses, largely due to the wide range of flow regimes they possess (Costigan et al., 2017; Jaeger et al., 2017) and include systems ranging from wide, alluvial channels to narrow V-shaped channels with coarse sediments (Costigan et al., 2017). Other influences upon geomorphology include climate and catchment properties such as soil, vegetation and topography (Bunn & Arthington, 2002; Jaeger et al., 2017). Hillslope gradients can change how water moves through the system; narrow, steep valleys mean that water movement is confined and moves quickly through the network, leading to increases in channel incision (Costigan et al., 2017; Kuo et al., 2017). Flat, wide valleys tend to have streams with more meandering and braided channels, due to the decreased sediment size and increased deposition (Allan & Castillo, 2007).

A stream channel cross-section is influenced by interactions between flow and sediment regime, substrate erodibility, and any vegetation or debris (Allan & Castillo, 2007; Jaeger et al., 2017). In most streams, channels are formed through erosion, with lowland streams also modified by depositional features like deltas (Williams, 2006). In temporary streams, however, channel morphology may not be as closely linked to fluvial processes in comparison to perennial watercourses, due to the cessation of flow. Bedforms may not have time to develop to reflect those typical of the flow if flow velocity and discharge change too quickly (Buttle et al., 2012).

The catchment position of a stream reach influences its channel morphology. Streams in upland areas are usually characterised by single thread channels and have little to no floodplain (Allan & Castillo, 2007; Jaeger et al., 2017), and lowland streams tend to have wider channels, with extensive floodplains (Jaeger et al., 2017). Mid-reach channels usually reflect an intermediate shape between upland and lowland streams, with more variable erosional and depositional conditions (Jaeger et al., 2017). These longitudinal patterns are usually concurrent with an increase in discharge as catchment size increases (Buttle et al., 2012). However, in temporary streams, there may be significant transmission losses, defined as the loss of water in channel from evaporation and infiltration to groundwater (Jarihani et al., 2015), resulting in decreases in discharge in lowland streams (Jaeger et al., 2017). These discharge decreases may result in considerable variation in the morphology of temporary streams in lowland areas, with some having particularly low sinuosity and shallow cross-sections (Jaeger et al., 2017).

Riffle and pool bedforms are usually characteristic of moderate to low gradient streams, and gravel or mixed sediment beds, (Emery et al., 2003; Allan & Castillo, 2007) including UK chalk streams (Holmes, 1999). The variations in riffle and pool distributions may impact on the surface sediments, bedform stability and flow patterns, providing a variety of microhabitats for communities (Emery et al., 2003; Marziali et al., 2010; Costigan et al., 2017).

1.2.4 Biological communities

Temporary streams can be considered as both aquatic ecosystems which dry, and terrestrial ecosystems that become inundated (Larned et al., 2010; Dell et al., 2014; Stubbington et al., 2017): the variations in flow creating a mosaic of aquatic and terrestrial habitats (Larned et al., 2010). These flow variations mean communities range from fully aquatic to fully terrestrial, the community composition, colonisation and succession changing between phases and according to phase duration (Sánchez-Montoya et al., 2016; Steward et al., 2017). As highly dynamic habitats, temporary streams can support high biodiversity including microorganisms, macrophytes, invertebrates, amphibians, reptiles, fish and mammals. Generalist taxa comprising of those found in the perennial reaches and riparian zones, can often dominate temporary stream communities, although specialists can also colonise the differing phases (Datry et al., 2014a; Corti & Datry, 2016; Stubbington et al., 2017). For example, some insect species in arid climates and in 'winterborne' chalk streams are specialists found only in temporary streams (Steward et al., 2011; Armitage & Bass, 2013). The evolution of adapted specialists can be promoted by predictable intermittence regimes (Stubbington et al., 2017).

Following flow cessation, lotic organisms die or survive in refuges (e.g. in pools or the hyporheic zone) as the aquatic habitat availability decreases, and are replaced by lentic and terrestrial taxa (Lake, 2003; Stubbington et al., 2011; Datry et al., 2014a). The biota that remains in the pools can be subjected to numerous stressors, particularly if the pools become isolated, such as high temperatures and a decrease in dissolved oxygen (Williams, 1997; Bogan et al., 2017). Terrestrial taxa can colonise the dry riverbed once flow recedes and sediments become exposed, entering the channel from the surrounding marginal and riparian habitats, or potentially reaches up or downstream (Steward et al., 2012; Datry et al., 2017). Recent research highlights that the dry sediments are an important habitat for terrestrial organisms (Steward et al., 2012; Rosado et al., 2015; Sánchez-Montoya et al., 2020), including in UK chalk streams (Bunting et al., 2021), and support persisting aquatic biota (Stubbington & Datry, 2013). Then once flow resumes, the terrestrial biota which inhabited the channel during the dry phase, and any organic matter which accumulated during this time are often flushed downstream (Corti & Datry, 2012; Rosado et al., 2015). Many terrestrial or dry-phase invertebrates can survive being flushed down stream by, for example, using any floating organic matter to escape flooding (Corti & Datry, 2012; Rosado et al., 2015). Following flow resumption, aquatic biota begin to recolonise the channel, typically from perennial reaches upstream but also the sediments, the rate of recolonisation influenced potentially by the dry phase duration (Dostine et al., 1997; Hill et al., 2019).

1.2.4.1 Perennial and temporary biodiversity comparisons

The alpha diversity, or local taxa richness, of aquatic invertebrate biota in temporary streams is generally lower than in perennial streams, and decreases with increased intermittence (Datry et al., 2014a; Soria et al., 2017; Gauthier et al., 2020). However, after extended flowing phases, temporary streams may support comparable alpha diversity to perennial streams, in comparison to dry or ponded phases when aquatic habitat availability is much lower or non-existent (Soria et al., 2017). Additionally, spatial and temporal beta diversity (i.e. the variability among communities in space and time), can be higher in temporary streams when considered over all phases and includes both aquatic and terrestrial taxa (Corti & Datry, 2015; Bogan et al., 2017), and contributes to regional (i.e. gamma) diversity (Clarke et al., 2008; Stubbington et al., 2017). This increase in beta diversity can be dependent on phase duration, and the taxonomic group. Streams with shorter dry phases may have higher beta diversity in aquatic organisms (Leigh and Datry, 2017) but potentially lower in terrestrial organisms in comparison to streams with longer dry phases. Equally, beta diversity can decrease as the harshness of disturbance increases through eliminating a large portion of poorly adapted species (Chase, 2007; Leigh and Datry, 2017).

1.2.4.2 Adaptations

Temporary streams are characterised by their changing flow regime, which has led to taxa with adaptations that enable persistence despite the cycling between flowing and dry (Lytle & Poff, 2004; Steward et al., 2012; Bonada & Resh, 2013). Physiological (an internal process of the body), behavioural (a response to the disturbance through reacting to an environmental cue), morphological (an advantageous modification to the body), and life history (the synchronisation of flow regime and life-cycle stages) strategies are all types of adaptations to enable taxa to avoid or cope with disturbance (Schwartz & Jenkins, 2000; Lytle & Poff, 2004). In intermittent streams, a natural predictable regime may mean communities are more likely to comprise taxa that have adapted to survive disturbance, leading to a more stable community over time (Adis and Junk, 2002; Sarremejane et al., 2017). However, these natural adaptations may be insufficient in streams with anthropogenic modifications such as water abstraction, which may influence the phase duration (Skoulikidis et al., 2017).

The two main categories of adaptation strategies can be defined as those promoting resistance or resilience. Resistance strategies confer the ability to tolerate disturbance events in situ, and resilience strategies enable taxa to recover from a disturbance (Lake, 2000; Bogan et al., 2017). Common adaptations conferring resistance include desiccation-resistant stages e.g. invertebrate eggs, or plant fragments and taking refuge in remaining pools or perennial reaches (Chester & Robson, 2011), whilst both active and passive dispersal are a common resilience strategy (Bogan et al., 2017). The resilience and resistance strategies may be influenced by the duration and intensity of drying, in addition to the proximity of perennial reaches (Bogan et al., 2017).

1.2.4.3 Temporary stream plant communities

As primary producers, the plants of temporary streams are at the base of the trophic network, making them an essential part of any temporary stream community (Sabater et al., 2017). Plants rely upon water availability as a main resource, which is limited in the dry, and potentially ponded, phases of a temporary stream regime. The loss of water during the ponded and dry phases also influences other habitat conditions, increasing solar radiation levels, gravitational pull, carbon dioxide levels, and light availability (De Wilde et al., 2014; Sabater et al., 2017). Despite these challenging conditions, temporary streams can often host a high diversity of plant species (Westwood et al., 2006a; Sabater et al., 2017), supporting vascular plants, mosses and algae (Sabater et al., 2017), during flowing and ponded phases, and also terrestrial mosses, herbs and grasses during the dry phase (Holmes, 1999; Westwood et al., 2006b).

Intermittent flow regimes can even have the highest riparian plant cumulative richness and beta diversity over time in riparian communities in comparison to perennial and ephemeral streams (Katz et al., 2012). This positive effect can be attributed to the multiple moisture conditions created at intermittent sites during non-flowing phases (Katz et al., 2012). Chalk streams, which are often intermittent, are recognised for their diversity, including their macrophyte communities, which are often dominated by species of water-crowfoot, (Westwood et al., 2006a), alongside other species such as whorl grass, lesser water-parsnip, water-starwort, creeping bent grass and marsh foxtail (Holmes, 1999; Westwood et al., 2006b). Whilst beta diversity has not been quantified for plant communities in chalk streams, longitudinal changes in communities have been characterised, indicating that intermittence also supports network-scale spatial beta diversity in these systems.

The substantial changes in habitat conditions between flowing and drying phases mean plants require adaptations to survive these conditions, with the duration and intensity of each phase influencing community resistance and resilience once flow returns (Sabater et al., 2017). Some species can endure drying above the bed, whilst in others, aboveground biomass may die but survive in the sediments through desiccation-resistant fragments and seeds (Steward et al., 2012; Sabater et al., 2017). Other common adaptations to drying include a reduction in leaf size, as well as an increase in leaf thickness, to decrease evapotranspiration, and higher energy allocation to roots, to increase water intake (Sabater et al., 2017). Phylogenetic position may also influence macrophyte survival (De Wilde et al., 2014; Sabater et al., 2017). Dicots tend to have increased survival in comparison to monocots when drying occurs due to monocots shifting earlier to aquatic life, meaning they developed more adaptations to deal with aquatic habitats at the cost of survival in dry conditions (De Wilde et al., 2014). In addition to adaptions to drying, some terrestrial plants combat inundation through decreasing in size, whilst others increased petiole length and leaf area to improve gas-exchange rates (Mommer et al., 2005; Stromberg and Merritt, 2016).

1.2.4.4 Temporary stream invertebrate communities

Similarly to plant communities, temporary stream invertebrate communities span the spectrum from fully terrestrial to fully aquatic. During the flowing phase, aquatic species are found throughout the channel with semi aquatic and terrestrial invertebrates, such as carabids and spiders, found at the water’s edge or on exposed gravel bars (Langhans & Tockner, 2014; Steward et al., 2017). As flow decreases, lotic biodiversity declines and some taxa may disperse to other wetted reaches through flight, swimming upstream or drifting downstream (Chester & Robson, 2011; Bogan et al., 2017). Any remaining aquatic biota may take refuge in any remaining pools and the hyporheic zone or, persist through life cycle or desiccation-resistant adaptations (Bogan et al., 2017; Hill and Milner, 2018). In the hyporheic zone conditions remain saturated (Boulton et al., 1998; Stubbington, 2012) and can be used by aquatic taxa through vertical migration from the channel (Vander Vorste et al., 2016). This loss of active lotic communities in channel occurs alongside an increase in lentic and terrestrial taxa (Datry et al., 2014a). Aquatic invertebrates may become concentrated in any remaining pool habitat, if available, meaning that abundance and richness within these habitats may be high after the initial flow cessation (Lake, 2003). However, as the time passes, these pools may become less inhabitable for some aquatic species as temperatures increase and oxygen availability declines, or due to predation (Williams, 1997; Lake, 2003).

As the riverbed dries, the adjacent riparian zones can become connected to the bed (Datry et al., 2012; Datry et al., 2015), allowing some terrestrial invertebrates such as ants, beetles and spiders (Steward et al., 2017; Steward et al., 2022) to colonise from the riparian zone, or from other dry reaches (Bogan et al., 2017). The dry riverbeds may have accumulated organic matter, nutrients and dead or dying aquatic taxa during the aquatic phase (Rosado et al., 2015), which colonising terrestrial taxa, such as ants, can consume and process (Wishart, 2000; Bogan et al., 2017; Steward et al., 2022). If any pools remain, predatory and scavenging terrestrial species may occur on their marginal sediment (Bonada & Resh, 2013; Rosado et al., 2015). Some taxa may remain following initial colonisation, whilst others may alternate between the bed and riparian zone (Bogan et al., 2017). Aquatic invertebrates may remain in the dry sediments as part of the 'seedbank', comprising all life stages of aquatic invertebrate biota, both active and dormant, which will remain viable during the dry phase until the sediments are rewetted (Stubbington and Datry, 2013; Bogan et al., 2017).

The resistance or resilience of aquatic taxa to the dry phase can allow quick recolonisation once the flowing phase returns (Bonada & Resh, 2013). Upon rewetting, active and dormant life forms emerge from the seedbank into the main channel (Stubbington & Datry, 2013). The hyporheic zone is also a key contributor to recolonisation by aquatic species when flow returns, and its inhabitation therefore represents a key resilience strategy (Vander Vorste et al., 2016). Other terrestrial taxa with aquatic larval stages may colonise from downstream or other wetted reaches through flight (Bogan et al., 2017; Stubbington et al., 2017). The terrestrial invertebrates remaining in the channel may be flushed downstream, alongside any material, which may provide a food source for aquatic species (Rosado et al., 2015) or drift downstream on floating organic matter to survive (Rosado et al., 2015). Other terrestrial and semi-aquatic invertebrates may have adaptations to escape inundation. For example, taxa may escape flow resumption by moving into the adjacent riparian zones and any exposed gravel bars either through flight, swimming and/or drifting (Adis & Junk, 2002; Kolesnikov et al., 2012; Steward et al., 2017). Other species may have developed morphological characteristics, such as wing dimorphism, to deal with inundation: fully winged where floods are irregular and short to allow quick dispersal, and shorter wings where floods are longer and regular. Plastrons are another morphological adaptation, allowing invertebrates to trap oxygen on their surface to counter the inability to respire whilst submerged (Adis & Junk, 2002). Other adaptations to inundation include univoltine life cycles timed to coincide with dry phases, becoming torpid during flooding, waterproof cocoons and inhabiting pieces of driftwood and floating debris (Adis & Junk, 2002).

1.2.4.5 The use of temporary streams by humans and other biota

In addition to the communities that inhabit the temporary streams, other biota benefit from the dry phase. Temporary streams provide food and water for other fauna from surrounding areas such as bats, birds, deer and small mammals (Steward et al., 2012, Seidman and Zabel, 2001; Stubbington et al., 2020), in addition to acting as a corridor, when dry, for many species (Steward et al., 2012; Coetzee, 1969). The provision of food and water are also true for humans, particularly in hotter climates where water can be scarce (Jacobsen et al., 1995; Hans et al., 1999; Steward et al., 2012).

Temporary streams provide numerous ecosystem services and processes, one of which is nutrient cycling (von Schiller et al., 2008), with microbial communities processing nutrients during the flowing phases, whilst during the dry-phase, nutrients are regulated through the uptake by terrestrial plants (Hefting et al., 2005). They can also contribute to carbon cycling, storing carbon during the dry phase through the accumulation of leaves and plants (organic matter), and as source of carbon during the wet phase where microbial and shredder communities process organic matter accumulation (Corti et al., 2011; Datry et al., 2018). The dry-phase communities also provide an ecosystem service in the form of pollination. Invertebrates which use the dry phase, whether for habitat or food provided by the dry-phase in-channel vegetation, may pollinate surrounding riparian areas and agricultural crops (Stubbington et al., 2020). Temporary streams also provide many cultural ecosystem services, as part of different cultures, featuring in indigenous stories or being used for recreation e.g. boating, walking and caving (Steward et al., 2012; Stubbington et al., 2020). In the UK, temporary chalk streams are considered a unique part of the countryside, eliciting differing emotions and providing a connection to a green space.

1.3 Threats to temporary streams

Even though naturally occurring, temporary river extent and dry-phase duration are expected to artificially increase due to water abstraction and climatic influences (Tramblay et al., 2020). Drought, defined as a water-deficit in comparison to the long-term average (Tallaksen & Van Lanen, 2004), is expected to increase along with the potential intensification of drying, but these are not the only expected changes to flow regime. Higher magnitude flooding is predicted due to climate change, with intense, but less frequent, rainfall events expected to increase (O’Gorman, 2015; Masson-Delmotte et al., 2021). These changes to flow regime, and the increased hydrological variability, can result in the loss of biodiversity, with aquatic taxa adapted to desiccation and terrestrial species adapted to flow resumption in natural temporary streams, struggling to persist in longer drying conditions or more frequent and shorted resumptions of flow, respectively (Chiu et al., 2017). Flow modifications and habitat degradation are two of the five main impacts on freshwater biodiversity (Dudgeon et al., 2006).

River ecosystems, including those in the UK, are also impacted by stressors resultant of human pressures such as land-use change and the alteration of channel morphologies (Addy et al., 2016; England & Wilkes, 2017), which often intensify the impact of, or reduce the ability of communities to recover from, flow regime alterations. The increase in urbanisation and agricultural practices has led to multiple interacting stressors impacting on the in-channel (and riparian) temporary stream habitat conditions and biological communities (Figure 1.2). Fine sediment introduced by agricultural practices, can lead to gill abrasion or clogging, sediment accumulation within macroinvertebrate organs, or the burial of organisms (Armitage et al., 1999; Wood et al., 2005; Jones et al., 2012). It also reduces the sediment heterogeneity and infills interstitial gaps, reducing the range of habitats and accessible refuge available to invertebrate communities.

Eutrophication, the artificial nutrient enrichment of a waterbody, is another major threat to stream biodiversity (Figure 1.2; Schindler, 2006; Conley et al., 2009; Hautier et al., 2009). This enrichment is often due to pollution from urban sources (e.g. septic tanks, wastewater) or agricultural practices (Schindler, 2006; Conley et al., 2009), and can lead to changes in vegetation community composition (Hautier et al., 2009; Kneitel & Lessin, 2010) and an increase in dominance of competitive or invasive species (Grime, 1979; Chase & Knight, 2006; Cleland & Harpole, 2010). These changes in vegetation can limit both plant biodiversity and that of aquatic and terrestrial invertebrates through reducing the number of habitats, food sources and range of differing morphological structures within the channel during flowing phases (Siemann et al., 1998; Clarke, 2002; Crist et al., 2006).

Alterations to channel morphology can impact the flowing, ponded and dry phase communities, potentially exacerbating other impacts associated with land use change such as excess fine sediment. Changes to channel morphology can involve modifications such as man-made banks and riverbeds, the straightening and widening of the river, and the removal of in-channel and riparian vegetation. Variations in flow, sediment, vegetation and channel features (i.e. berms, in-channel islands) create a mosaic of habitats of differing microhabitats which are often lost due to channel modifications, reducing habitat heterogeneity and impacting biodiversity (Stanley et al., 1997; Rosenfeld, 2017; Beerman et al., 2018).

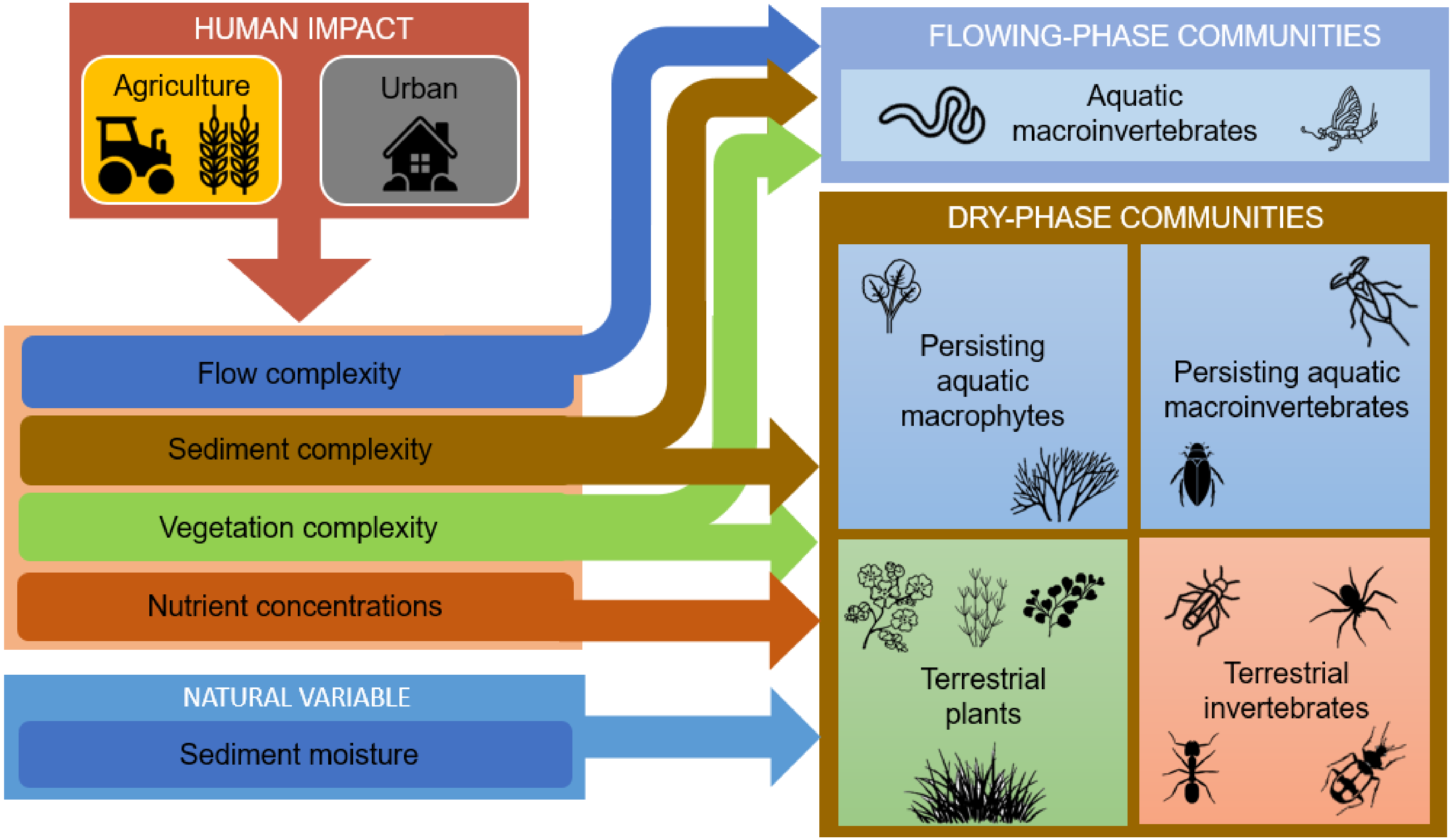

Figure 1.2. A conceptual model displaying the human pressures and corresponding stressors that impact temporary stream communities, and the potential dry-phase biomonitors for each stressor.

1.4 Biomonitoring and restoration

A biomonitor is a biological tool to measure or collect information about an ecosystem, typically on the physical and chemical properties (Andersen, 1999). Biotic groups (typically a community, e.g. macroinvertebrates) are biomonitors, and can be represented by taxonomic or functional metrics. Biomonitors range from individual species (indicator species) to entire communities, the composition of which responds to specific environmental conditions. Biomonitors have been routinely used in freshwater and terrestrial ecosystems to assess the impact of human activities (Cairns & Pratt, 1993; Mainstone, 1999; Hodkinson & Jackson, 2005 Birk et al., 2012), such as those mentioned in Section 1.4. Often, reference conditions are defined for specific river types (e.g. chalk streams) to characterise the communities indicative of undisturbed or least impacted conditions, against which communities from assessed sites can be compared. Useful biomonitors need to be abundant, sensitive to stressors, and easily sampled and identified (Andersen, 1999; Holmes, 1999; Steward et al., 2018). Bonada et al. (2006) provides twelve criteria for the “ideal” biomonitor (Table 1.1).

Table 1.1. The twelve criteria defined by Bonada et al. (2006) for the “ideal” biomonitor.

Rationale
(I) Derived from sound theoretical concepts in ecology
(II) A priori predictive
(III) Potential to assess ecological functions
(IV) Potential to discriminate overall human impact (i.e., to identify anthropogenic disturbance)
(V) Potential to discriminate different types of human impact (i.e., to identify specific types of anthropogenic disturbance)
Implementation
(VI) Low costs for sampling and sorting (field approaches) or for standardised experimentation (laboratory approaches)
(VII) Simple sampling protocol
(VIII) Low cost for taxa identifications (no specialists in taxonomy required)
Performance
(IX) Large-scale applicability (across ecoregions or biogeographic provinces)
(X) Reliable indication of changes in overall human impact
(XI) Reliable indication of changes in different types of human impact
(XII) Human impact indication on linear scale

The EU Water Framework Directive 2000/60/EC (WFD), which remain in force in the UK, requires that all watercourses are of good ecological status (ES; i.e. only slightly different from undisturbed conditions/limited anthropogenic impact; European Commission, 2000) and in order to assess ecological status, effective biomonitors are needed. Despite this, the biomonitoring of temporary streams remains lacking in comparison to perennial counterparts, even within the WFD which has only one category (R-M5) for temporary streams, and it is only for the Mediterranean region (European Commission, 2000). Additionally, due to the cycling of flowing and dry ES can be wrongly assessed through perennial biomonitors (Reyjol et al., 2014; Crabot et al., 2021), there is a need for dry-phase biomonitors which respond to environmental variability despite drying in order for managers to assess ES regardless of instream conditions.

1.4.1 Plants and invertebrates as biomonitors

Plants and invertebrates (both aquatic and terrestrial) have many benefits as biomonitors and have been used in other freshwaters and ecosystems (Birk et al., 2012). Both taxonomic groups are abundant and easily sampled/surveyed by cost-effective means, with plants having the additional benefit of being sessile. The ecological preferences of both groups are well studied, and they are responsive to changes in environmental conditions. Invertebrates have the advantage of average growth levels and turnover times in comparison to mammals or mosses, as well as being effective dispersers, allowing for recolonisation after a disturbance or impact (Perner & Malt, 2003; Hodkinson and Jackson, 2005). These qualities could make invertebrates more responsive to short-term impacts and could be used to determine restoration success. Terrestrial invertebrate communities are known to respond to habitat complexity (Siemann et al., 1998; Crist et al., 2005), such as sediment and vegetation complexity, indicative of fine sediment inputs and nutrient enrichment. Whilst plants have longer turnover times in comparison and are slower dispersers, meaning they are more useful for detecting longer term impacts (Hodkinson & Jackson, 2005) and are known to respond to nutrient enrichment (Birk et al., 2012; Stromberg & Merritt, 2016). These differences highlight that multiple biotic indices may be needed to fully assess ecological status during the dry phase (Marshal & Negus (2019).

Benthic macroinvertebrates have been used frequently in freshwater monitoring of perennial streams. These biomonitors can be represented by metrics to assess human impacts, which are most frequently used for fine sediments (e.g. EPSI; Turley et al., 2014) and organic pollution (e.g. Whalley Hawkes Paisley Trigg Index; Paisley et al., 2014; Figure 1.2). However, the current macroinvertebrate biomonitoring methods for temporary streams are likely unsuitable in many circumstances due to their concurrent responses to natural drying and human impact (Figure 1.2; Soria et al., 2019; Stubbington et al., 2021). Terrestrial invertebrates are also used often for monitoring conditions in exposed riverine sediments, a habitat similar to temporary streams in that they are frequently inundated (Eyre and Luff, 2002), and their potential as dry-phase indicators highlighted in other climates (Steward et al., 2018; Corti & Datry, 2015; Sánchez-Montoya et al., 2020), and in UK chalk streams (Bunting et al., 2021).

Aquatic plants are currently used to monitor the impacts of nutrient enrichment (e.g. LEAFPACS2; WFD-UK TAG, 2014; Figure 1.2), and have been demonstrated to be useful as indicators of flow regime, with the research of Stubbington et al. (2019) and Westwood et al. (2021), indicating further research needs to be conducted to assess their potential as dry-phase bioindicators.

1.4.2 Restoration and its links to biomonitoring

Given the threats to temporary streams and the general degradation of freshwaters globally (Karr & Chu, 1999; Gleick, 2003), river restoration projects are done to reduce, prevent or reverse human impacts to improve ecosystem biodiversity, services and functions. (Palmer et al., 2005; Wohl et al., 2015; Kaiser et al., 2020). Restoration can, for example, involve improvements to habitats, dam removals and the reinstatement of a natural flow regime. In general, restoration schemes in countries including the UK, are often only carried out reactively rather than proactively, and can be limited by time and funding availability (Kondolf, 1998; England et al., 2008). These limitations can lead to restoration projects that are small-scale sometimes lacking appropriate methods to improve habitat conditions for target communities and/or species (England et al., 2008). However, there is some progress towards a more multi-faceted, scientifically led approach to restoration (Palmer et al., 2005; Johnson et al., 2019; Kaiser et al., 2020). The River Restoration Centre, in particular, is helping to support the development of evidence-informed restoration in the UK, by providing guidance at national level and conducting projects in collaboration with partners such as water companies, non-profit organisations and the Environment Agency (River Restoration Centre, 2014).

Despite these efforts, similarly to biomonitoring, temporary stream restoration is led by methods based on our knowledge of perennial streams and, their communities and preferences (Leigh et al., 2016; Stubbington et al., 2017), which may differ from temporary streams. This lack of knowledge, time and funding may lead to potentially ineffective temporary stream restoration. A solution to this is to improve the understanding of the systems and produce efficient biomonitors. These biomonitors are a key facet of any restoration plan (Skinner & Bruce-Burgess, 2005; England et al., 2008), allowing for the assessment of ecological status after restoration has been carried out, and informing resource allocations (Dobbie & Negus, 2013).

1.5 Thesis rationale, aims and structure

1.5.1 Thesis rationale

Temporary streams are under threat, in the UK and globally, impacted by historical and current anthropogenic pressures and stressors, which are modifying their habitats and detrimentally affecting the communities they support. Without considering both aquatic and terrestrial taxa occurring in lotic, lentic and terrestrial phases, temporary stream biodiversity may not be accurately estimated, and therefore not fully understood (Corti and Datry, 2016; Stubbington et al., 2017; Hill & Milner, 2018). Our knowledge of the dry phase communities and their responses to environmental variables, including those indicative of human impact, is particularly lacking. This leads to an inability to monitor the health of these ecosystems accurately and efficiently, which in turn impacts on our ability to assess restoration success, limiting the capacity of managers to improve methods. Improvements to our knowledge on dry-phase communities and their responses to environmental variables are needed to inform the development of effective biomonitoring tools to assess the ecological status of temporary streams regardless of the in-channel state in order to meet legislative requirements, monitor restoration success and protect temporary streams.

1.5.2 Aims

There are significant knowledge gaps in temporary stream research, predominantly relating to dry-phase community composition and their responses to environmental variables. Additionally, the differences in aquatic macroinvertebrate responses to environmental variables in temporary and perennial streams requires further study. Research into aquatic macroinvertebrate communities across a variety of flow regimes, and dry phase-biota, including their responses to environment conditions (including human impacts) is needed to improve our understanding of temporary stream systems as a whole to inform the biomonitoring and restoration of temporary streams. Therefore, this research has three key aims:

1. To identify the responses of macroinvertebrate communities to flow, sediment and vegetation, and how temporary stream responses differ to perennial communities, to inform restoration (Chapter 3).
2. To characterise the dry-phase plant communities and explore their responses to environmental conditions to identify potential biomonitoring metrics (Chapter 4).

3. To characterise the dry-phase invertebrate communities and explore their responses to environmental conditions to identify potential biomonitoring metrics (Chapter 5).

1.5.3 Thesis structure

This thesis is structured to address each of the aims in a different results chapter, with a final chapter to summarise and conclude:

Chapter 3: Macroinvertebrate community responses to environmental conditions in perennial and intermittent streams

This chapter analyses an Environment Agency, a government body in the UK, macroinvertebrate dataset, and incorporates both biological metrics and community compositional responses to environmental conditions across a range of flow regimes, with particular focus on comparisons between perennial and intermittent streams. The results from this chapter highlight potential differences between perennial and temporary communities to help inform priorities for temporary stream restoration.

Chapter 4: Dry-phase plant communities and their potential as biomonitors

This chapter involves novel data collection, using a modified biomonitoring method currently used for aquatic plants, to characterise dry phase plant communities (including terrestrial and persisting aquatic species) and examine how plant metrics summarising community composition respond to a range of environmental conditions indicative of human impact. This chapter will improve our understanding of the dry phase biodiversity, characterising a previously unknown community, and evaluate potential biomonitors of specific environmental drivers indicative of human impact.

Chapter 5: Dry-phase invertebrate communities and their potential as biomonitors

This chapter uses a well-known method, pitfall trapping, to sample and characterise dry-phase invertebrates, and their responses to environmental drivers including vegetation and sediment conditions. This chapter will improve our knowledge of dry-phase invertebrates and identify potential biomonitors of environmental variables indicative of human impact.

Chapter 6: General discussion

This chapter summarises and discusses the previous chapter’s findings, the advancements made to temporary stream research, and the implications for temporary stream biomonitoring and restoration. It also highlights the priorities for future research to further advance these topics.

Chapter Two: Study sites and general methods

2.1 Chalk streams

Chalk is a porous calcareous rock with fracturing, allowing surface water to infiltrate into the ground into an aquifer, an important source for groundwater flow within the UK (Westlake et al., 1972; Allan et al., 1997). As a result, chalk streams are groundwater dominated with predictable flow regimes, and often have naturally intermittent sections, typically in their upper reaches (Holmes, 1999; Allan et al., 1997). These naturally intermittent sections have largely seasonal hydrological regimes, with flow reducing towards the end of spring and peaking during late winter, with the possibility for channel bed drying within the summer months. Due to this seasonal regime, these streams are often termed 'winterbournes'. However, not all chalk streams have seasonally intermittent flows; some have perennial and near perennial reaches or have multi-year low and high flows.

Usually chalk streams have low energy flows, which influences sediment composition and geomorphological processes (Mainstone, 1999; Harvey et al., 2008). Chalk streams often have a shallow cross section with gentle slopes and are sinuous, unless modified. Common in-channel features include riffles and pools, and sometimes exposed bedrock and gravel shoals (Mainstone, 1999). When unimpacted by humans, these streams often have unpolluted, crystal-clear waters, which support a diverse community of flora and fauna, including species such as water-crowfoot (*Ranunculus* spp.), otter (*Lutra lutra*), kingfisher (*Alcedo atthis*) and brown trout (*Salmo trutta;* Rangeley-Wilson, 2021). Many of these taxa, along with species such as grayling and lamprey are protected under UK legislation (e.g. Biodiversity Action Plan Priority Species and Wildlife and Countryside Act 1981).

Despite this, many have been historically, heavily modified in their physical morphology and flow through a variety of human impacts, so much so that there are no British examples of a chalk stream with natural morphology (Mainstone, 1999). The main impacts include water abstraction, water-cress farms and mill works, in addition to changes in land use (i.e. increasing urbanisation and agricultural intensification) that have affected many ecosystems in the UK (Westlake et al., 1972; Mainstone, 1999; Rangeley-Wilson, 2021). Water abstraction can further reduce the natural seasonal or multi-year flows, exacerbating in low flows and extending dry phases, whilst water-cress farms and other agriculture may input silt, organic matter and nutrients into the system (Westlake et al., 1972; Rangeley-Wilson, 2021).

UK chalk streams account for a significant proportion of chalk streams found globally and are mostly found in the south and east of England (Chilterns AONB, 2020; WWF-UK, 2022). In addition to supporting protected species, chalk streams are also a priority habitat under the UK Biodiversity Action Plan and their protection is a focus of regulatory bodies such as the Environment Agency, thus the protection of these ecosystems and their communities from human impact is crucial. Additionally, chalk streams provide a variety of ecosystem services such as a fresh water supply for drinking water and agriculture, fishing, and provides a space for people to interact and feel close to nature. Therefore, chalk streams in southern England were selected as the study streams for this research, to improve the knowledge of these naturally drying ecosystems and their communities and identify biomonitors that can monitor the human impacts to inform management actions.

2.1.1 Study catchments

This thesis studied two groundwater catchments: the Upper Lee and the Colne, located within the Thames River Basin District in southern England (Figure 2.1). Areas of the Colne and the Lee catchments form part of in the Chilterns Area of Outstanding Natural Beauty (AONB), a 839 km^2 stretch of countryside from south Oxfordshire to Hertfordshire (Chilterns AONB, 2020). The AONB and the two catchments have predominantly underlying chalk geology with some glacial deposits and boulder clay cover (National River Flow Archive, 2022a-f), and comprise numerous habitats such as chalk grasslands, woodland and chalk streams. Land cover in the area is predominantly arable with some grassland and woodland cover, and mostly rural communities outside of the major cities and towns such as Hemel Hempstead, Welwyn Garden City and St. Albans (National River Flow Archive, 2022a-f).

The rivers Beane and Mimram form the Upper Lee catchment, and the Ver, Gade, Bulbourne, Chess and Misbourne for the Colne catchment are used to address the aims of this thesis (Figure 2.1). The rivers studied within the catchment range from poor to moderate ecological status, largely due to poor or moderate macrophyte and phytobenthos conditions (Environment Agency, 2021a and b). This assessment has only represented aquatic taxa for reasons outlined in Chapter 1. Reasons for the poor to moderate ecological status are mostly due to physical modifications and pollution from sources including agriculture and urban/transport (Environment Agency, 2021a and b). All of the study rivers are chalk streams and all sites are temporary streams. Although water abstraction affects flow regimes within these catchments, the streams are naturally intermittent, with flows occurring when the water table is above the channel bed (Chapter 1.2.1).

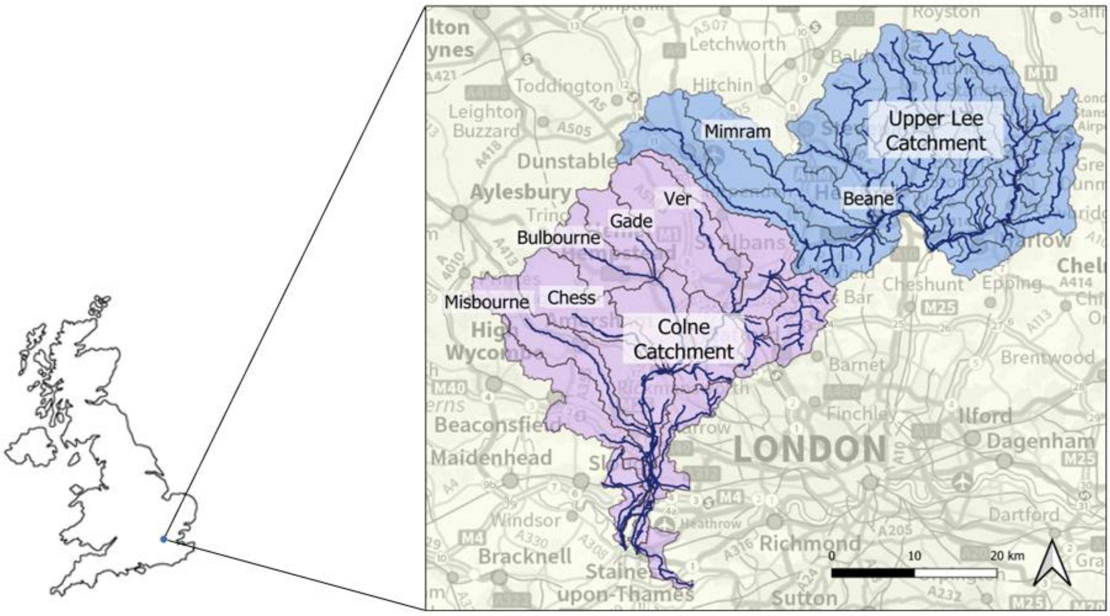

Figure 2.1. The location and a map of the study catchments (Colne and Upper Lee) in the UK. The map of the catchments highlights the Colne (purple shading) and the Upper Lee (blue shading) with main rivers and tributaries represented as dark blue lines.

2.2 Dry-phase data collection methods

Two biological groups were selected as potential biomonitors for environmental variables indicative of human impact: plants and ground-dwelling invertebrates. As described in the introduction (section 1.4.1), both plant and invertebrates have qualities necessary for an 'ideal' biomonitor such as being easily sampled, responsive to change and their ecological preferences are well-known, making them suitable biomonitors for the dry phase. Additionally, their use in perennial streams and marginal habitats, further supports their use as potential dry-phase biomonitors (Birk et al., 2012). Plants are typically more responsive to changes in nutrients and shading (Stromberg & Merritt, 2016), whilst invertebrates are known to respond to changes in habitat structure, such as sediment composition (Crist et al., 2005). Therefore, to effectively monitor dry-phase habitats both taxonomic groups are needed to cover a range of environmental variables.

2.2.1 Dry-phase plant survey methods

Dry-phase plant community data were collected using a modified version of LEAFPACS2 (WFD-UK TAG, 2014; formerly Mean Trophic Rank; Holmes et al., 1999; similar to that in Stubbington et al., 2019), which was expanded beyond aquatic macrophytes to include terrestrial taxa. The presence and estimated percentage cover of each taxon of aquatic, semi-aquatic and terrestrial plants were recorded at each site. Visual percentage cover estimates have been widely used in plant ecology to effectively characterise communities and to monitor community responses to environmental variability (Greig-Smith, 1983; Kennedy & Addison, 1987; Bonham and Clark, 2005). Total cover of all taxa combined may exceed 100% due to the different layers that may occur due to plant height differences (Greig-Smith, 1983).

At each site, a 100 m section was measured by selecting two bankside points, to define the survey reach (Holmes et al., 1999; WFD-UK TAG, 2014). In-channel communities were surveyed at each site, with the area at the bottom of the stream between the two bank margins defined as in channel. Bank and riparian vegetation were also surveyed but are not considered further, based on preliminary analyses. Surveys were conducted in channel by crossing from bank to bank in a zigzag formation, as per WFD-UK TAG (2014). This was repeated over the 100 m survey section at least twice, or until percentage cover estimates were deemed accurate. Once vegetation had reached peak growth in the summer months, crossing the channel became more difficult at two sites on the River Ver, which may have reduced the efficiency and accuracy of percentage cover estimates.

Taxa were recorded to species in most cases. In some circumstances, such as when riparian areas had been mown or in earlier surveys when plants which are difficult to identify without flowers or fruits had not fully grown, taxa were recorded to as low a taxonomic resolution as possible (e.g. Poaceae spp., *Ranunculus* spp.). Where taxa (e.g. *Galium* spp.) could not be identified to species, a sample was taken and further identified in the laboratory. I conducted all plant surveys, facilitating consistent taxa identification and percentage cover estimations, and avoiding variation in estimations between surveyors (Greig-Smith, 1983; Kennedy & Addison, 1987).

2.2.2 Dry-phase invertebrate sampling methods

Pitfall traps are a method extensively used to examine terrestrial invertebrate community composition, particularly for ground-dwelling invertebrates such as Araneae, Carabidae and Formicidae, which are the focus of this project (Spence & Niemelä, 1994; Wishart, 2000; Work et al., 2002; Corti et al., 2013; Skvarla et al., 2014). A pitfall trap consists of two plastic cups with a diameter of 10 cm, placed into a hole in the sediments to a depth at which the rim of the cup is flush with the soil/sediment. The traps are filled with a preservative (typically an ethylene-glycol solution) then left for a period of time before the trap is collected, by removing one of the cups to empty the sample for preservation and leaving the other in the ground to reset.

Pitfall traps should be spaced apart (> 1 m) to avoid depleting populations and increase the richness of taxa caught (Ward et al., 2001; Skvarla et al., 2014; Webb et al., 2017).

Recommended pitfall trap numbers per site range usually between 4-11, with 8-11 being the ideal to capture 70-80% of taxa present (Corti et al., 2013). The method is passive, as traps are left for invertebrates to fall into rather than actively searching for invertebrates (Wishart, 2000), meaning sampling can occur for longer periods (days to weeks), rather than for minutes to hours as with hand searching and quadrat sampling. Pitfall traps allow the collection of invertebrates during both day and night, which is useful as some families/groups such as Carabidae are most active at night (Wishart, 2000; Gobbi et al., 2018) and can be missed by other methods such as hand searching and quadrating which require daylight. Sampling throughout a diel cycle is particularly useful when sampling dry riverbeds which are subject to higher temperatures and low moisture availability during the day, meaning some invertebrates become more active at night (Broza, 1979). Pitfall traps are simple in design, require no expensive or specialist equipment, and are not impacted by operator skill, meaning that any help I received during fieldwork and my own increasing experience did not influence the taxa caught (Work et al., 2002; Skvarla et al., 2014).

The limitations of pitfall sampling include their characterisation of activity densities (mean number of taxa captured per trap) rather than absolute abundances, meaning they are influenced by vegetation, weather and species/organism behaviour (Corti et al., 2013; Engel et al., 2017). A higher vegetation density can mean that certain organisms or species have reduced movement and less likely to encounter the trap, and inclement weather can also reduce activity levels (Corti et al., 2013; Engel et al., 2017). Differences in species morphology, relating to mainly body size, can mean that more larger taxa are captured because smaller taxa can escape more readily due to the material of the trap supporting their small mass (Luff, 1975; Wishart, 2000; Skvarla et al., 2014). Behavioural differences also introduce a bias towards the capture of more mobile/active species such as Carabidae and Lycosidae (Skvarla et al., 2014), which are more likely to encounter the traps although sedentary taxa are still captured.

2.3 Characterising environmental variables

The Modular River Survey is a method that enables citizen scientists to record and monitor the physical habitat of rivers and streams (Gurnell et al., 2016). It includes the Modular River Physical survey (MoRPh), which was used to assess the study sites. The MoRPh survey relates the influence of geomorphology (the channel shape and physical characteristics i.e. sediment characteristics) to the hydrology of the stream, focusing on the physical structures relevant to the ecology (England et al., 2017; Beach et al., 2018). MoRPh also incorporates both natural features (e.g. sediment composition, vegetation, channel shape and pattern of flow types) and human pressures such as bank modifications and artificial land use (England et al., 2017; Shuker et al., 2017).

For each survey, the dimensions of the river are noted: the water width, water depth, bank height, bank-full width and MoRPh width (i.e. channel width including any marginal areas; England et al., 2017). The length of the survey is determined by the MoRPh width and is approximately double (e.g. 5 m MoRPh width means a 10 m survey length is needed). MoRPh is currently not suitable for any river wider than 30 m. All of the rivers and streams surveyed for this project were either < 5 m or between 5 m and < 10 m, falling into the 10 m and 20 m survey length categories, respectively.

The survey includes three lateral sections: the channel bed, bank face and channel margins, and bank top. The latter section extends 10 m from the bank top, recognising the influence of bank top land use and vegetation on the hydrology (England et al., 2017; Beach et al., 2018). Within each section, features are recorded based on categories relating to a percentage abundance/area: A (absent), T (trace, <5%), P (present, 5-<33%) and E (extensive, >33%). Vegetation morphotypes are recorded, with distinctions for terrestrial vegetation made mostly according to vegetation height, and for aquatic vegetation according to leaf shape and whether they are emergent or submerged (Table 2.1). For the bank top, land use, natural vegetation cover, non-native vegetation and water features (ponds, wetlands and tributaries) are recorded. Bank profile, materials, features (e.g. a berm or cliff) and vegetation (including marginal aquatic vegetation) are recorded for the bank face and channel margins. For the channel bed, information is gathered on channel bed materials, flow types, channel features (e.g. exposed boulders, pools and riffles) and aquatic vegetation (Table 2.1). I adapted this standard method to also record terrestrial morphotypes in-channel.

Table 2.1. The variables collected during MoRPh surveys and a description of each category as defined in the MoRPh manual (Gurnell et al., 2016).

MoRPh variables	Category descriptions
Flow types	Free fall = near-vertical falling water with no contact to the channel bed Chute flow = steep water surface, mostly with contact to the channel bed Broken waves = waves that have a foaming/breaking crest Unbroken waves = waves which do not have a foaming/breaking crest Ripples = small waves which move gradually Smooth = water that is clearly moving downstream but has no features

	No perceptible flow = water is not moving Dry channel = no water in the channel
Sediment types	Artificial = if artificial materials obscure the natural sediments Bedrock = exposed bedrock Boulder = mineral, > 256 mm diameter Cobble = mineral, >64-256 mm diameter Gravel-pebble = mineral, >2-64 mm diameter Sand = mineral, > 0.0625-2 mm diameter Silt = mineral, 0.00195-0.0625 mm diameter Clay = mineral, < 0.00195 mm diameter Organic = intact dead plant matter (e.g. leaves, twigs) Earth = a mixture of mineral and organic matter Not visible = if natural sediments are obscured from view
Terrestrial vegetation	Unvegetated Mosses/lichens Short/creeping herbs and grasses Tall herbs/grasses Scrub or shrubs Saplings or trees
Aquatic vegetation	Lichens, mosses and liverworts Emergent broad-leaved = above the water surface, leaf length < 4 × leaf width Emergent linear-leaved = above the water surface, leaf length > 4 × leaf width Floating leaved = rooted to the bed but with leaves on the surface Free floating = leaves on or below the surface and not rooted Submerged broad-leaved = below the water surface, leaf length < 4 × leaf width Submerged linear-leaved = below the water surface, leaf length > 4 × leaf width Submerged fine-leaved = below the water surface, string like leaves Filamentous algae = fine filaments covering the channel bed or other plants below the surface

Bank profile	Vertical Vertical with top overhang = banks with a vertical face and only a shallow vegetated section protruding over the edge Undercut or vertical with undercut = banks with/without a vertical face that have eroded away at the base, leaving an overhanging section Vertical with toe = banks with a vertical face that then shallow into the water Steep = banks > 45 degrees Gentle = banks < 45 degrees Composite = composition of differing slope angles Reshaped = banks have been obviously made steeper, wider, narrower, etc. Artificial two-stage = the banks moved further into the riparian zone Embanked = an embankment at the bank edge Set-back embankment = an embankment has been created away from the channel Poached bank = evidence of trampling

Survey data can be entered into the Modular River Survey database (Gurnell et al., 2016) alongside at least 1-4 photos taken at the site facing upstream, downstream and across the river. From this, 14 indices are calculated automatically by the MoRPh system to reflect the physical habitat and vegetation (Table 2.2).

Table 2.2. Indices calculated in the MoRPh system and the range for the index. T = Trace, P = Present and E = Extensive abundance/area category.

	Index	**Index range**
Channel characteristics	1: Number of present/extensive flow types	1-10 (count)
	2: Highest energy present/extensive flow type	Flow > Chute > Broken standing wave > Unbroken standing wave > Rippled > Smooth > No perceptible flow > Dry

	3: Number of present/extensive bed material types	1-10 (count)
	4: Coarsest present/extensive mineral bed material type	Bedrock > Boulder > Cobble > Gravel-pebble > Sand > Silt > Clay
	5: Average bed material size (phi units)	The score is based on abundance categories: T=2, P=19, E=67, multiplied by material value from boulder = - 9 to clay = 10. Higher values reflect smaller sizes.
	6: Average bed material size class	Bedrock, boulder, cobble, gravel-pebble, sand, silt and clay
	7: Extent of superficial bed siltation	Patchy thin silt layer: T=1, P=9.5, E=33.5 Continuous silt layer: T=2, P=19, E=67
	8: Channel physical habitat complexity	1 (minimal complexity) – 10 (extremely high complexity) base on the weighted average of four sub-indices
	9: Number of aquatic vegetation morphotypes	0 (no aquatic vegetation) – 10 (all aquatic vegetation morphotypes present)
Riparian characteristics	10: Riparian physical habitat complexity	0 (extremely low complexity) – 10 (extremely high complexity)
	11: Riparian vegetation structural complexity	Number of riparian vegetation morphotypes with P or E abundance
Human pressures	12: Degree of human pressure imposed by bank top land cover	0 (minimal modification) – 10 (high modification)
	13: Channel reinforcement	0 (no reinforcement) – 10 (fully reinforced)
	14: Non-native invasive plant extent	0 (no non-natives) – 10 (extensive and diverse invasion)

2.4 Data analysis

In all research elements (Chapters 3-5), both a univariate (biological metrics) and multivariate (community composition) analytical approach were used to fully represent community responses to environmental variables. All statistical data analysis was conducted in R (the version dependent on chapter) and all data preparation was conducted in Microsoft Excel.

2.4.1 Biological metrics

In Chapters 3-5, biological metrics were calculated to summarise communities for use in analyses, all of which can be responses to environmental variability. Richness, a count of the different taxa, was calculated either to represent overall richness (taxonomic) or of certain taxonomic groups (e.g. grasses and Ephemeroptera, Plecoptera and Trichoptera; EPT). The Shannon-H diversity index uses taxa richness and evenness (i.e. the relative abundance of each taxon) to give an overall diversity value which typically ranges between 1.5 and 3.5. Berger-Parker dominance indicates the proportional abundance of the most abundant taxon, which can be useful for measuring impacts such as nutrient enrichment.

Functional diversity metrics were also analysed in Chapter 3: functional richness, diversity and redundancy. Taxa have specific functional traits relating to their biological (e.g. morphology, feeding strategies, etc.) and ecological (habitat tolerances, distribution, etc.) characteristics, and can respond to environmental variables (Statzner et al., 2001). Trait-based analyses can have advantages over taxonomic analyses such as providing a generic result regardless of region, unlike the taxonomic differences seen geographically, (Menezes et al., 2010) and simplify species responses (Zakharova et al., 2019), thus they were incorporated into Chapter 3. Functional richness measures the functional niche space occupied by the taxa in a community and functional diversity describes the range of traits and their distribution within a community (Schleuter et al., 2010). Functional redundancy is the difference between functional diversity and taxonomic diversity, and the taxa which contribute comparably to ecosystem functioning.

In addition to diversity metrics, biomonitoring indices were calculated to represent aquatic macroinvertebrate and plant communities in Chapters 3 and 4. In Chapter 3, the Whalley Hawkes Paisley Trigg (WHPT; Paisley et al., 2014), Drought Effect of Habitat Loss on Invertebrates (DEHLI; Chadd et al., 2017) and Empirical-weighted Proportion of Sediment-sensitive Invertebrates (EPSI; Turley et al., 2016) indices were used to characterise macroinvertebrate communities. These biomonitoring indices were developed from expert judgement, with individual taxa scores assigned based upon their sensitivity or tolerance to stressors. WHPT ASPT was developed from the well-known BMWP index (Armitage et al., 1983), and measures the sensitivity of taxa to organic pollution, however, WHPT ASPT has also been used as a measure of overall habitat degradation and was therefore selected as a potential index to represent communities. The DEHLI index quantifies macroinvertebrate community responses to changes in flow and the habitat availability that occur during drought (Chadd et al., 2017; Sarremejane et al., 2019). DEHLI was selected over the well-know LIFE index because macroinvertebrate responses to hydrological variability are already well studied. EPSI is an index that measures the sensitivity of taxa to fine sediments and was used to characterise community responses sediment quality (Turley et al., 2016). In Chapter 4, the Ellenberg index, specifically Ellenberg nitrogen, was used to represent plant communities (Hill et al., 1999). The Ellenberg index calculates the overall mean tolerance score of a community to sediment nitrogen concentrations, and other stressors, based upon individual taxa tolerances. Ellenberg N can also be considered a measure of general sediment fertility, indicative of nutrient concentrations including phosphorus and nitrogen.

2.4.2 Ecological modelling

Ecological modelling is the use of mathematical models to understand complex relationships and interactions between different biological (i.e. species richness, abundance and diversity), chemical (i.e. soil and water chemistry) and physical (i.e. channel morphology, sediment composition) variables in an ecosystem. Models can also make predictions and simulations based upon these relationships on how these ecosystems may change.

In Chapters 3-5, linear regression modelling (general and generalised) was used to analyse the biological metrics described above (further details of which metrics were used can be found in sections 3.2, 4.2 and 5.2). These models identify associations between the dependent variable (response variable) and one or more independent variables (explanatory variables), and model predictions based upon these association. Ecological data can often be grouped by a random variable (random factor) which is not of interest in the study but can influence the independence of data points (Bolker et al., 2009; Bates et al., 2015). A mixed model approach accounts for this random variation through incorporating both random factors and fixed factors (explanatory variables of interest) in the model. Data collected throughout this thesis had potential to be influenced by random factors, such as site or date, and so a mixed modelling approach was used to improve modelling accuracy. Where multiple models were conducted, the Akaike's Information Criterion (AIC; Akaike, 1973) values were used in selecting the model that is the most adequate model or best fitting. Models with the lowest AIC value (ΔAIC) or values ΔAIC ≤ 2 were considered the best fitting model or models.

2.4.3 Model assumptions

Linear models make assumptions regarding normality, homogeneity, independence of variables, overdispersion and zero-inflation. Assumptions were tested on both the raw data and the model residuals (the differences between the observed and predicted values of the data). Ecological data often does not conform to the model assumptions of normality and homogeneity, are often not wholly independent with collinearity between variables, and can often be over-dispersed or zero-inflated (Bolker et al., 2009; Zuur & Ieno, 2016).

A normal or Gaussian distribution is a probability distribution in which response variable data points fall symmetrically around the mean, where data points occur more frequently around the mean, forming a bell-curve. Ecological data can also fit distributions which are non-normal such as Poisson (count data) and beta (proportional data) distributions. The homogeneity of variance (homoscedasticity) means any random variance in the data is equal across all data points. Variables (both dependent and explanatory) should also be independent from one another and not connected in any way not accounted for in a model. Multi-collinearity occurs where two or more explanatory variables are correlated in a linear manner. This influences the accuracy of the model, potentially causing the parameters to be incorrectly deemed insignificant (Zuur et al., 2010). Finally, overdispersion occurs when the observed variance in model residuals is higher than that predicted by a theoretical model, and zero-inflation is a high number of zeros in the data.

Assumptions of normality of the response variables were checked initially using both graphical checks (histograms and QQ-plots) and Shapiro-Wilk’s tests (Shapiro & Wilk, 1965). Both methods, in particular the graphical checks, inform decisions about which mixed model (LMM or GLMM) and distribution to use (Gaussian for LMM and Poisson for GLMM; Zuur et al., 2009). QQ-plots with data points following roughly a linear line through the plot and histograms which follow the bell curve distribution were considered indicative of a normal distribution. Then during model validation, histograms and QQ-plots were also applied to the model residuals to assess normality.

The homogeneity of each response variable was assessed visually for categorical and continuous variables using boxplots and scatterplots respectively, by plotting the response variables against the fixed factors. Categorical variables were considered of equal variance if the box and whiskers followed a similar distribution for each category. Continuous variables were considered of equal variance if data points follow a similar distribution along the independent variable gradient. Following modelling, the residuals were visually assessed using scatterplots, supported by Levene's tests (Levene, 1960). Residuals were considered to be of equal variance if data points showed no obvious patterns around the central line.

Data were collected from multiple sites, with differing flow regimes, across multiple rivers over multiple dates. Therefore, to count any potential violations of the assumption that data were independent, random factors were incorporated into models. Data were explored initially by plotting response variables against potential random factors (e.g. variables relating to site, time and flow). If a random factor resulted in a model with a singular fit (i.e. it did not impact on the independence of variables) it was removed.

Outliers were visually assessed for the categorical and continuous variables using boxplots and scatterplots respectively, and supported by Cook's distance plots, which were also used to assess the model residuals.

Overdispersion and zero-inflation within the data were both assessed on the model residuals using the 'check_overdispersion' and "check_zeroinflation" function in the "Performance" package in R (Lüdecke et al., 2020). If the models have a dispersion ratio value > 1, supported by a P value < 0.05 then models are overdispersed. If the number of observed zeros is larger than the number of predicted zeros, the zero-inflation function will indicate zero-inflation within the data (Lüdecke et al., 2020).

If assumptions of the raw data were met then a linear mixed model (LMM) was used, and if assumptions of the raw data were not met then a generalised linear mixed model (GLMM) was used. Where model residuals did not meet assumptions, further distributions were tested or failing that, the response variables were transformed.

2.4.4 Generalised Linear Mixed Models (GLMM)

Generalised linear mixed models allow for data that do not meet the assumptions of a Gaussian distribution to be modelled accurately through specifying error distributions and link functions. For data with response variables consisting of count data, such as taxa richness, a Poisson distribution and log link function or square-root link function were initially used in the GLMM. If the model residuals of this GLMM were over dispersed a negative binomial GLMM was used, which does not assume that the variances are equal around the mean (Feld et al., 2016; Zuur & Ieno, 2016). Where zero-inflation occurred a hurdle model with a Poisson distribution was used, as these models make assumptions that zeros in the data do not occur by chance (Brooks et al., 2017). For proportional response variables, a GLMM with a beta distribution and logit link function was used.

2.4.5 Community analysis

Community composition analysis is another facet of understanding biotic responses to environmental variables including those indicative of human impacts, and is enabled by measures that quantify compositional dissimilarity between communities. The Bray-Curtis dissimilarity was used in this thesis and indicates the differences in taxa occurrences and abundances between samples, given as a number between 0 (all are the same taxa between samples) and 1 (no shared taxa between samples). This measure of dissimilarity was used because it is not a true distance, and therefore does not assume multivariate normality (unlike Euclidean distances) and often community composition data is non-normal (Anderson & Santana-Garcon, 2015).

Using Bray-Curtis dissimilarities, three methods were used to analyse community compositional changes: permutational multivariate analysis of variance (PERMANOVA; Anderson, 2014) and non-metric multidimensional scaling (NMDS). NMDS simplifies data from multiple dimensions into a few, typically two, dimensions, which can then be visualised as an ordination. NMDS is rank-based, comparing which communities are most or least distant from each other and ranking and plotting them accordingly (Rabinowitz, 1975). For NMDS ordinations a stress value is assigned to each dimension, with values > 0.2 generally considered uninformative. However, stress values are influenced by sample sizes, meaning in larger datasets, higher values can still be considered informative (Dexter et al., 2018). PERMANOVA identifies differences in community composition in relation to environmental variable groups using a dissimilarity measure (e.g. Bray-Curtis; Anderson, 2014). PERMANOVA was selected because it is semiparametric, meaning there is flexibility around assumptions such as normality and zero-inflation, and also allows the use of ordinal data (Anderson, 2014). The main assumption of NMDS and PERMANOVA is that the distribution of samples within-groups is homogeneous among groups, although PERMANOVA is robust to heterogeneity in balanced designs than other methods (i.e. ANOSIM; Anderson and Walsh, 2013). This assumption was checked using the ‘permdisp’ function from the vegan package (Oksanen, 2015). Similarity Percentage Analysis (SIMPER) was used to identify species which contribute towards the dissimilarity between pairs of environmental variable groups, as detected by the PERMANOVA analyses (Clarke & Gorley, 2006). SIMPER results described the contribution of each species to the dissimilarity, their average abundance in each group.

Beta diversity describes differences in community composition among sites (spatial) or at one site over time (temporal) and is another component of community composition and biodiversity (Anderson et al. 2011). Total beta diversity comprises turnover and nestedness-resultant dissimilarity, which is not considered true nestedness but will be referred to hereafter as nestedness (Baselga, 2010). Turnover describes the substitution of lost species by other species between sites, and nestedness, the variability in communities according to richness differences (Baselga, 2010; Aspin et al., 2018). In this research, beta diversity was measured using Sørensen dissimilarity (βsor), turnover using the Sørensen dissimilarity index (βsim) and nestedness as the difference between the two (βnes) using the package 'betapart' (Baselga & Orme, 2012).

2.4.5.1 Taxon-specific responses

Two methods were used to analysis taxon-specific responses to environmental variables: Indicator Species Analysis (IndVal; de Caceres, 2010) and Threshold Indicator Taxa ANalysis (TITAN; Baker & King, 2010). IndVal is a widely used method to identify taxa associated with, and therefore potentially indicative of, categorical habitat conditions (e.g. land use; Dufrêne & Legendre, 1997). IndVal scores can be split into two components: specificity, the probability of taxa occurring at all sites within the habitat category, and fidelity, the probability of taxa being found only in the habitat category.

TITAN defines an ecological threshold on a continuous environmental gradient using both change-point analysis and IndVal (Baker & King, 2010). It uses IndVal scores to identify change points in taxa occurrence and abundance along the continuous environmental gradient, calculating the midpoint and magnitude of change to indicate taxa which increase or decrease along the gradient (Baker & King, 2010). Bootstrap resampling is used to produce diagnostic indices to indicate the quality of the response: purity (the number of bootstrap replicate responses which agree with the overall responses) and reliability (the proportion of bootstrap replicates with $P < 0.05$). For both these indices a value of ≥ 0.95 is considered pure or reliable (Baker & King, 2010).

Chapter Three: Macroinvertebrate community responses to habitat conditions across differing flow regimes

3.1 Introduction

Streams have long been subjected to various anthropogenic impacts, which influences the taxonomic composition of their resident macroinvertebrate communities (Dudgeon et al., 2006; Reid et al., 2019). In southern England, modifications to channel morphology have been made historically to accommodate water mills and agricultural activities including water-cress farming (Wilson et al., 2021). These systems also face increasing pressures from land use changes (e.g. agriculture and urban expansion), and both human-altered channel morphologies and anthropogenic land uses can increase fine sediment inputs into streams (Wood & Armitage, 1997; Jones et al., 2011). Concurrently, increasing demands for water supplies – particularly in regions with high and expanding urbanisation (e.g. southern England; Poff et al., 2003; Richter et al., 2003; Dumont et al., 2012) – coupled with climatic changes – potentially including an increase in the frequency and severity of both floods and droughts (Döll & Schmied, 2012; Watts et al., 2015) – are exacerbating hydrological variability in river ecosystems (Jones, 2013; Ledger & Milner, 2015).

Droughts manifest as low flows in perennial rivers (Wood and Petts, 1999; Dewson et al., 2007), rare drying events in near-perennial systems (Hill et al., 2019), and extended dry phases in seasonally intermittent streams (Sarremejane et al., 2020). Across these streams, low flows and drying can lead to reduced dissolved oxygen levels, increased channel temperatures and decrease the capacity for taxa to disperse (Williams, 1977; Boulton, 2003). The extremity of these conditions is influenced by the different flow regime responses to drought, which can in turn affect macroinvertebrate community responses and the potential recovery following a drought period (Boulton, 2003; Stubbington et al., 2015; Sarremejane et al., 2021;). The effects of drought on aquatic communities may be expected to manifest in different ways depending on the intermittence regime (Figure 3.1). The impacts may differ in morphologically modified channels, by further reducing hydrological variability, sediment complexity and vegetation diversity in already homogenous channels (Wood and Petts, 1994; Dunbar et al., 2009).

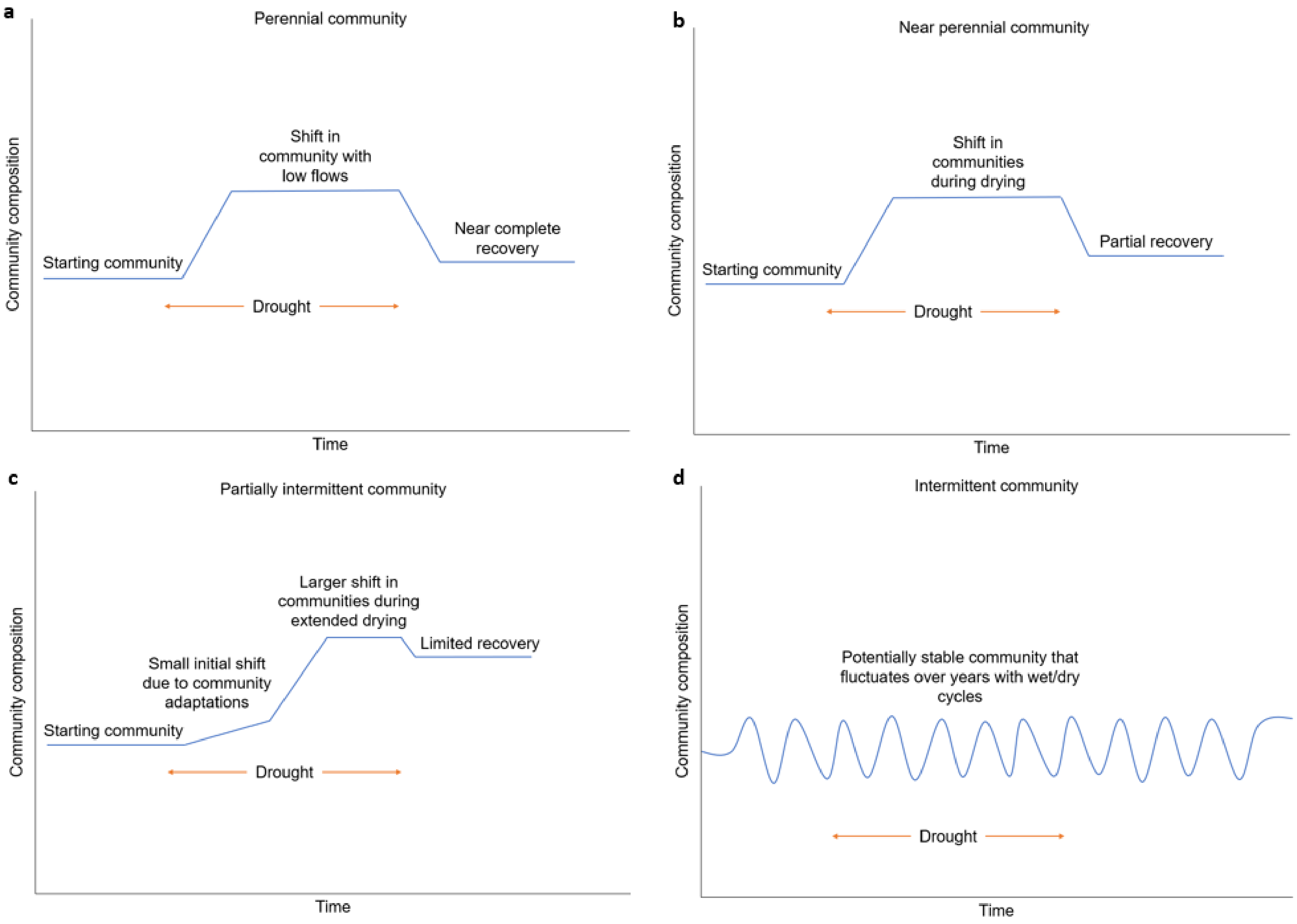

Figure 3.1. Conceptual models for the community responses to drought according to flow regime: a) perennial, b) near-perennial, c) partially intermittent (dry unpredictably) and d) intermittent. The community composition is arbitrarily defined.

River and stream ecosystems comprise a variety of spatiotemporally variable habitat patches with differing environmental characteristics, in particular reflecting variability in hydrology, sediment and vegetation (Rempel et al., 2000). Many freshwater taxa have specific environmental preferences (Extence et al., 1999), in particular reflecting flow conditions (e.g. rippled flow or broken waves, sensu Environment Agency, 2003; Shuker et al., 2017), sediment sizes (e.g. sand, gravels, cobbles; William & Mundie, 1978) and vegetation (structural morphologies e.g. broad-leaved, fine-leaved; Scheffer et al., 1984; Schröder et al., 2013; Beermann et al., 2018). Therefore, the spatiotemporal heterogeneity and diversity of these habitat qualities influence the taxonomic composition of instream communities including benthic macroinvertebrates.

Flow and sediment are closely linked, with declining flow velocities reducing bedload transport and increasing fine sediment deposition (Beermann et al., 2018; Blöcher et al., 2020), especially in low-energy systems such as chalk streams (Acornley & Sear, 1999). Vegetation also interacts with both flow velocity and sediment, with different plant morphotypes having contrasting effects on these physical parameters (Clarke, 2002; Gurnell, 2014). For example, the dissected leaves and trailing stems of dense *Ranunculus* stands—which often occur in perennial chalk streams—reduce flow velocities and increase fine sediment deposition, creating habitats suitable for other plant species (Clarke, 2002; Gurnell et al., 2006). Studies investigating macroinvertebrate community responses often focus on the independent and interacting effects of just one or two of these environmental factors (e.g. Rempel et al., 2000; Beermann et al., 2018; Blöcher et al., 2020), with few investigating the influence of all three (Khudhair et al., 2019), and none encompassing both perennial and intermittent flow regimes and quantifying interactive effects.

Macroinvertebrate communities typically differ between perennial and temporary streams (Datry et al., 2014a; Soria et al., 2019), and the latter largely comprise generalist taxa, with a few specialists also occurring in systems with predictable, long-term dry phases (Armitage & Bass, 2013; Bogan et al., 2017; Stubbington et al., 2017). Research exploring differences between macroinvertebrate communities in perennial and temporary streams have rarely focused on systems with impacted morphologies, with few studies characterising responses to hydrological variability and drought in regions dominated by modified channels (e.g. Sarremejane et al., 2019, 2020). As such, temporary stream restoration, and monitoring, typically rely heavily on approaches developed for perennial systems, leading to potential poor performance (Leigh et al., 2016; Stubbington et al., 2017). Additionally, macroinvertebrate communities change over time, responding to hydrological interannual variability including floods and droughts (Poff et al., 1997).

Morphological modifications may influence the survival of macroinvertebrates during extreme flow conditions due to resistance and resilience strategies (Dunbar et al., 2009). However, the differences in responses between perennial and intermittent communities over time, with particular interest in inferences to climate change, and how morphology can influence these temporal responses needs further study.

To address the knowledge gaps mentioned, the research presented in this chapter aims to characterise the independent and interactive macroinvertebrate community responses (both composition and as metrics such as taxa richness and indices) to spatial and temporal variability in flow, sediment and vegetation conditions. Sampling sites encompassed a range of flow permanence regimes (from perennial to intermittent) and morphological modification levels, which were sampled over a 23 year period). The results will inform the design of restoration schemes that support biodiversity within river networks by increasing morphological naturalness of sites spanning a breadth of flow permanence regimes. To address the aims of this chapter, I hypothesised that macroinvertebrate community compositional change, and community-based biological metrics increased, in response to increasing complexity in (H1) flow, (H2) sediment and (H3) aquatic vegetation structures, with (H4) responses to these environmental characteristics differing between perennial and intermittent macroinvertebrate communities. I also hypothesise that (H5) community composition differed over time with greater temporal change in communities at perennial compared to intermittent sites, in particular during droughts.

3.2 Methods

3.2.1 Study sites

The six study streams (Beane, Chess, Gade, Mimram, Misbourne and Ver) are located within the Colne and Upper Lee catchments, UK. All streams have underlying chalk geology, with some reaches having naturally intermittent flow regimes due to the porous nature of the chalk (Westlake et al., 1972; Shand et al., 2003). This natural intermittence is often exacerbated by anthropogenic impacts (e.g. water abstractions; Shand et al., 2003) and further impacted morphologically, influencing flow, for historic mills and water cress farms (River Colne Catchment Action Network, 2021; Ver Valley Society, 2021). The flow permanence regimes at the study sites included perennial (PR; 0% no flow; i.e. ponded, wet bed or dry bed states), near-perennial (near PR; >0-20% no flow), partially intermittent (partial IR; >20-60% no flow) and intermittent (IR; >60% no flow; sensu Sarremejane et al., 2019). Land use within the catchments is predominantly agricultural with increasing urban extent (summarised in Table 3.1).

Table 3.1. The land use percentage cover for the catchment of each of the six study streams (National River Flow Archive, 2021).

	Woodland	Agricultural	Grassland	Urban
Beane	10.9	59.5	16.7	12.9
Chess	17.9	34.5	33.5	12.4
Gade	17.1	36.3	25.0	21.5
Mimram	12.6	56.5	18.3	12.6
Misbourne	22.4	42.0	23.7	11.1
Ver	9.9	55.7	24.7	8.9

3.2.2 Macroinvertebrate dataset

A macroinvertebrate community dataset provided by the Environment Agency (EA) was used comprising 799 taxa in 20,175 samples collected between 1990-2019, from 97 sites on the six study streams. Data were harmonised and some sites were removed (as described below), to produce a final dataset.

Macroinvertebrate samples were collected using the standard 3-minute kick-sampling method, which represents all instream habitats in proportion to their occurrence, supplemented by a 1-minute hand search (ISO, 2012). Abundance recording methods varied among years; samples collected pre-1995 were recorded on a 33rd logarithmic scale (3, 33, 333) as opposed to actual abundance from 1995, and thus pre-1995 samples were removed from the dataset. Macroinvertebrates were identified to different taxonomic levels, mainly to genus or species but family (e.g. Chironomidae and other Diptera) and higher levels (e.g. Oligochaeta) for some taxa. The lowest possible taxonomic level was used in the dataset and the taxa list was harmonised across samples to ensure consistency in taxonomic resolution, following Sarremejane et al. (2019), who characterised macroinvertebrate communities in the same six study rivers as included here.

3.2.3 Site and sample selection

The first process of site selection involved prioritising sites (n = 31) with more temporal replicates (e.g. samples collected in most years) and which already had environmental data (see section 3.4.2). For the remaining sites (n = 66) without environmental data, further selections were made according to expert recommendations based on knowledge of site hydrology, geomorphology and vegetation, and again, prioritising those with higher replication (n = 38). From the prioritised sites (n = 69), two sites were excluded due to poor water quality, which may have influenced macroinvertebrate communities, masking the effects of the habitat conditions of interest. Five sites were initially excluded as sites were dry when environmental data were collected (see section 3.2.4). Environmental data were not always collected at the time of the macroinvertebrate sampling and would therefore not be representative of the conditions found during the flowing phase needed for macroinvertebrate community survival.

Finally, the EA dataset included surveys conducted in all seasons, introducing seasonality as a potential influence on macroinvertebrate communities. Seasonal influence upon macroinvertebrate communities is well documented (Carlson et al., 2013), therefore – informed by both previous research (Environment Agency, 1999; Šporka et al., 2006) and data exploration (box plots, analysis of variance and permutational multivariate analysis of variance, Anderson, 2014; see section 2.5.2) – summer and winter surveys were removed. Data exploration revealed differences in community composition and biological metrics (e.g. taxonomic richness) between seasons when winter samples were included, and previous research suggesting spring and autumn macroinvertebrate samples as the least likely to be influenced by season (Environment Agency, 1999; Šporka et al., 2006). Linear mixed models (LMM) and generalised linear mixed models (GLMM) identified differences between biological metrics between spring and autumn communities, which were therefore combined in later analysis. PERMANOVA identified compositional differences between spring and autumn communities, and each season was therefore analysed separately.

3.2.4 Environmental data

Each site’s flow permanence regime was characterised primarily using monthly observations of instream conditions made by the EA throughout the macroinvertebrate sampling period (1995-2018). These observations characterised hydrological state as overbank flow, high flow, flowing, low flow, trickle flow, ponded, wet bed and dry bed. Macroinvertebrate sampling sites were matched to observation sites with 39 of the sample sites being co-located, seven <100 m apart, ten 100-500 m apart and eight 500-800 m apart, and all experiencing comparable flow conditions. Observations were used to calculate the number of months since no flow (i.e. ponded, wet bed or dry bed states; hereafter, ‘month since’). Additional information on abstraction changes and licences in the area over the survey period were used to infer abstraction influence over time. A drought period occurred between 2005-2008, with the years before 2005 considered as pre-drought and those after 2008 considered post-drought.

To characterise the hydrology, sediment characteristics and in-channel vegetation of each site Modular River Physical Surveys (MoRPh; Shuker et al., 2017) data were used (see section 2.4.x for full details on each variable). Existing MoRPh survey data were accessed via http://modularriversurvey.org/ and matched to macroinvertebrate sampling sites using grid references, for 31 of the 69 sites. The remaining 38 sites were surveyed on 25th–26th Nov 2019 and 20th Jan 2020, as described in Chapter 2.3. Despite limited characterisations of vegetation, MoRPh surveys were done in winter for logistic reasons and produced acceptable results. For the 62 finalised sites, the 14 MoRPh indices were calculated (see section 2.3). Indices 1–7 and 9 were initially selected to represent the complexity of flow, sediment and in-channel vegetation. Index 9 (the number of vegetation morphotypes; *NumVegMorph*) was then adapted by splitting cover into four categories (absent, minimal = <5%, moderate = 5-33%, and extensive = >33%) for each of six morphotypes (emergent linear leaved, emergent broadleaved, submerged fine leaved, submerged broadleaved, submerged linear leaved, filamentous algae). Data exploration was conducted to assess the suitability of the categorical indices (2,4 and subsets of 9) and continuous indices (1, 3, 5, 6, 7, 9). For categorical indices, the basic R function *table* was to assess the distribution and balance of samples across each index category, resulting in removal of four subdivisions of index 9 with low replication (e.g. submerged fine leaved vegetation cover) and two indices due to imbalance between categories (index 4: coarsest sediment size, and subset 9: emergent linear leaved). For categorical variables, scatterplots were produced to assess distributions, on the basis of which three indices were removed due to representation by other indices (e.g. average bed sediment size).

The number of flow types (NumFlow; index 1) and the highest energy flow type (*HighestEFlow*; index 2) were selected to represent flow complexity, the number of sediment types (*NumSed;* index 3) and the extension of silt covering the channel bed (*SiltBedCover* index 7) to represent sediment complexity, and *NumVegMorph* (index 9) and emergent broad-leaf vegetation cover (*EmBroadVeg*; index 9 subdivision) to represent in-channel vegetation complexity.

Table 3.2. The 62 sites included in the final dataset and their environmental properties, as characterised by flow permanence regime (FPR) and six MoRPh indices representing flow complexity, sediment complexity and in-channel vegetation. IR, intermittent river; partial IR, partially intermittent river; near PR, near-perennial river; PR, perennial river.

Waterbody	Site name	FPR	Highest energy flow type	Number of sediment types	Extent of silt over bed	Number of aquatic vegetation morphotypes	Emergent broadleaf presence
BEANE	Below Church End Ford, Walkern	IR	No perceptible flow	5	1.9	0	Absent
	At Aston End Pumping Station	partial IR	Smooth	1	0	1	Absent
	Watton-At-Stone	partial IR	Smooth	3	0	2	Absent
	At Hartham Common	PR	Smooth	3	0.95	1	Absent
	At Waterford	partial IR	Smooth	3	0	0	Absent
	U/S Frogmore Hall	IR	Smooth	2	0	2	Moderate
	U/S Watton-At-Stone	near PR	Unbroken standing waves	2	0	2	Moderate

	U/S Mill Lane	partial IR	Smooth	0	0	0	Absent
	U/S Stapleford	near PR	Unbroken standing waves	3	0	1	Absent
CHESS	Above Chenies STW	PR	Unbroken standing waves	3	0.1	1	Extensive
	Below Broadwater Bridge	partial IR	Smooth	3	3.35	0	Absent
	Above Valley Farm Ford	PR	Broken standing waves	3	0	1	Absent
GADE	Above Gade Bridge Lane, Hemel Hempstead	PR	Rippled	2	0.1	2	Moderate
	At Great Gaddesdon, D/S Pipers Lane	partial IR	Rippled	3	0.1	2	Extensive
	At Gade Water Nurseries	PR	Rippled	4	1.9	0	Minimal
	Gade Bridge Park Behind Park and Ride	PR	Unbroken standing waves	2	0	1	Minimal

	Below Fish Farm at electric sub station	near PR	Rippled	3	0.2	3	Moderate
	Us Link Road	PR	Smooth	0	0	2	Minimal
	U/S Plough Roundabout	near PR	Rippled	3	0.95	1	Absent
	D/S Plough Roundabout	near PR	Smooth	1	0	1	Absent
	U/S Piccotts End Ps	near PR	Unbroken standing waves	3	0	1	Extensive
MIMRAM	Below Whitwell, at Hoo End, Whitwell	near PR	Rippled	1	0	3	Extensive
	At Welwyn Town	near PR	No perceptible flow	1	6.7	2	Extensive
	Above Welwyn Town	partial IR	Unbroken standing waves	2	0	3	Moderate
	At Digswell Park	partial IR	Smooth	2	0	2	Moderate
	At Whitwell	near PR	Free fall	3	3.35	2	Moderate
	At Codicote Bottom	near PR	Unbroken standing waves	2	0	1	Minimal
	At Panshanger	PR	Rippled	4	0.95	2	Moderate

	Below Codicote Bottom	partial IR	Unbroken standing waves	2	0	2	Moderate
	D/S Kimpton Mill	PR	Rippled	1	0	3	Extensive
	Within Sherrardswood School control site	near PR	Rippled	4	0	3	Extensive
	Within Sherrardswood School - Site of Old Weir	near PR	Rippled	1	0	1	Moderate
	D/S Hertford Road	partial IR	No perceptible flow	3	0.95	3	Extensive
	At Digswell Lakes Nature Reserve (D/S)	PR	Smooth	1	0.2	1	Absent
	Tewin Water School	PR	Free fall	3	0.95	2	Minimal
MISBOURNE	Below Deep Mill Lane, Great Missenden	partial IR	Smooth	4	6.7	0	Moderate
	At Little Missenden	partial IR	Rippled	4	2.85	2	Extensive
	At Bottom House Farm Lane, Chalfont St.Giles	IR	Rippled	4	0	2	Moderate
	At Community Centre, Chalfont St.Peter	IR	Dry	1	0	0	Moderate
	D/S Gerrards Cross STW	PR	Rippled	3	1.9	2	Moderate

	Above Old Amersham at A415	partial IR	Unbroken standing waves	5	0	1	Moderate
	U/S Gerards Cross STW	PR	Unbroken standing waves	2	0	1	Extensive
	Below Denham Village	PR	Smooth	4	6.7	1	Moderate
	Below Misbourne Farm	partial IR	Rippled	3	0	0	Minimal
	Below Quarrendon Mill	partial IR	Smooth	4	0.95	2	Moderate
	Below Bottom House Farm	IR	Rippled	3	0	1	Absent
	D/S Little Missenden GS	near PR	Unbroken standing waves	4	0.2	2	Moderate
	Amersham Cemetery	partial IR	Unbroken standing waves	4	1.9	0	Absent
VER	Above Pre Mill House, St. Albans	near PR	Rippled	3	0.95	2	Extensive
	At River Hill, Flamstead	IR	No perceptible flow	0	6.7	2	Extensive

	At Chequer Lane, D/S Redbourne	partial IR	No perceptible flow	2	0	2	Extensive
	Below Redbourne Road (A5183)	partial IR	Unbroken standing waves	3	0.95	5	Extensive
	Below Burydell Lane, Park Street	PR	Broken standing waves	3	0	1	Minimal
	Above Colne	PR	Unbroken standing waves	2	0	4	Absent
	Below Redbournbury Farm Ford	partial IR	No perceptible flow	0	0	2	Extensive
	At Sopwell	near PR	Smooth	0	0	1	Moderate
	Below Kingsbury Mill, St Albans	near PR	Rippled	2	0.1	0	Minimal
	Us Shafford Farm next to Works	PR	No perceptible flow	1	6.7	4	Moderate
	Us Shafford Farm next to A5183	PR	Smooth	3	0	2	Moderate
	Hyde Lane	PR	Smooth	0	0	2	Moderate

	Above Cottonmill Bridge and Weir	PR	Rippled	0	0	1	Moderate
	New Barnes Mill	PR	Smooth	2	6.7	0	Absent

3.2.5 Perennial and intermittent community datasets

To enable comparison of community responses at sites with contrasting flow permanence regimes, two macroinvertebrate datasets were created, one including all samples from intermittent sites (n = 100) and one including 100 randomly selected samples from perennial sites. Three samples were moved from the intermittent dataset due to the low replication of sites with smooth flow as the HighestEFlow, although these were retained for visual analyses, and ten samples were removed from the perennial dataset due to the low replication of free fall and broken wave sites as the HighestEFlow.

3.2.6 Statistical analysis

Three separate analyses were conducted for each method described below, one for the dataset which included all flow regimes (PR, near PR, partial IR and IR; termed all-regime hereafter), and separate analyses for perennial and intermittent datasets. All data analyses were conducted in R version 4.0.0 (R Core Team, 2020). Prior to analysis, initial data exploration was conducted using both Variance Inflation Factors (VIF; see section 2.5.1) and correlation plots to check for collinearity between independent variables (i.e. environmental variables) and no collinearity was found (GVIF <3).

Boosted regression trees (BRT; Elith et al., 2008; Feld et al., 2016) were used to assess the contribution of each independent variable to variation in the macroinvertebrate data, to inform selection of sediment and vegetation variables to include in further analysis. The NumFlow did not explain any variation and so was excluded.

3.2.7 Community composition

Non-metric multi-dimensional scaling (NMDS) analysis (999 iterations) and ordination were conducted using Bray-Curtis similarity coefficients (‘vegan’ package; Okansen et al., 2007), to visualise variability in macroinvertebrate community composition over time and in space. Environmental variables (year, HighestEFlow, NumSed and EmBroadVeg), were colour coded according to categories on the NMDS plot.

PERMANOVA tests, including pairwise comparisons (‘vegan’ package; Oksanen et al., 2007; Anderson, 2014) were conducted to identify statistical differences in community composition between years and between the environmental variables to investigate spatial changes. For all PERMANOVA analyses, the function betadisper (‘vegan’ package) was also applied to the data to check for the multivariate homogeneity of group dispersions. Similarity percentage analysis (SIMPER; Clarke, 1993) was used to identify the species contributing towards any dissimilarity identified by PERMANOVA.

To further examine the temporal changes in community composition and the responses of communities to drought conditions, four NMDS ordinations were produced for a representative PR, near PR, partial IR and IR site, with PERMANOVAs conducted to identify site-specific differences between years. Visual assessments were also made to identify changes from pre-drought, drought and post-drought periods. As site-specific environmental parameters were characterised for the study period had only one temporal replicate, the environmental analysis (mentioned above) was not conducted for individual sites. Instead, environmental parameters were considered for inference when between-site comparisons were made, to assess if environmental conditions can influence the recovery to pre-drought conditions. Once analysis was completed, comparisons between the community responses to drought and the conceptual model were made in the discussion.

3.2.8 Biological indices

From the all-regime dataset, ten biological metrics (six taxonomic and four functional) representative of macroinvertebrate communities were calculated for each sample. Taxonomic richness, Shannon-H diversity, Whalley Hawkes Paisley Trigg Average Score Per Taxon (WHPT ASPT, Paisley et al., 2014), Drought Effect of Habitat Loss on Invertebrates index (DEHLI, Chadd et al., 2017), the family-level Proportion of Sediment-sensitive Invertebrates (EPSI family, Turley et al., 2016) and Ephemeroptera, Plecoptera and Trichoptera richness (EPT) were used to investigate taxonomic community responses. All metrics were calculated using the R package ‘biomonitoR’ (Laini et al., 2020) and described in full in section 2.4.1. Functional richness and diversity were calculated in R using the ‘FD’ package (Laliberté et al., 2014) from Gower distance community matrices, which can be more accurate than Bray-Curtis at identifying responses along an environmental gradient and deals with missing values (de Bello et al., 2007). Functional redundancy was calculated in ‘biomonitoR’ (Laini et al., 2020) using the Gini-Simpson index (de Bello et al., 2007).

To investigate the influence of hydrology, sediment and in-channel vegetation on the biological metrics, generalised linear mixed models (GLMMs) and LMMs were applied to the three datasets: all-regime, perennial and intermittent. GLMMs were used for taxonomic richness and EPT richness, and LMMs for all other metrics, using the ‘glmmTMB’ (Brooks et al., 2017) and ‘lme4’ (Bates et al., 2015) packages in R, respectively. Guided by previous research (Chapter 1 and section 3.1) and the hypotheses, for each model, a flow variable, sediment variable and vegetation variable were selected, dependent on RF results and data exploration plots (all model variables are summarised in Table 3.3). All continuous independent variables were scaled prior to analysis to make them comparable. For all models marginal R^2 and conditional R^2 were calculated in the “performance” package in R (Lüdecke et al., 2021), to quantify the proportion of variation in the response explained by fixed factors and fixed + random factors, respectively.

Table 3.3. The flow, sediment and vegetation variables initially included in the mixed-effect models (before model selection based on AIC) for each of the biological metrics for the all-regime, perennial and intermittent analysis.

Metric	Flow variable	Sediment variable	Vegetation variable
All regime			
Richness	HighestEFlow	SiltBedCover	NumVegMorph
Diversity	HighestEFlow	NumSed	NumVegMorph
WHPT ASPT	HighestEFlow	SiltBedCover	EmBroadVeg
DEHLI	HighestEFlow	SiltBedCover	EmBroadVeg
EPSI family	HighestEFlow	NumSed	EmBroadVeg
EPT richness	HighestEFlow	SiltBedCover	NumVegMorph
Functional richness	HighestEFlow	NumSed	EmBroadVeg
Functional diversity	HighestEFlow	NumSed	NumVegMorph
Functional redundancy	HighestEFlow	SiltBedCover	EmBroadVeg
Perennial			
Richness	HighestEFlow	NumSed	EmBroadVeg
Diversity	HighestEFlow	SiltBedCover	NumVegMorph
WHPT ASPT	HighestEFlow	SiltBedCover	NumVegMorph
DEHLI	HighestEFlow	NumSed	EmBroad
EPSI family	HighestEFlow	NumSed	NumVegMorph
EPT richness	HighestEFlow	NumSed	NumVegMorph
Functional richness	HighestEFlow	SiltBedCover	NumVegMorph
Functional diversity	HighestEFlow	NumSed	NumVegMorph
Functional redundancy	HighestEFlow	NumSed	EmBroadVeg
Intermittent			
Richness	HighestEFlow	NumSed	NumVegMorph

Diversity	HighestEFlow	NumSed	EmBroadVeg
WHPT ASPT	HighestEFlow	SiltBedCover	EmBroadVeg
DEHLI	HighestEFlow	SiltBedCover	EmBroadVeg
EPSI family	HighestEFlow	SiltBedCover	NumVegMorph
EPT richness	HighestEFlow	SiltBedCover	NumVegMorph
Functional richness	HighestEFlow	NumSed	NumVegMorph
Functional diversity	HighestEFlow	SiltBedCover	NumVegMorph
Functional redundancy	HighestEFlow	SiltbedCover	EmBroadVeg

For the all-regime analysis, in all but the H and functional diversity models, site, month since, and year were used as random factors. For H and functional diversity models, month since was removed as it explained no variation in the response variable, meaning the models had a singular fit (see section 2.4.3). For the analysis conducted on perennial and intermittent communities, month since was removed from diversity, WHPT ASPT, EPT richness, and functional diversity models as it had no influence on the response variables.

Multiple models were produced from the hydrological, sediment and vegetation variables and their interactions and the best fitting models selected using Akaike's Information Criteria (AIC) as per section 2.4. For all-regime taxonomic richness, a negative binomial model (R function "glmer.nb") with a quasi-poisson distribution and log link function was used due to overdispersion which was found after initial GLMM Poisson model residuals were inspected and AICs consulted. For perennial and intermittent datasets, a GLMM Poisson model was applied as there was no overdispersion. For EPT richness, for models based on all three datasets, a hurdle GLMM (R function "glmmTMB") with a Poisson distribution and log link function was used after model residuals revealed zero-inflation.

3.3 Results

The final macroinvertebrate dataset comprised of 1,376,165 individuals from 234 taxa from 1128 samples (the mean number of samples ± SD per river: Beane, 15 ± 11.7, Chess, 23 ± 13, Gade, 14.9 ± 16, Mimram, 18.8 ± 11.12, Misbourne, 19.4 ± 16.3, Ver, 18.6 ± 10.4) collected at 62 sites (Beane = 10, Chess = 3, Gade = 9, Mimram = 14, Misbourne = 12, Ver = 14) in spring (n = 552) and/or autumn (n = 576) between 1995-2018.

3.3.1 Environmental factors

3.3.1.1 All sites

Site-specific flow conditions varied from free fall to no perceptible flow (NPF) as the highest energy flow type (*HighestEFlow*), and the number of flow types (*NumFlow*) per site ranged from 1–5. The most widespread HighestEFlow types were rippled (387 samples), unbroken waves (299), smooth (252) and NPF (105). The number of sediment types (*NumSed*) ranged from 0 (not visible, reflective of heavily silted conditions) to 5, with dominant sediment types including bedrock, cobbles, gravels, sand and silt. The extent of silt on the channel bed (*SiltBedCover*) ranged from 0–6.7. Emergent broadleaf vegetation cover (*EmBroadVeg*) encompassed all categories, from absent to extensive.

3.3.1.2 Perennial and intermittent sites

At perennial sites, the HighestEFlow included smooth flow, rippled flow and unbroken waves, with the number of flow types ranging from 1–3 per site. Sediment composition included cobbles, gravels and silt, with 0–4 sediment types per site and SiltBedCover ranging between 0 and 6.7. All categories of EmBroadVeg were represented and the number of vegetation morphotypes per site varied between 0–4.

At intermittent sites the HighestEFlow ranged from NPF to rippled flow. Between 0–5 sediment types were recorded per site, with SiltBedCover ranging from 0 to 6.7. Sites only supported 0–2 vegetation morphotypes, and EmBroadVeg was absent, moderate or extensive.

3.3.2 Differences in perennial and intermittent community composition

Despite some overlap, community composition differed between P and I sites (PERMANOVA, F = 8.68, df = 1, P = < 0.001, Figure 3.2). Perennial sites had higher abundances of taxa including *Gammarus pulex/fossarum, Baetis rhodani/atlanticus, Elmis aenea* and *Potamopyrgus antipodarum* (SIMPER, Table A1.1), and supported taxa which were absent from intermittent sites, including *Sericostoma personatum* and *Sphaerium* spp. (Table A1.1). Some taxa were moderately more abundant at intermittent sites, such as *Asellus aquaticus* and *Pisidium* spp. but these differences were non-significant (SIMPER, P > 0.05). All biological metrics were higher in perennial communities than their intermittent counterparts.

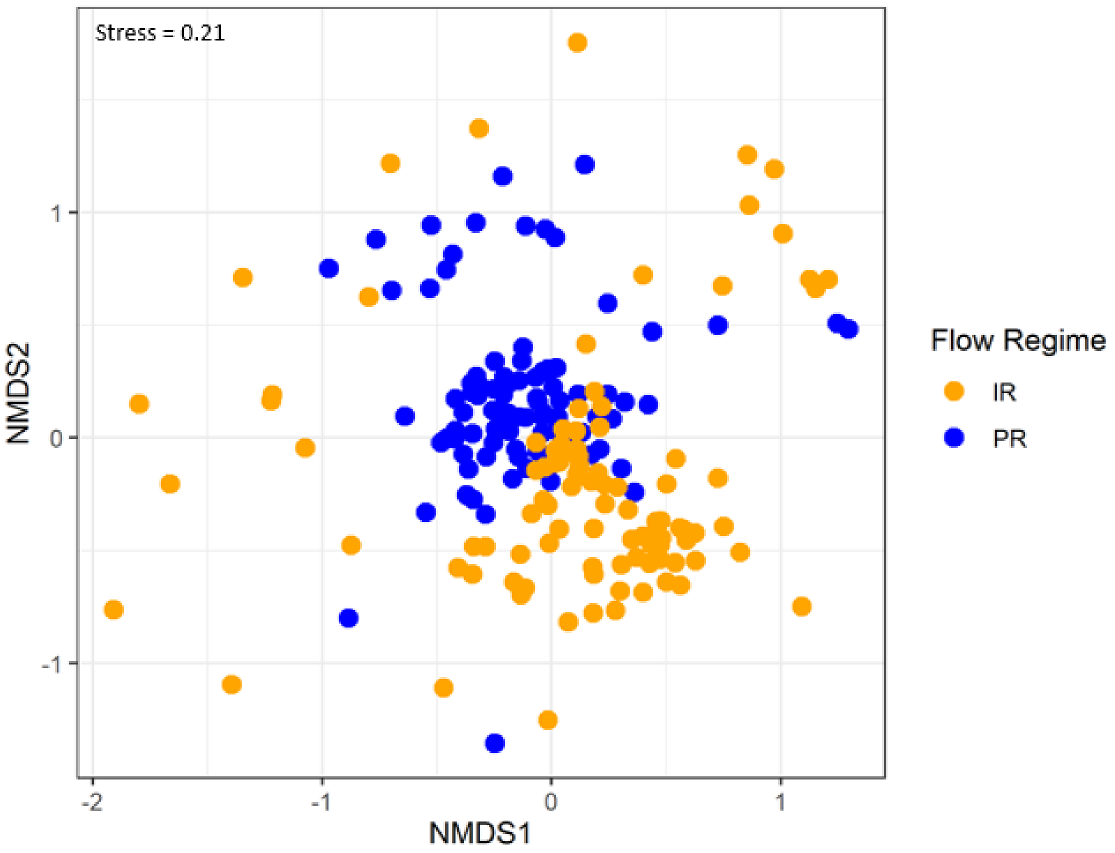

Figure 3.2. Non-metric multidimensional scaling (NMDS) ordination of abundance-based variability in macroinvertebrate community composition of the 100 perennial (PR) and intermittent (IR) sites.

3.3.3 All-regime responses to environmental parameters

3.3.3.1 Community compositional responses

Flow (i.e. HighestEFlow) explained the most variation in community composition in both spring and autumn, although the proportion explained was low (R^2 = 0.052). The HighestEFlow at a site influenced community composition in both seasons, as both an individual factor (PERMANOVA, spring: F = 6.77, df = 5, P < 0.001; autumn: F = 7.29, df = 5, P < 0.001) and as an interaction with sediment (spring R^2 = 0.035: F = 5.71, df = 4, P < 0.001; autumn R^2 = 0.039, df = 4, P < 0.001) and vegetation (PERMANOVA, spring R^2 = 0.051: F = 4.12, df = 8, P < 0.001; autumn R^2 = 0.055: F = 4.77, df = 8, P < 0.001).

Vegetation (i.e. EmBroadVeg) explained comparable, low variation in community composition in spring (PERMANOVA; R^2 = 0.020) and autumn (PERMANOVA; R^2 = 0.021). EmBroadVeg influenced community composition as an individual variable (PERMANOVA, spring: F = 4.33, df = 3, P = 0.001, autumn; F = 4.75, df = 3, P = 0.001) and as part of an interaction with SiltBedCover (spring R^2 = 0.025, df = 3, P = 0.001; autumn R^2 = 0.026, df = 3, P = 0.001). Sediment (i.e. SiltBedCover) explained very little variation in community composition (spring R^2 = 0.008, autumn R^2 = 0.007), but community composition differed between sites with varying SiltBedCover (PERMANOVA, spring: F = 5.16, df = 1, P = 0.001; autumn: F = 4.52, df = 1, P = 0.001). Community composition varied considerably both within and between flow, sediment and vegetation categories (Figure 3.3).

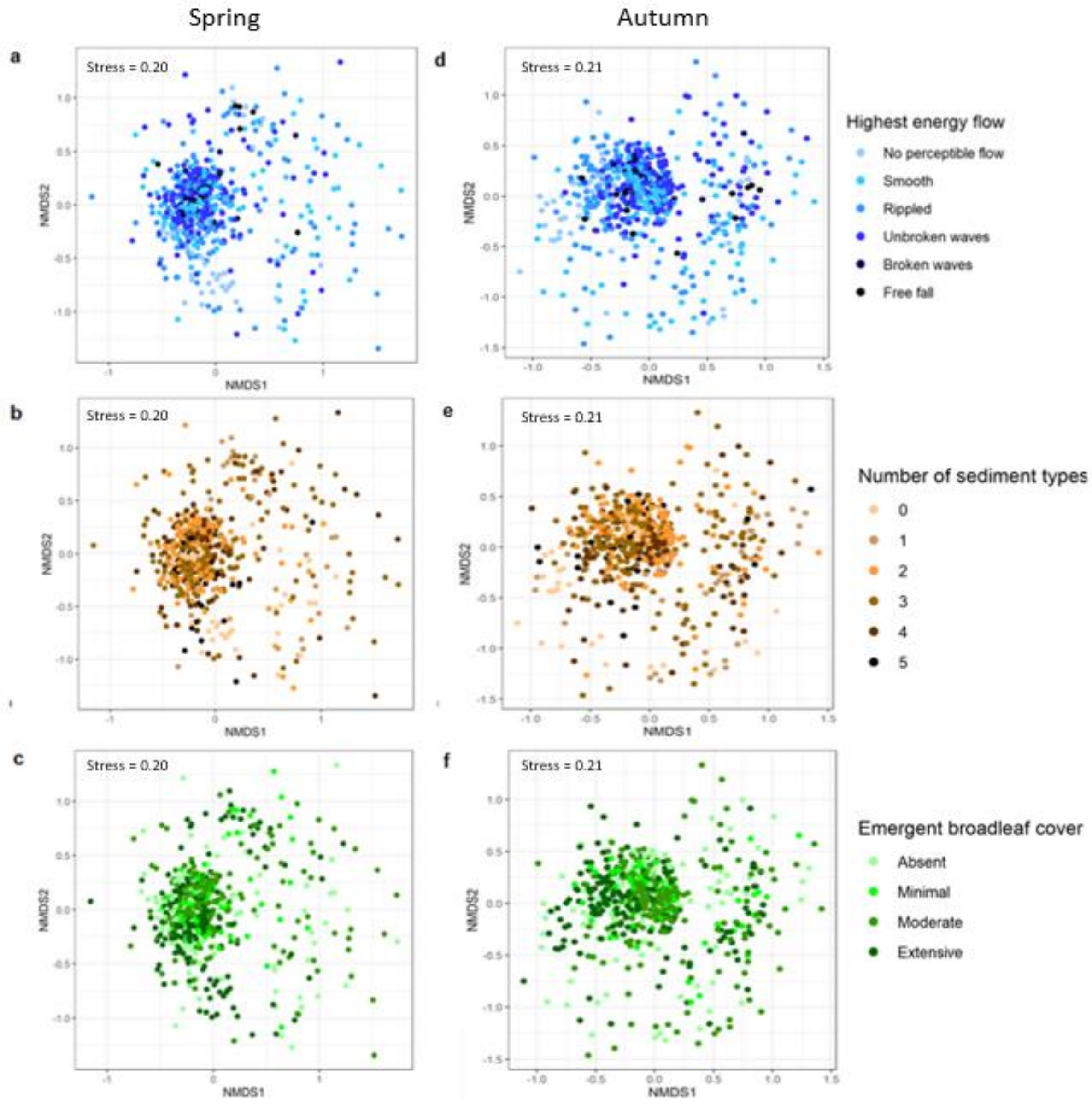

Figure 3.3. Non-metric multidimensional scaling (NMDS) ordination of macroinvertebrate community composition of spring (a, b, c) and autumn (d, e, f) communities, coloured to reflect their occurrence at sites with different flow, sediment and vegetation: (a–b) highest energy flow type (light blue – dark blue = NPF – free fall); (c–d) number of sediment types, and (e–f) vegetation (light green – dark green = absent – extensive) cover of emergent broadleaf vegetation.

3.3.3.2 Taxonomic metric responses

Flow (i.e. HighestEFlow) occurred in the best models for four metrics: taxonomic richness, WHPT ASPT, DEHLI and EPSI (Table 3.1), all of which, except for EPSI which was comparable at all HighestEFlow categories, were significantly influenced by flow (Table A1.8). DEHLI and WHPT ASPT were higher at sites at which unbroken waves were the HighestEFlow compared to sites with NPF (Figure 3.4a, Table A1.8). DEHLI was also higher at sites with broken waves as the HighestEFlow (Figure 3.4b, Table A1.8). WHPT ASPT and taxonomic richness were non-significantly higher at sites with broken waves than at sites with NPF (WHPT ASPT: estimate = 0.984, SE = 0.501, P = 0.055; taxonomic richness: estimate = 0.494, SE = 0.276, P = 0.07; Figure 3.4a and c).

Table 3.4. The all-regime models with ΔAIC < 2 for each metric with respective marginal and conditional R^2 values. Flow is the HighestEFlow; sediment is SiltBedCover or NumSed; vegetation is NumVegMorph or EmBroadVeg; × indicates interactions.

Metric: model	**R^2 marginal**	**R^2 conditional**
Taxonomic richness: flow × sediment × vegetation	0.32	0.67
Shannon-H diversity: sediment	<0.001	0.46
Shannon-H diversity: vegetation	0.02	0.46
WHPT ASPT: flow	0.11	0.79
WHPT ASPT: sediment	0.04	0.78
EPSI: flow × sediment × vegetation	0.25	0.61
DEHLI: sediment	0.02	0.64
DEHLI: flow	0.09	0.65
EPT richness: sediment	0.06	0.67
EPT richness: sediment × vegetation	0.07	0.67
Functional redundancy: sediment	<0.001	0.28
Functional richness: sediment	<0.001	0.44
Functional diversity: sediment	<0.001	0.19

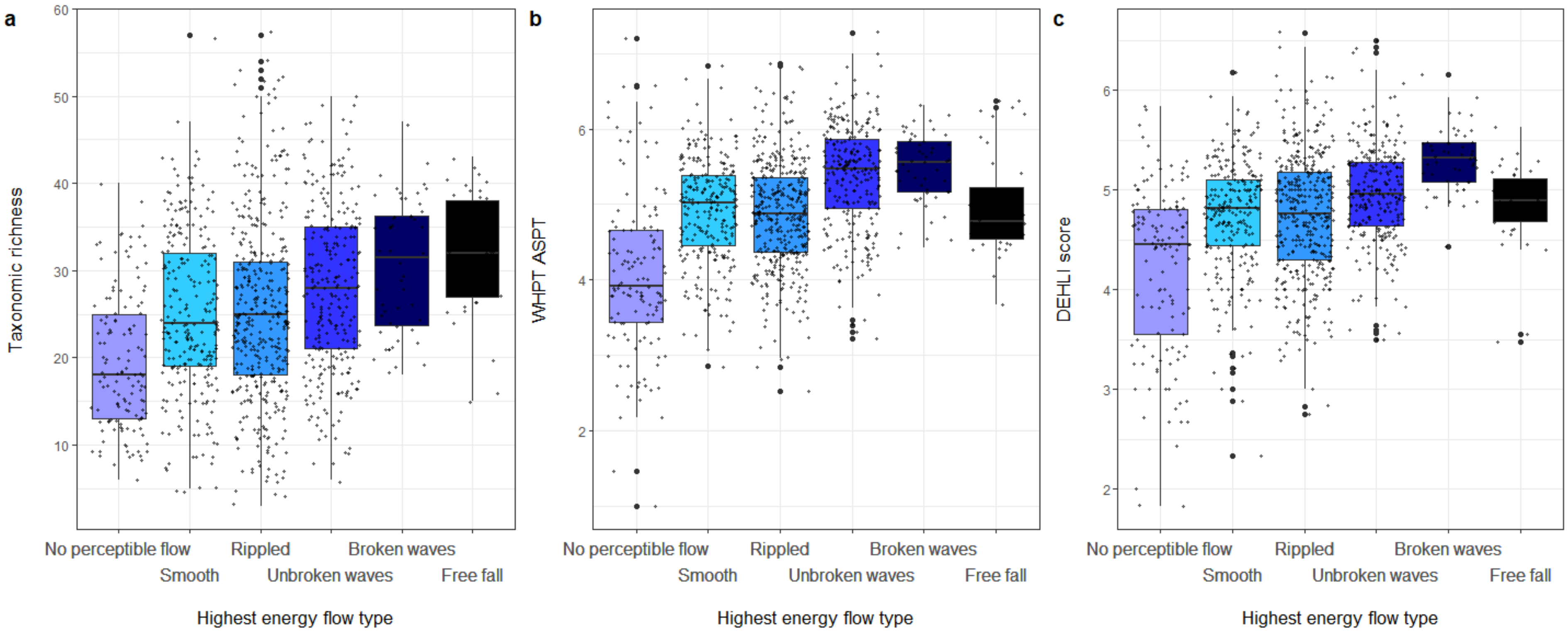

Figure 3.4. The median, interquartile range and 95% confidence intervals with individual sample points (jittered) for (a) taxonomic richness, (b) WHPT ASPT and (c) DEHLI responses to the highest energy flow type at a site. Big dots are outliers.

Sediment-related predictors (i.e. SiltBedCover and NumSed) occurred in the best models for all taxonomic metrics (Table 3.4) and significantly influenced four metrics: taxonomic richness, WHPT ASPT, EPSI and EPT richness (Table A1.8). Taxonomic richness and DEHLI were comparable across all SiltBedCover conditions, and EPSI and diversity are comparable across NumSed (Table A1.8). The sediment conditions explained less variation (4%) than flow conditions (11%) in WHPT ASPT, but did respond significantly, decreasing as SiltBedCover increased (Figure 3.5a, Table A1.8). EPT richness also decreased significantly as the extent of SiltBedCover increased (Figure 3.5b, Table A1.8).

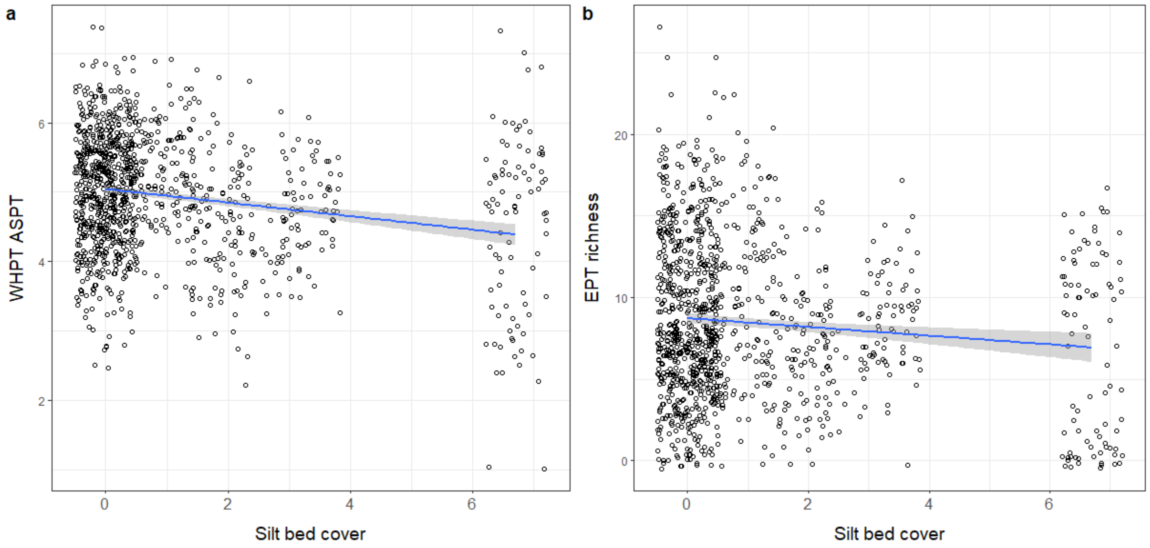

Figure 3.5. The response of a) WHPT ASPT and b) EPT richness to the extent of silt on the channel bed (i.e. silt bed cover). Points are jittered to avoid overplotting. The shaded area represents 95% confidence intervals.

Sediment also affected the macroinvertebrate communities in an interaction with flow, significantly influencing both taxonomic richness and EPSI (Table A1.8). At sites with unbroken waves as HighestEFlow, richness decreased strongly with increasing SiltBedCover (Figure 3.6 and Figure 3.7b), compared to sites with NPF, at which richness decreased only slightly (Figure 3.6 and Figure 3.7a). EPSI decreased slightly as NumSed increased at sites with rippled flow in comparison to those with NPF, where EPSI increased with NumSed (Figure 3.8a). This interaction may reflect differences in EmBroadVeg at rippled sites (Table A1.8): EPSI decreased as NumSed increased at sites with extensive cover but increased with NumSed at sites with absent or present EmBroadVeg cover (Figure 3.7b).

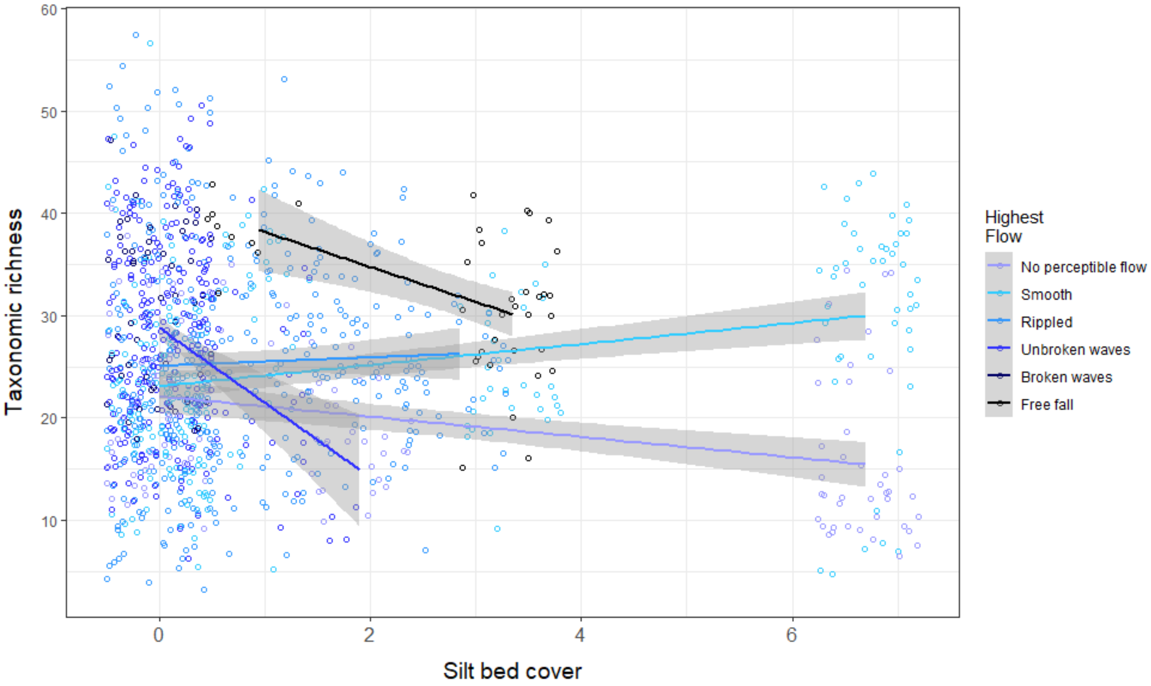

Figure 3.6. The relationship between taxonomic richness and the extent of silt on the channel bed (i.e. silt bed cover) across all highest energy flow types. Points are jittered to avoid overplotting. The shaded area represents 95% confidence intervals.

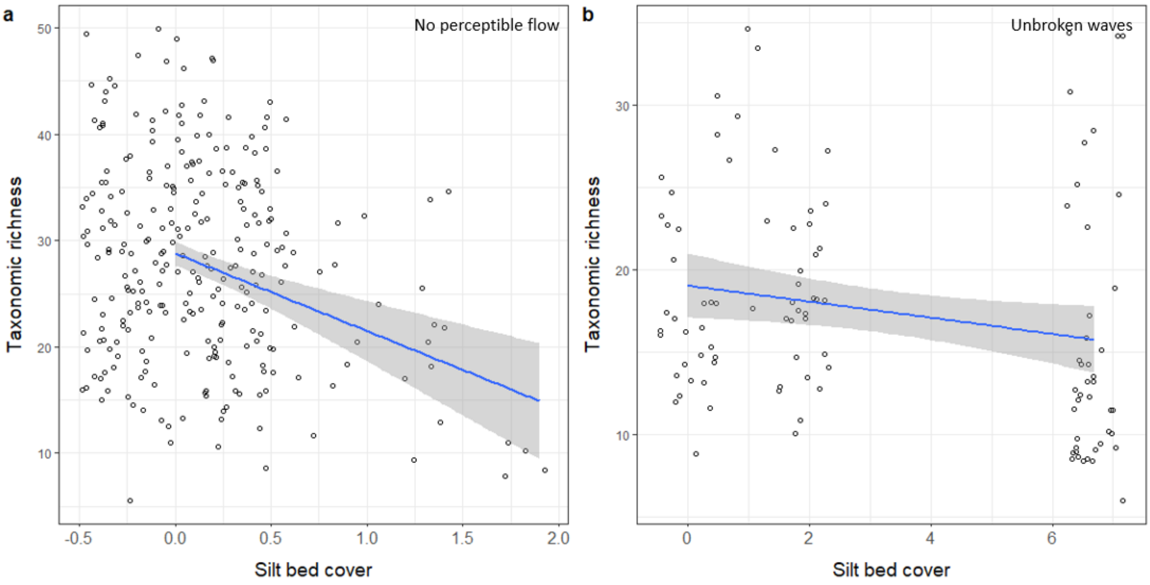

Figure 3.7. The relationship between taxonomic richness and the extent of silt on the channel bed (i.e. silt bed cover) at sites with the highest energy flow as (a) no perceptible flow and (b) unbroken waves. Points are jittered to avoid overplotting. The shaded area represents 95% confidence intervals.

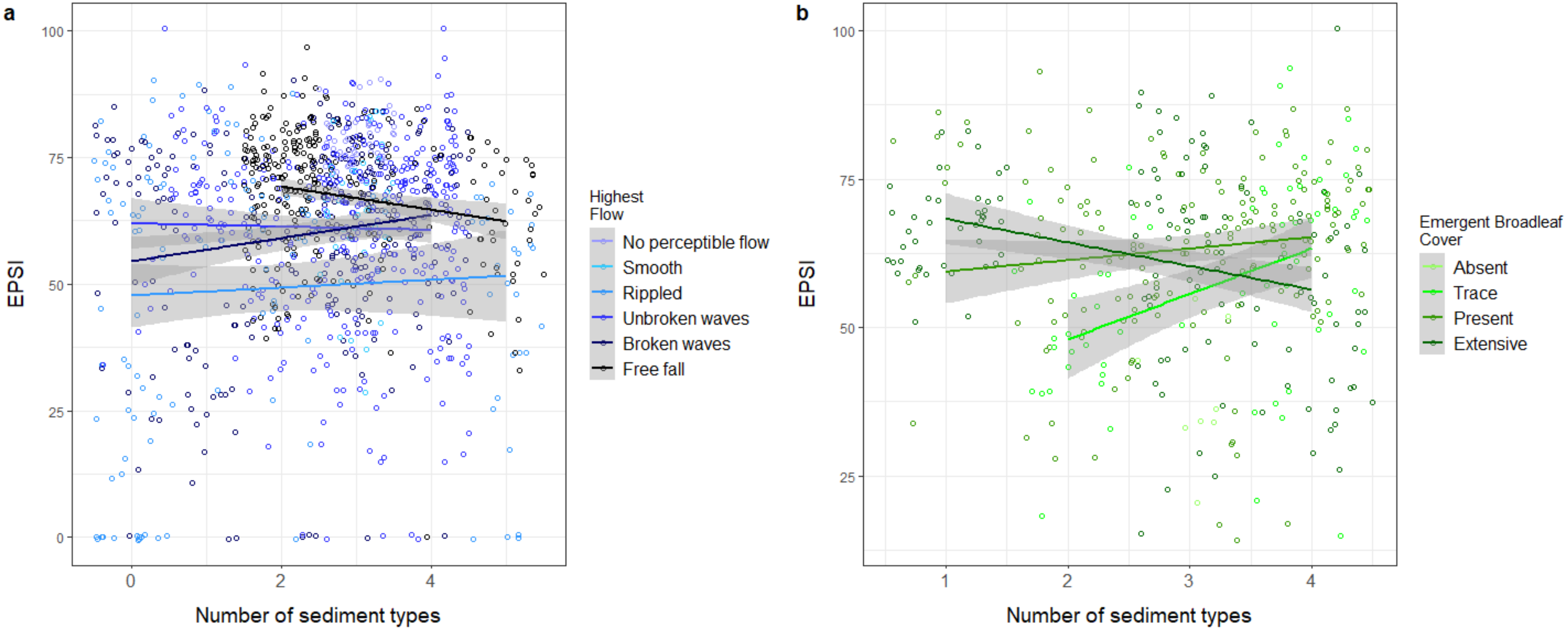

Figure 3.8. The relationship between EPSI family and the number of sediment types at (a) sites with different highest energy flow types and (b) at rippled sites with different cover of emergent broadleaf plants. The shaded area represents 95% confidence intervals.

The two vegetation variables (NumVegMorph and EmBroadVeg) occurred in the best models for taxonomic richness, diversity, EPSI and EPT richness. Vegetation only significantly influenced taxonomic richness – as part of an interaction (Table A1.8) – with diversity, EPSI and EPT richness comparable across all vegetation conditions (Table A1.8). At sites with smooth flow, taxonomic richness responded positively to both an increase in SiltBedCover and NumVegMorph (Figure 3.9). At sites with rippled flow, a non-significant decrease in richness occurred as both SiltBedCover and EmBroadVeg increased (estimate = -0.368, SE = 0.196, P = 0.061).

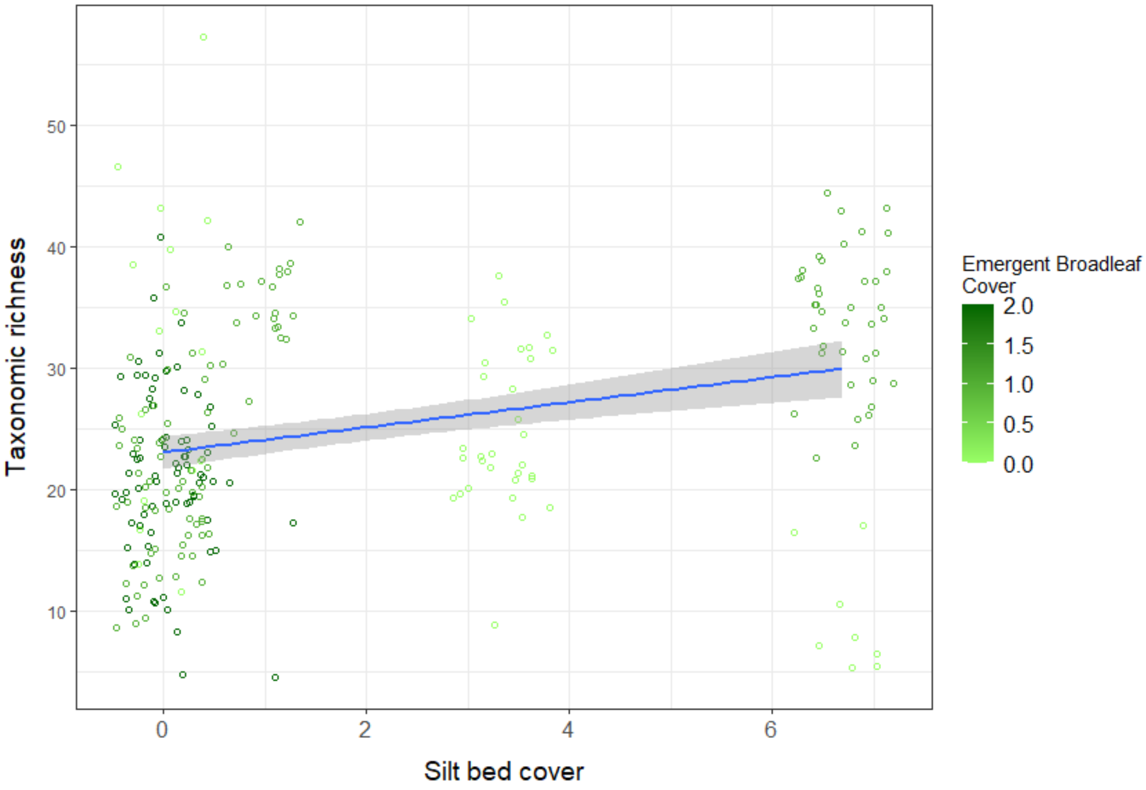

Figure 3.9. Taxonomic richness response to the extent of silt on the channel bed (i.e. silt bed cover) with different numbers of aquatic vegetation morphotypes at sites with smooth flow. Points jittered to avoid overplotting. The shaded area represents the 95 % confidence intervals.

3.3.3.3 Functional metric responses

Only sediment-related predictors occurred in the top models for all three functional metrics: richness, diversity and redundancy. These metrics were comparable across all sediment conditions (Table A1.8), with predictors accounting for a negligible proportion of the variation in each metric (Table 3.4).

3.3.4 Perennial and intermittent communities

3.3.4.1 Community composition

Vegetation explained the most variation in community composition for perennial sites ($R^2 = 0.11$), and flow was the most influential variable on intermittent community composition ($R^2 = 0.14$), with vegetation explaining a similar amount of variation ($R^2 = 0.11$). EmBroadVeg influenced community composition (Figure 3.10, Figure 3.11, PERMANOVA, perennial: F = 4.7, df = 3, P = 0.001, intermittent: F = 8.02, df = 2, P = 0.001), with communities at intermittent sites clearly differing between categories (Figure 3.10c). Composition differed between all emergent broadleaf categories. The differences between communities at sites with absent and extensive EmBroadVeg accounted for the most variation in composition for perennial (pairwise PERMANOVA; $R^2 = 0.13$, F = 3.95, df = 1, P = 0.002) and intermittent communities ($R^2 = 0.15$, F = 11.7, df = 1, P = 0.001). In perennial communities all taxa except Chironomidae and *Micronecta poweri/scholtzi* increased between sites with absent and extensive emergent broadleaf cover, such as *Agapetus* spp.*, S. personatum* and *Limnephilus lunatus* (SIMPER, Table A1.3). In intermittent communities, taxa such as *Pisidium* spp., *Helobdella stagnalis* and *Dugesia lugubris/polychroa* increased in abundance from sites with no EmBroadVeg to sites with extensive cover, whereas taxa such as *G. pulex/fossarum, Anisus vortex* and Hydracarina decreased (SIMPER, Table A1.6). Vegetation also interacted with sediment at perennial sites, influencing community composition (PERMANOVA, $R^2 = 0.2$, F = 3.45, df = 1, P = 0.001) and flow (PERMANOVA, $R^2 = 0.1$, df = 3, P = 0.001).

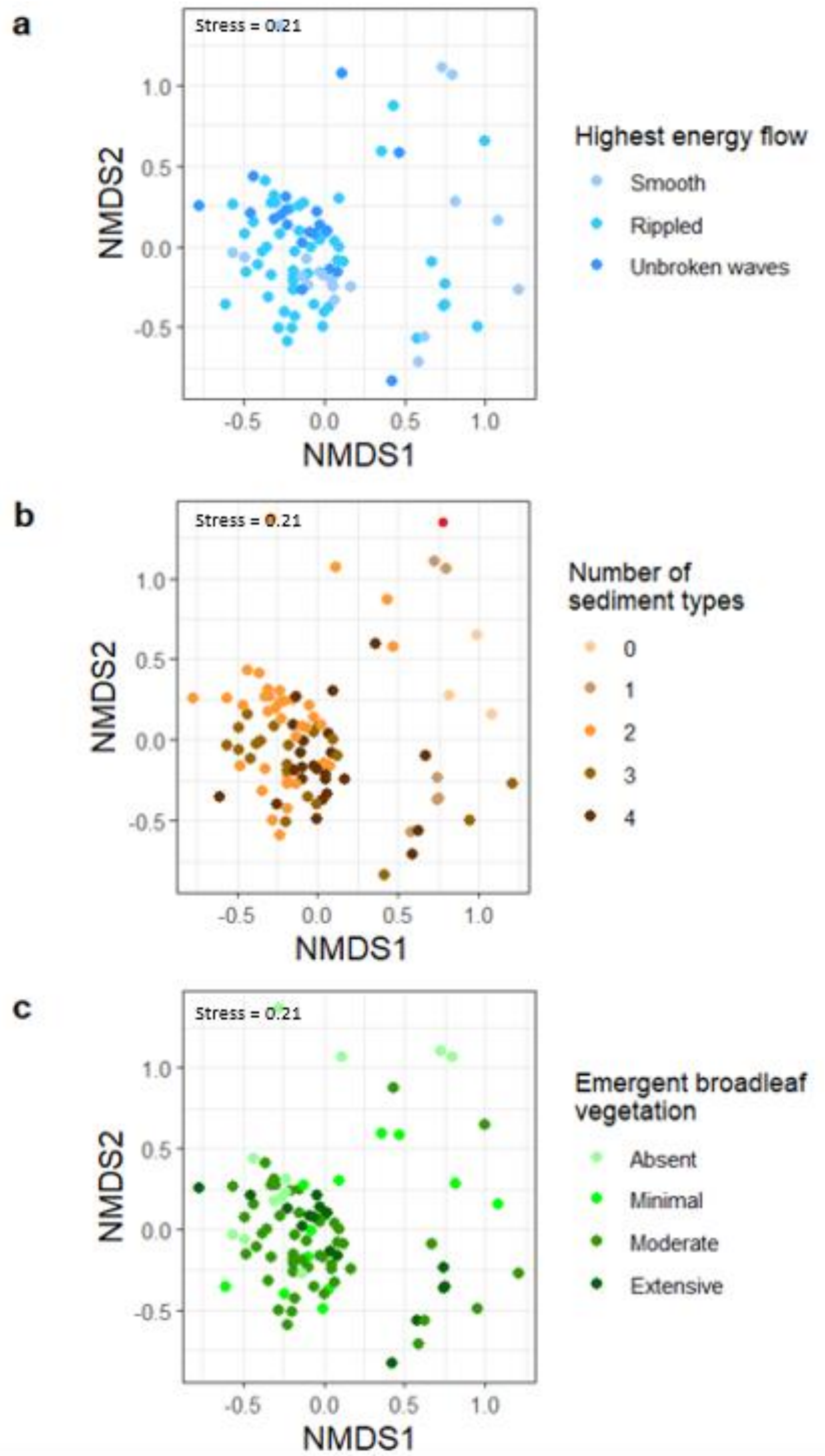

Figure 3.10. Non-metric multidimensional scaling (NMDS) ordination of macroinvertebrate community composition at perennial sites in relation to environmental variables representing flow, sediment and vegetation: (a) highest energy flow type; (b) number of sediment types; and (c) cover of emergent broadleaved vegetation.

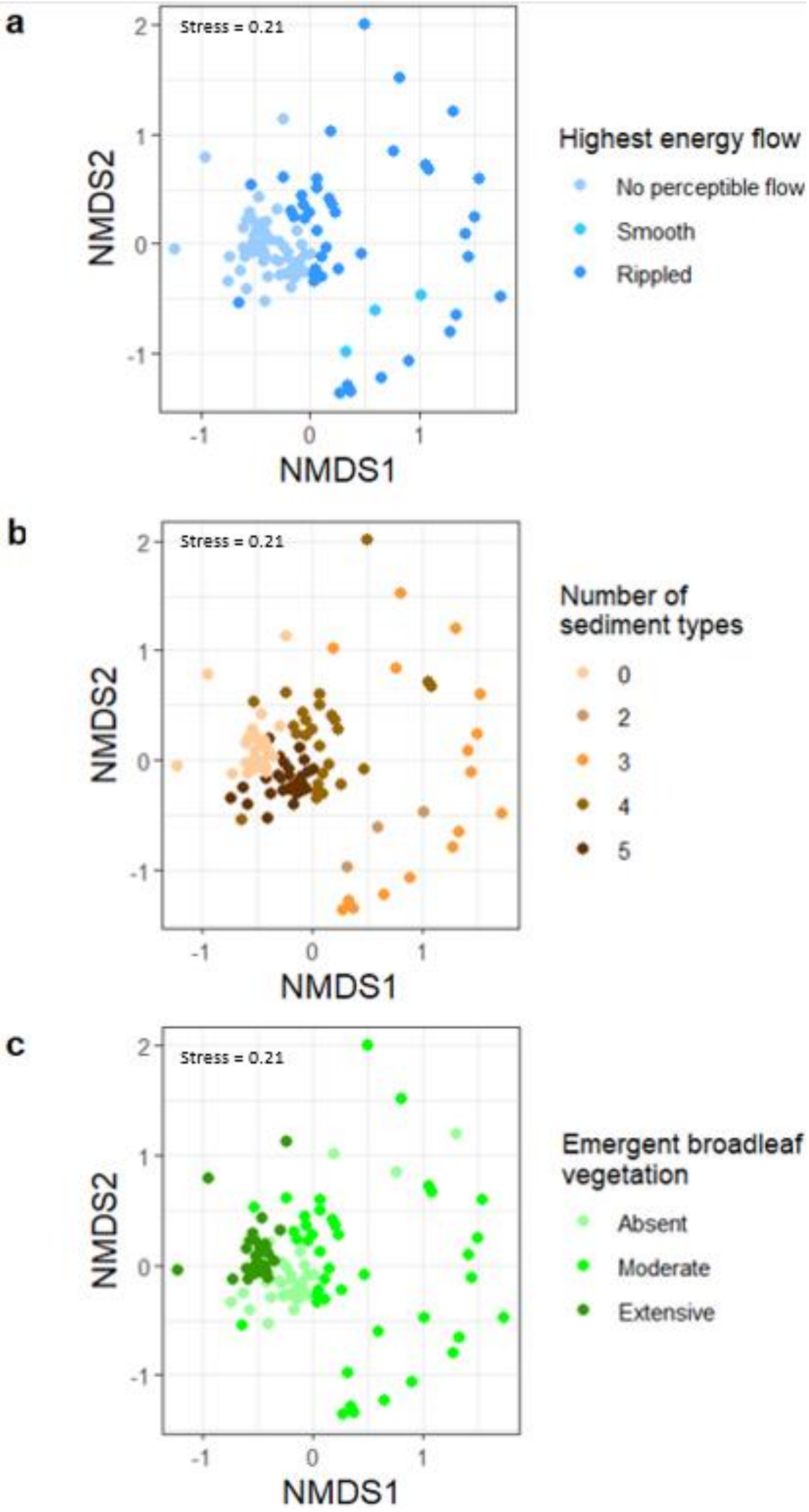

Figure 3.11. Non-metric multidimensional scaling (NMDS) ordination for the composition of macroinvertebrate communities at intermittent sites in relation to environmental variables representing flow, sediment and vegetation: (a) highest energy flow type; (b) number of sediment types; (c) cover of emergent broadleaved vegetation.

Flow influenced community composition at both perennial (PERMANOVA, $R^2 = 0.08$, F = 5.64, df = 2, P = 0.001) and intermittent sites ($R^2 = 0.14$, F = 10.35, df = 2, P = 0.001), with greater dispersion within flow categories for perennial communities (betadisper permutest, F = 3.23, df = 2, P = 0.040; Figure 3.10a). Perennial communities differed between all flow categories (smooth, unbroken waves and rippled), with compositional differences between smooth and unbroken waves explaining most variation (pairwise PERMANOVA, $R^2 = 0.10$, df = 1, P = 0.003). Most of the significant changes in taxa abundances involved increases in abundance at sites with smooth flow in comparison to sites with unbroken waves (e.g., *G. pulex/fossarum, Simulium* spp. and *Ephemera danica*). Few taxa decreased from smooth to unbroken wave sites (e.g. *Limnius volckmari, Physa heterostropha*) (SIMPER, Table A.12). Additionally, 4% of compositional differences were explained by an interaction between the HighestEFlow and NumSed (PERMANOVA, $R^2 = 0.04$, F = 2.83, P = 0.001). Variation in community composition at intermittent sites was driven largely by differences at sites with NPF and rippled flow as the HighestEFlow (pairwise PERMANOVA, $R^2 = 0.12$, F = 12.89, df = 1, P = 0.003; Figure 3.11). The abundance of taxa including Chironomidae, Oligochaeta and *G. pulex*/*fossarum* was lower at sites with rippled flow than at sites with NPF as the highest energy flow type, whereas taxa including *Hydropsyche angustipennis* and *Simulium* spp. were more abundant at sites with NPF (SIMPER, Table A1.5).

Sediment accounted for the least amount of variation in both perennial and intermittent communities (perennial: $R^2 = 0.04$, intermittent: $R^2 = 0.08$). Community composition varied between sites with different NumSed (PERMANOVA; perennial: F = 5.62, df = 1, P = 0.001; intermittent: F = 12.14, df = 1, P = 0.001), with significant differences found between all NumSed. Compositional variation between perennial sites with no visible sediments (0) and 1 sediment type (pairwise PERMANOVA, $R^2 = 0.25$, F = 2.34, df = 1, P = 0.045), and between 1 and 3 sediment types (pairwise PERMANOVA, $R^2 = 0.21$, F = 6.57, df = 1, P = 0.001) accounted for nearly half of the variation in community composition relating to sediments. Of the 26 taxa that significantly increase, 22 increased in abundance between 1 and 3 sediment types (e.g., *L. lunatus*, *Pisidium* spp. and *E. danica*)*,* but *G. pulex/fossarum,* Chironomidae, Oligochaeta and *Baetis rhodani/atlanticus* decreased in abundance (SIMPER, Table A1.4). Variation in composition between intermittent sites with 3 and 5 sediment types accounted for 28% of variation attributed to sediment (pairwise PERMANOVA; F = 16.8, df = 1, P = 0.01). Taxa such as *G. pulex/fossarum*, Oligochaeta and *Agapetus* spp. increased from 3 to 5 sediment sites, and taxa such as *L. lunatus, E. aenea* and *Musculium lacustre* decreased (SIMPER, Table A1.7).

3.3.4.2 Taxonomic metric responses

For each taxonomic metric at both perennial and intermittent sites, most best models included an independent or interactive effect of vegetation, and for most metrics with multiple top models (ΔAIC < 2), vegetation was in the model explaining the greatest variation (Table 3.5 and Table 3.6). All metric responses to vegetation were significant except WHPT and EPT richness, which did not respond to any environmental variables at perennial sites, and diversity, which did not respond at intermittent sites (Table A1.9 and Table A1.10). Additionally, environmental conditions explained more variation in the metric responses in intermittent sites ($R^2M = 0.44 \pm 0.23$ per model) than at perennial sites ($R^2M = 0.18 \pm 0.11$ per model).

Table 3.5. The perennial community models with the lowest AIC (ΔAIC < 2) for each metric with respective marginal and conditional R^2 values. Further details are provided in Table 3.4, NS = not significant; × indicates interactions.

Metric: model	R^2 marginal/ adjusted	R^2 conditional
Taxonomic richness: sediment × vegetation	0.41	0.61
Shannon-H diversity: sediment × vegetation (NS)	0.14	0.70
Shannon-H diversity: flow × sediment × vegetation	0.22	0.66
WHPT ASPT: flow × sediment (NS)	0.13	0.75
WHPT ASPT: flow (NS)	0.13	0.68
EPSI: flow × sediment × vegetation	0.31	0.61
DEHLI: flow (NS)	0.07	0.80
DEHLI: flow × vegetation	0.17	0.80
EPT richness: sediment (NS)	0.04	0.49
EPT richness: sediment × vegetation (NS)	0.14	0.51
Functional redundancy: sediment	0.10	0.54
Functional redundancy: vegetation	0.17	
Functional richness: vegetation	0.10	0.28
Functional diversity: sediment	<0.001	0.60
Functional diversity: vegetation	0.07	0.56

Table 3.6. The intermittent community models with the lowest AIC (∆AIC <2) for each metric with respective marginal and conditional R^2 values; Further details are provided in Table 3.4, NS = not significant; × indicates interactions.

Metric and model	**R^2 marginal**	**R^2 conditional**
Taxonomic richness: flow × sediment × vegetation	0.48	0.61
Taxonomic richness: sediment × vegetation	0.48	0.61
Shannon-H diversity: flow (NS)	0.03	0.15
Shannon-H diversity: vegetation (NS)	0.02	0.17
WHPT ASPT: flow × sediment	0.61	0.78
WHPT ASPT: flow × vegetation	0.61	0.78
EPSI: sediment	0.41	0.43
DEHLI: vegetation	0.42	0.64
DEHLI: flow × vegetation	0.42	0.63
DEHLI: sediment	0.40	0.62
EPT richness: flow × *vegetation	0.67	0.72
EPT richness: sediment × vegetation	0.67	0.72
Functional redundancy: flow (NS)	0.14	0.38
Functional richness: flow (NS)	<0.001	0.34
Functional diversity: flow (NS)	0.05	0.37
Functional diversity: vegetation (NS)	0.06	0.39

At intermittent sites, taxonomic richness, DEHLI and WHPT ASPT were lower at sites with extensive EmBroadVeg, and taxonomic richness was also lower at sites with moderate cover, compared to those at which such vegetation was absent (Figure 3.12, Table A1.10). Although non-significant, WHPT ASPT was also higher at sites with moderate EmBroadVeg compared to sites with no such vegetation (Figure 3.12a). Whilst the models for taxonomic richness and EPT richness suggested an increase with NumVegMorph (Table A1.10), there was no actual relationship once plotted. At perennial sites, DEHLI scores were higher at sites with minimal or moderate EmBroadVeg compared to absent EmBroadVeg (Figure 3.12d, Table A1.9).

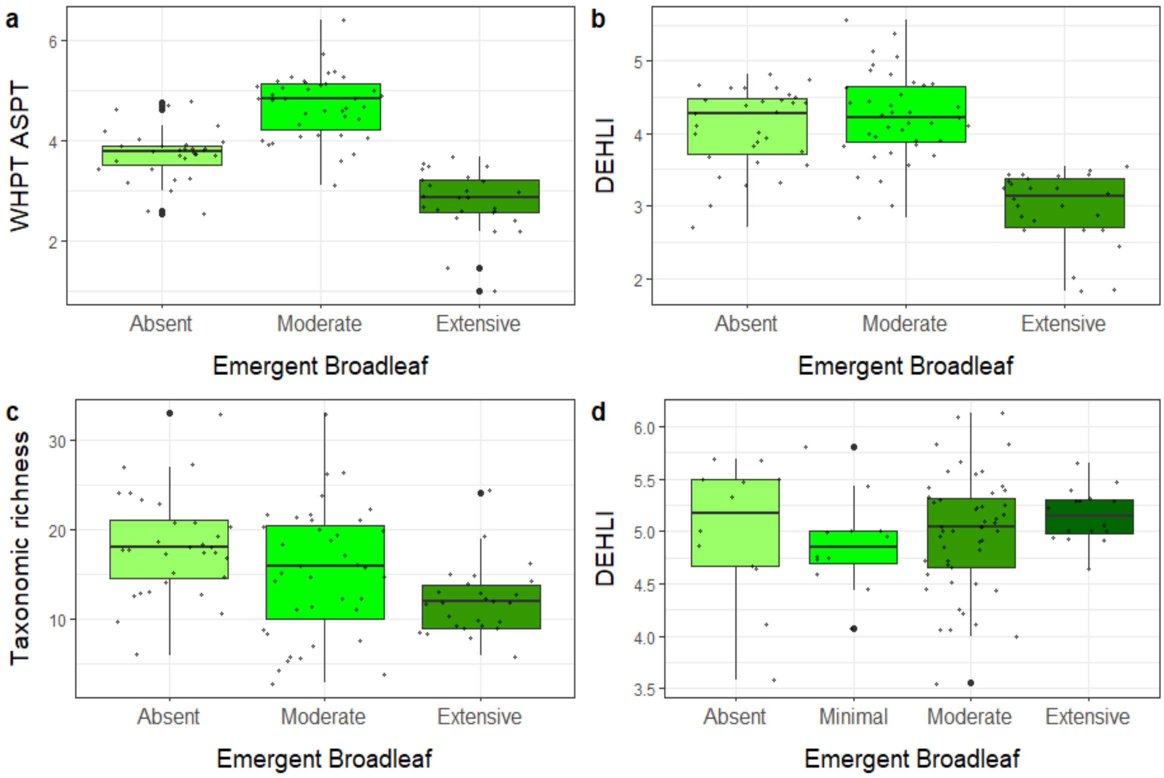

Figure 3.12. The median, interquartile range and 95% confidence intervals with individual sample points (jittered) for (a) WHPT ASPT, (b) DEHLI and (c) taxonomic richness at intermittent sites; (d) DEHLI at perennial sites with different emergent broadleaf vegetation cover categories. Big dots are outliers.

Metrics also responded to vegetation as part of an interaction with sediment at both perennial and intermittent sites. The increase in taxonomic richness with the NumSed was greater at intermittent sites with moderate EmBroadVeg compared to absent EmBroadVeg (Figure 3.13a; Table A1.10 and Table A1.11). In contrast, at perennial sites, taxonomic richness increased with the number of sediment types at a greater rate at sites with absent EmBroadVeg compared to those with minimal EmBroadVeg, and decreased at sites with extensive EmBroadVeg (Figure 3.13b; Table A1.9 and Table A1.11). Models indicated diversity responded to the interaction between vegetation and sediment at perennial sites, but there was no visible relationship (Table A1.9 and Table A1.11).

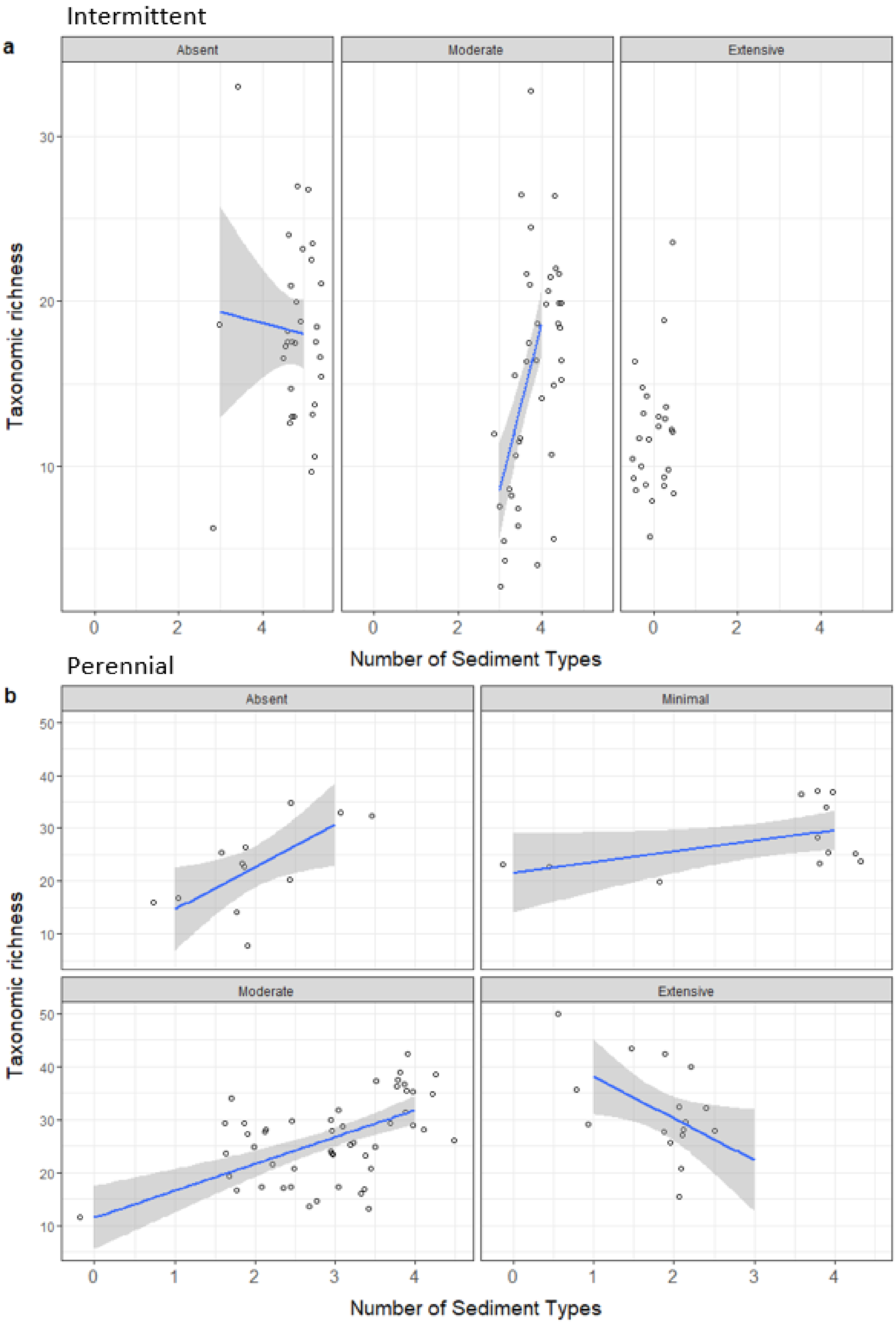

Figure 3.13. The relationship between taxonomic richness and the number of sediment types at a) intermittent and b) perennial sites at which emergent broadleaf vegetation cover was absent, minimal, moderate and extensive. The shaded area represents 95% confidence intervals.

Vegetation influence communities at perennial and intermittent sites through an interaction with flow. At perennial sites with rippled flow and unbroken waves as the HighestEFlow, an interaction with minimal EmBroadVeg caused a reduction in DEHLI in comparison to sites where vegetation was absent at smooth sites (Figure 3.14, Table A1.9 and Table A1.11). At intermittent sites with NPF, EPT richness decreased with increasing NumVegMorph, with the highest EPT richness values occurred only at 0 NumVegMorph (Figure 3.15, Table A1.10 and Table A1.11). At sites with rippled flow, EPT richness increased with increasing NumVegMorph, with the EPT richness much more variable at sites with 2 NumVegMorph (Figure 3.15, Table A1.10 and Table A1.11).

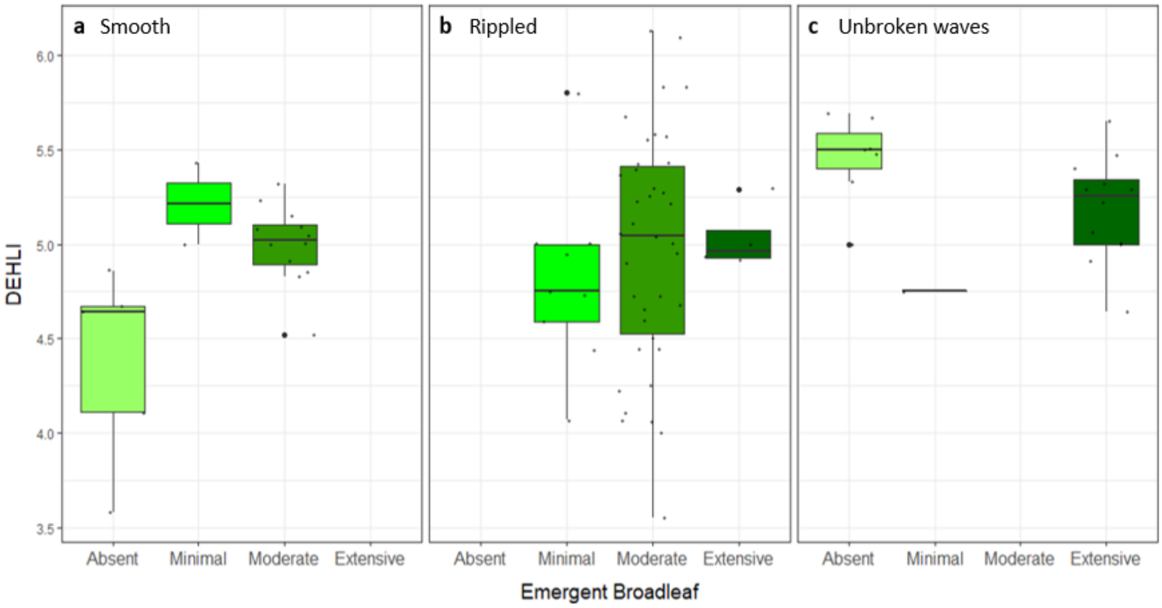

Figure 3.14. The median, interquartile range and 95% confidence intervals with individual sample points (jittered) DEHLI scores in each emergent broadleaf vegetation cover category at perennial sites with (a) smooth, (b) rippled, and (c) unbroken wave as the highest energy flow type. Big dots are outliers.

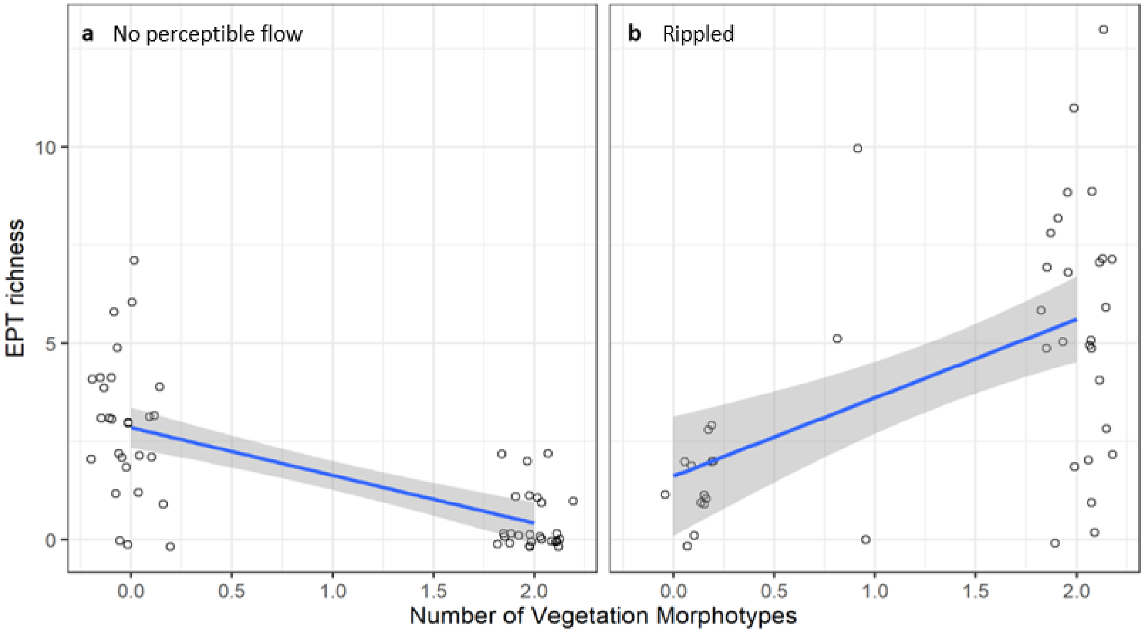

Figure 3.15. The relationship between EPT richness and the number of vegetation morphotypes at intermittent sites with (a) no perceptible flow and (b) rippled flow. The shaded area represents 95% confidence intervals.

Both sediment variables occurred in the top models for taxonomic richness, diversity and EPSI at perennial sites (Table 3.4) and for the top models for taxonomic richness, DEHLI, WHPT ASPT, EPSI and EPT richness at intermittent sites (Table 3.5). At perennial sites, diversity and EPSI were non-significant (Table A1.9). At intermittent sites, DEHLI, WHPT ASPT, EPSI and EPT richness all decreased as SiltBedCover increased (Figure 3.16, Table A1.10 and Table A1.11). At perennial and intermittent sites, richness increased at perennial and intermittent sites as the NumSed increased (Figure 3.17, Table A1.10 and Table A1.11). Richness at intermittent sites also responded to an interaction between sediment and flow: occurring at a greater rate at rippled sites with increase of 1 NumSed category in comparison to the increase at NPF sites which spanned 5 NumSed categories (Figure 3.18, Table A1.10 and Table A1.11).

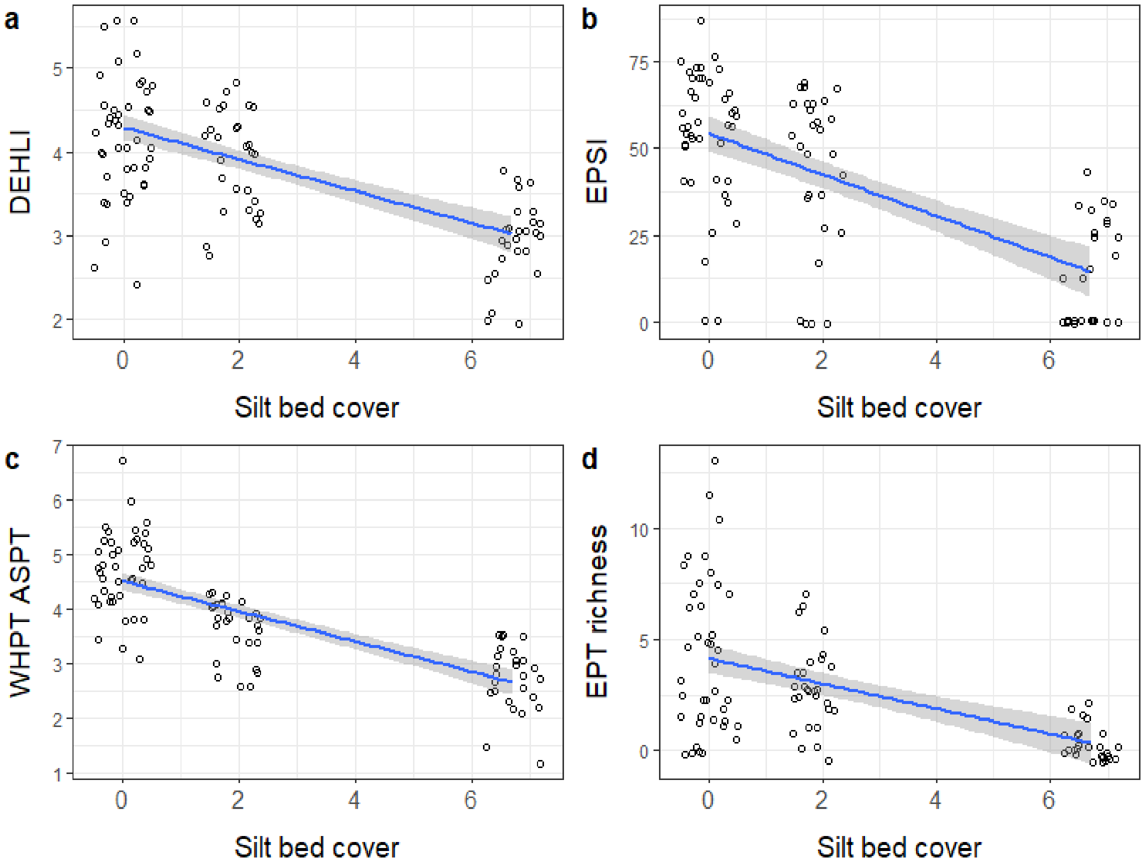

Figure 3.16. The relationship between (a) DEHLI, (b) EPSI family, (c) WHPT ASPT and (d) EPT richness, and the extent of silt bed cover at intermittent sites. The shaded area represents 95% confidence intervals.

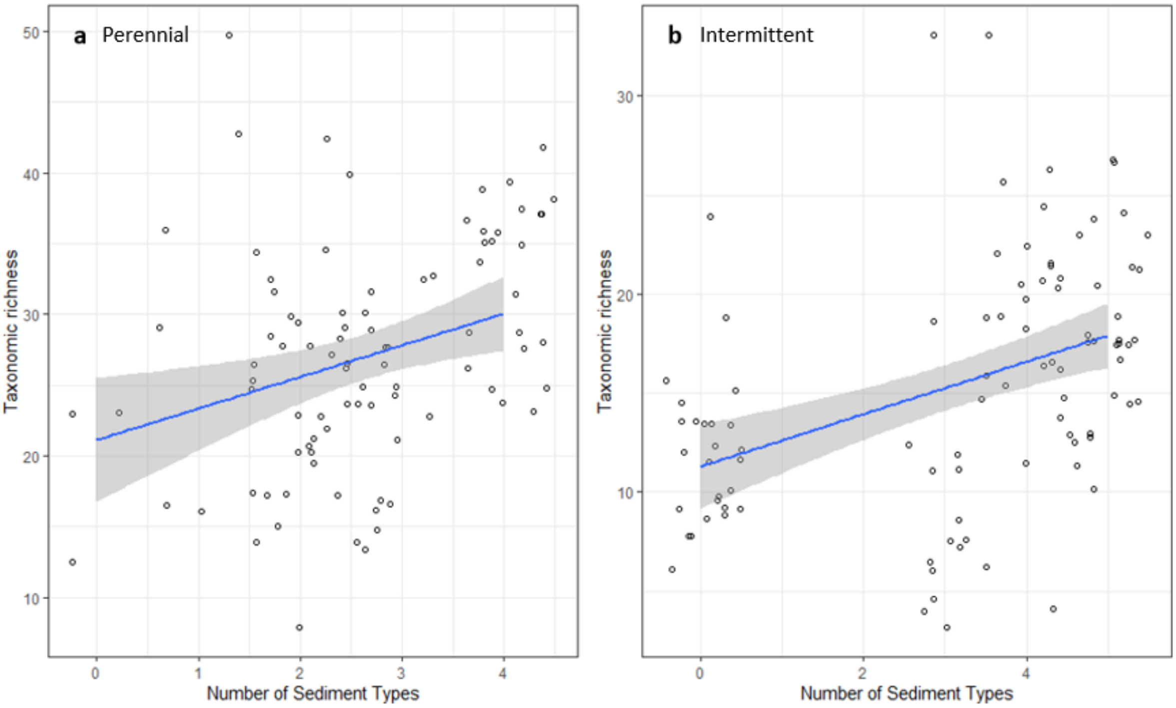

Figure 3.17. The response of taxonomic richness to the number of sediment types at (a) perennial and (b) intermittent sites. The shaded area represents 95% confidence intervals.

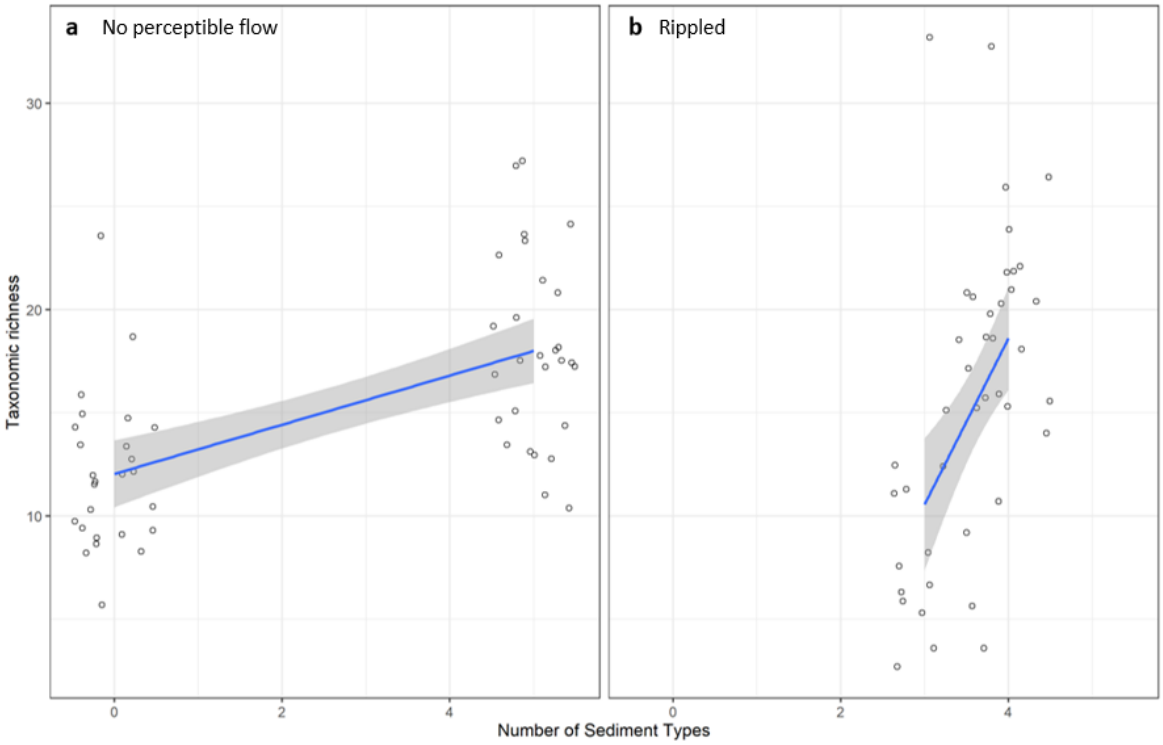

Figure 3.18. The relationship between taxonomic richness and the number of sediment types at intermittent sites with (a) no perceptible flow and (b) rippled flow. The shaded area represents 95% confidence intervals.

Flow occurred in fewer best models than both sediment and vegetation but these models often explained more of the variation in the metrics (Table 3.4 and Table 3.5). At intermittent sites, taxonomic richness, WHPT ASPT and EPT richness were higher at sites with rippled flow than at those with NPF as the HighestEFlow (Figure 3.19; Table A1.10 and Table A1.11). At perennial sites, DEHLI and EPSI were higher at perennial sites with rippled rather than smooth flow as HighestEFlow, and DEHLI and EPSI were also higher at sites with unbroken waves, although EPSI was non-significant (Figure 3.20; Table A1.9 and Table A1.11).

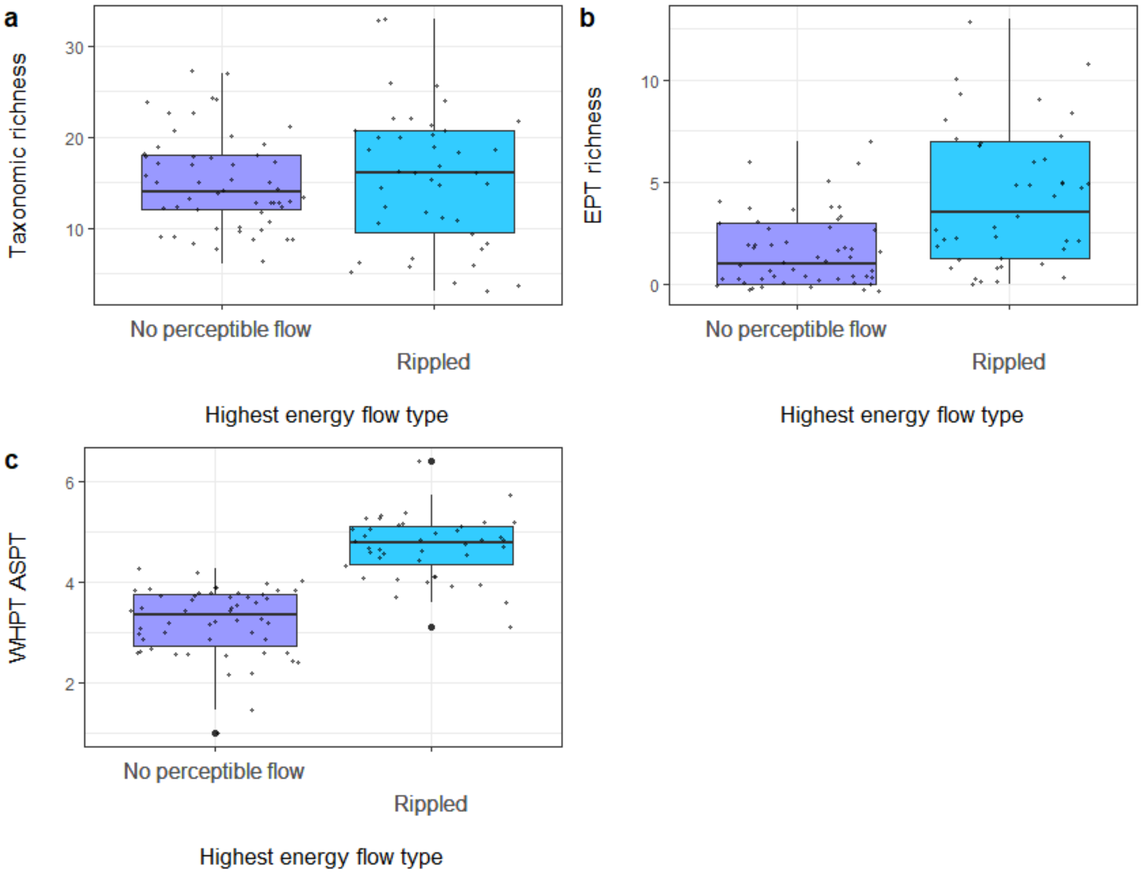

Figure 3.19. The median, interquartile range and 95% confidence intervals for (a) Taxonomic richness, (b) EPT richness and (c) WHPT ASPT at intermittent sites with no perceptible flow and rippled flow as the highest energy flow type. Big dots represent outliers.

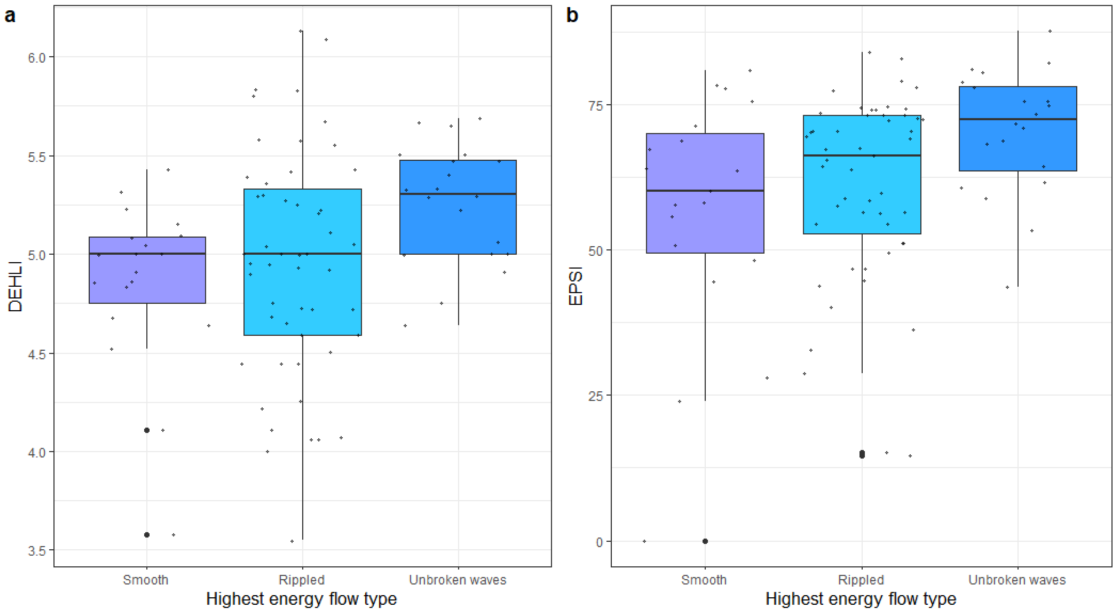

Figure 3.20. The median, interquartile range and 95% confidence intervals for (a) DEHLI and (b) EPSI family index scores at perennial sites with smooth flow, rippled flow and unbroken waves as the highest flow type. Big dots represent outliers.

3.3.4.3 *Functional Metrics*

For perennial sites, vegetation, but not flow or sediment, influenced functional metrics (Table 3.5). In contrast, flow alone was included in a top model for each metric at intermittent sites (Table 3.6), but did not have significant influence on functional metrics. Vegetation was the sole predictor in a second non-significant top model for functional diversity (Table 3.5). At perennial sites, functional redundancy was higher sites with minimal to extensive EmBroadVeg compared to with no such cover (Figure 3.21a; Table A1.9 and Table A1.11). In contrast, functional richness had a limited response, slightly decreasing, at perennial sites as the NumVegMorph increased (Table A1.9 and Table A1.11). Functional redundancy models indicated that the metric increased with NumSed at perennial sites, however, there was no relationship (Table A1.9 and Table A1.11).

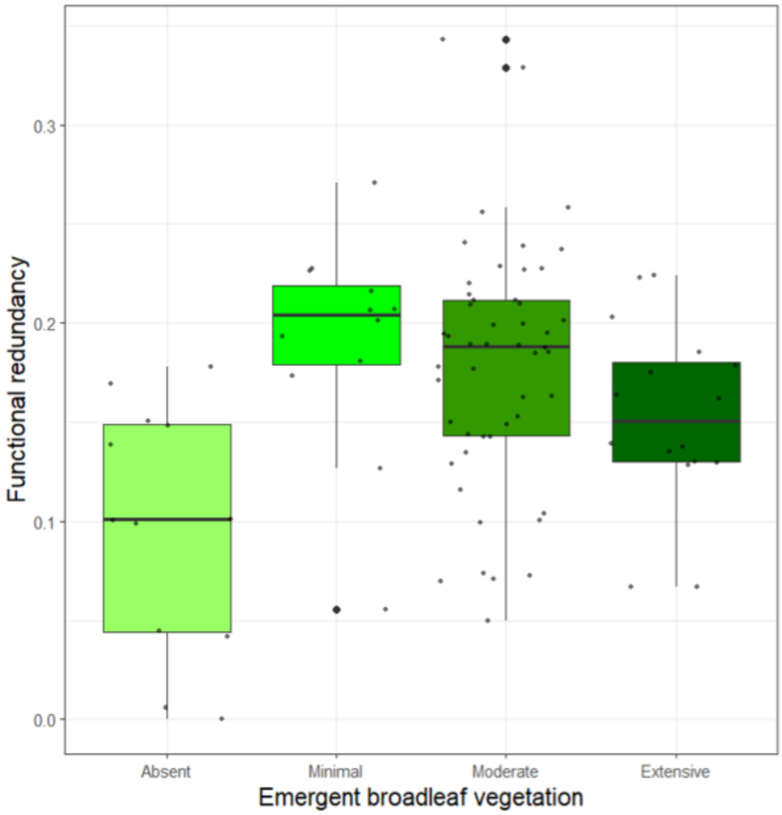

Figure 3.21. The median, interquartile range and 95% confidence intervals with individual sample points (jittered) for functional redundancy in each emergent broadleaf vegetation cover category at perennial sites. Big dots are outliers.

3.3.5 Temporal community composition differences

3.3.5.1 All-regime communities

In both spring (Figure 3.22a) and autumn (Figure 3.22b), community composition across all-regimes changed over time, with differences between years (PERMANOVA, spring: F = 4.33, df = 20, P = 0.001; autumn: F = 4.56, df = 20, P = 0.001), explaining comparable variation in community composition in both seasons ($R^2 = 0.14$). Communities had comparable composition in earlier years (1998–2013), clustering at the centre of NMDS2 and towards the lower end of NMDS1 in both seasons, whereas in the later years (2014–2018), communities had higher NMDS1 scores and were dispersed along NMDS2. Community composition also showed intra-annual variation, with later-year communities having greater intra-annual dispersion than those in earlier years (Figure 3.22; betadisper, spring: F = 7.87, df = 20, P <0.001, autumn: F = 6.67, df = 20, P <0.001).

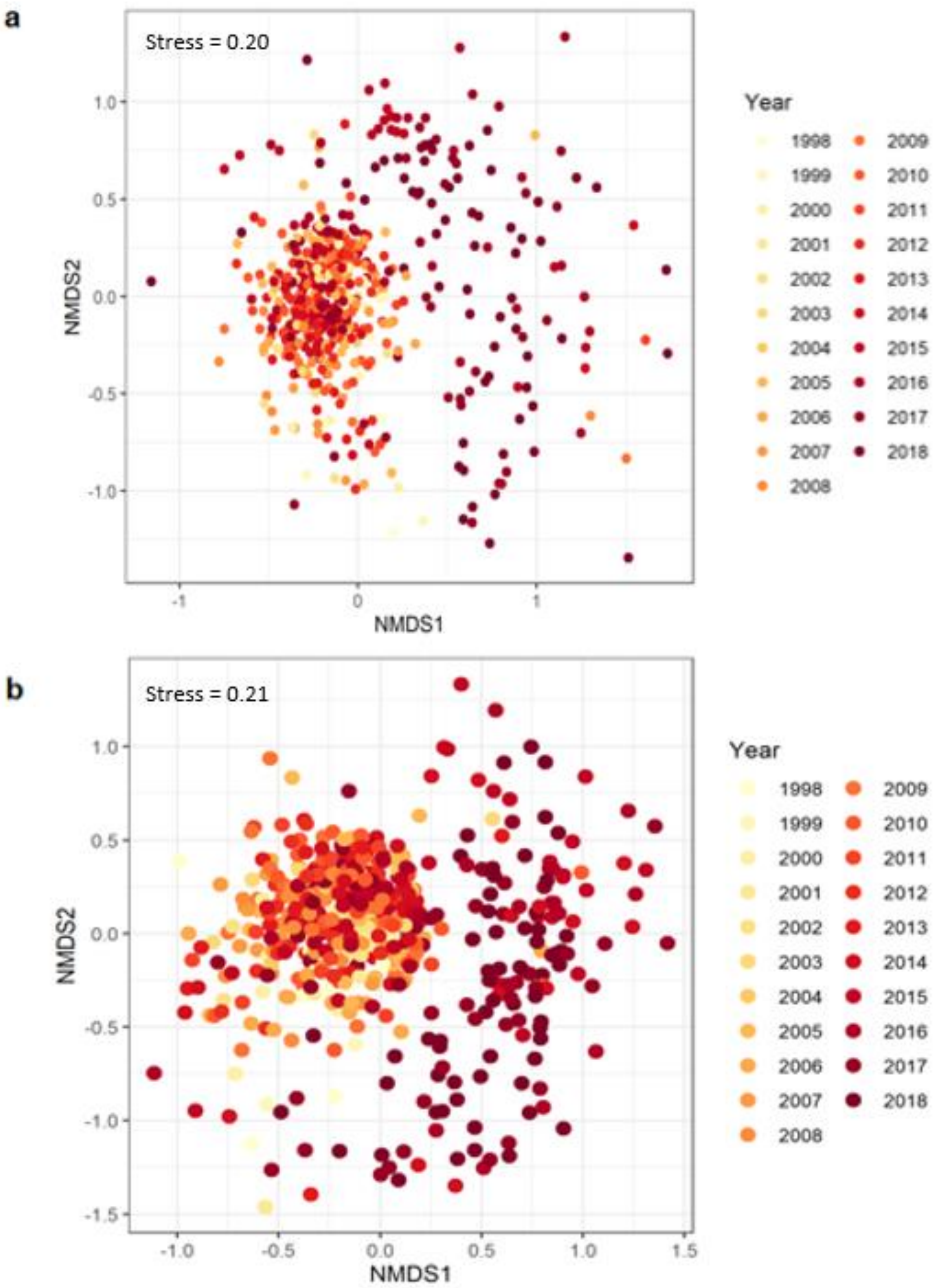

Figure 3.22. Non-metric multidimensional scaling (NMDS) ordination of macroinvertebrate community composition in (a) spring and (b) autumn 1995–2018.

3.3.5.2 Perennial and intermittent communities

Differences between years accounted for a substantial proportion of variation in community composition at both perennial sites (PERMANOVA; $R^2 = 0.35$, F = 1.52, df = 23, P = 0.001) and intermittent sites ($R^2 = 0.28$, F = 1.44, df = 20, P = 0.001). Intra-annual variability in community composition was higher in later years at both perennial and (betadisper; F = 5.72, df = 23, P <0.001) and intermittent sites (F = 3.06, df = 20, P <0.001), but changes were less pronounced in intermittent (Figure 3.23b) compared to perennial communities (Figure 3.23a), with both earlier (1995-2013) and later years (2014-2018) plotting in the main cluster.

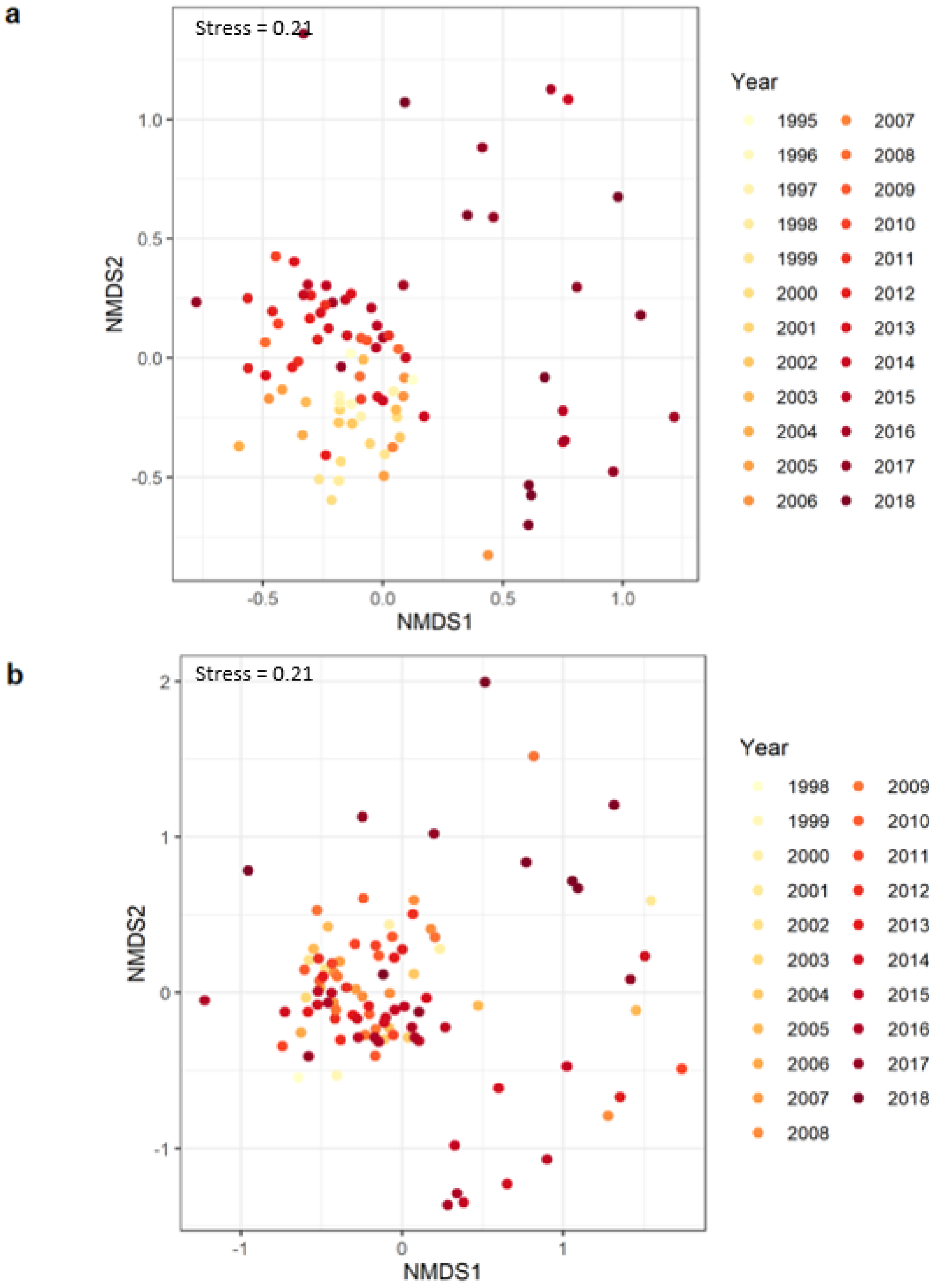

Figure 3.23. Non-metric multidimensional scaling (NMDS) ordination of macroinvertebrate composition of communities at (a) perennial and (b) intermittent sites from 1995–2018.

3.3.5.3 Individual sites

Communities at the perennial site differed among samples collected pre (1999-2005; n = 7), during (2006-2008; n = 3) or post-drought (2009-2016; n= 8; PERMANOVA, $R^2 = 0.47$, F = 6.55, df = 2, P = 0.001). Changes in composition were seen mostly along NMDS1

(39% of total variation) with pre and post communities at opposite ends (Figure 3.24). Drought year communities were span NMDS1: 2006 was closer in composition to the pre-drought communities and 2007 and 2008 were closer in composition to post-drought communities. Drought communities also had higher NMDS2 scores in comparison to pre and post communities but this accounted for less of the variation (15%).

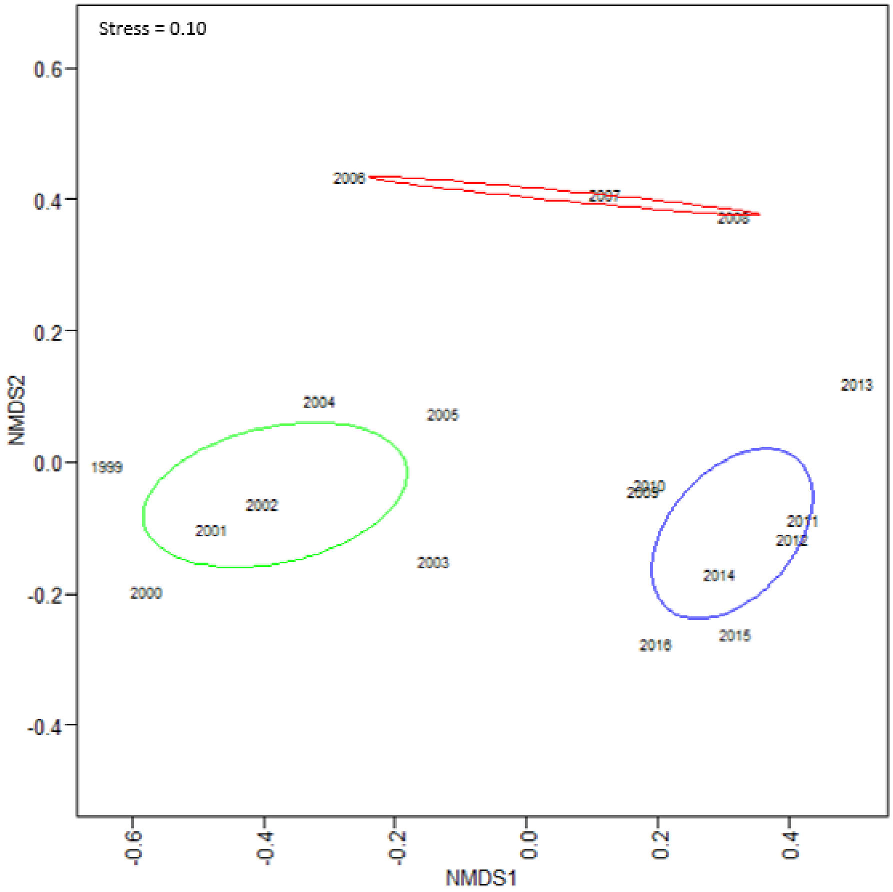

Figure 3.24. Non-metric multidimensional scaling ordination of macroinvertebrate community composition of a site on perennial stream (located on the Gade) over time with drought conditions indicated by ellipses: pre-drought (green), during drought (red) and post (blue).

Pre and post-drought community composition differed at the perennial site (pairwise PERMANOVA: $R^2 = 0.43$, $F = 9.71$, $df = 1$, $P = 0.001$) with an overall decrease in the abundance of 31 taxa from pre to post-drought, 27 of which were only found before the drought occurred and 17 taxa were only found at low abundances in pre-drought communities; SIMPER, Table A1.12) and three taxa increased: *G. pulex/fossarum, Halesus digitatus* and *Simulium* spp.. Pre and during-drought community composition also differed (pairwise PERMANOVA: $R^2 = 0.35$, $F = 4.31$, $df = 1$, $P = 0.01$). There was an increase in abundance from pre to during drought conditions in two invasive taxa (*Physella acuta* and *Pacifastacus leniusculus*), Empididae and Chironomidae, whilst several molluscs and two caddisfly taxa decreased (SIMPER, Table A1.12). Once drought conditions ended, increases were seen *G. pulex/fossarum,* Limoniidae, Oligochaeta, two caddisfly taxa and *Baetis rhodani/atlanticus*, whilst the two invasive taxa that increased during drought (*P. acuta* and *P. leniusculus*) decreased alongside *P. antipodarum* (which is also invasive)*, Sialis lutaria, Mystacides azurea* and *A. aquaticus,* leading to overall differences between drought and post-drought community composition (pairwise PERMANOVA: $R^2 = 0.33$, $F = 4.52$, df = 1, $P = 0.009$, SIMPER, Table A1.12).

At the near-perennial site, community composition also changed in response to drought state (PERMANOVA: $R^2 = 0.29$, $F = 2.25$, df = 2, $P = 0.004$). Pre-drought (2000 and 2005; n = 2) community composition was split across NMDS1, however, 2005 was most similar to post-drought communities (Figure 3.25). Drought years (2006-2007; n = 2) plot distinctly from 2005 and post-drought (2008-2017; n = 10) communities on both axes, although mostly on NMDS1 (27.1% of total variation). Differences in taxa between during and post-drought were driven by increases in 13 taxa such as *Agapetus* spp.*, E. aenea, H. angustipennis* and *Ancylus fluviatilis* (all of which had decreased from pre-drought to during-drought conditions) and *Erpobdella octoculata* and *H. stagnalis* decreased (SIMPER, Table A1.13).

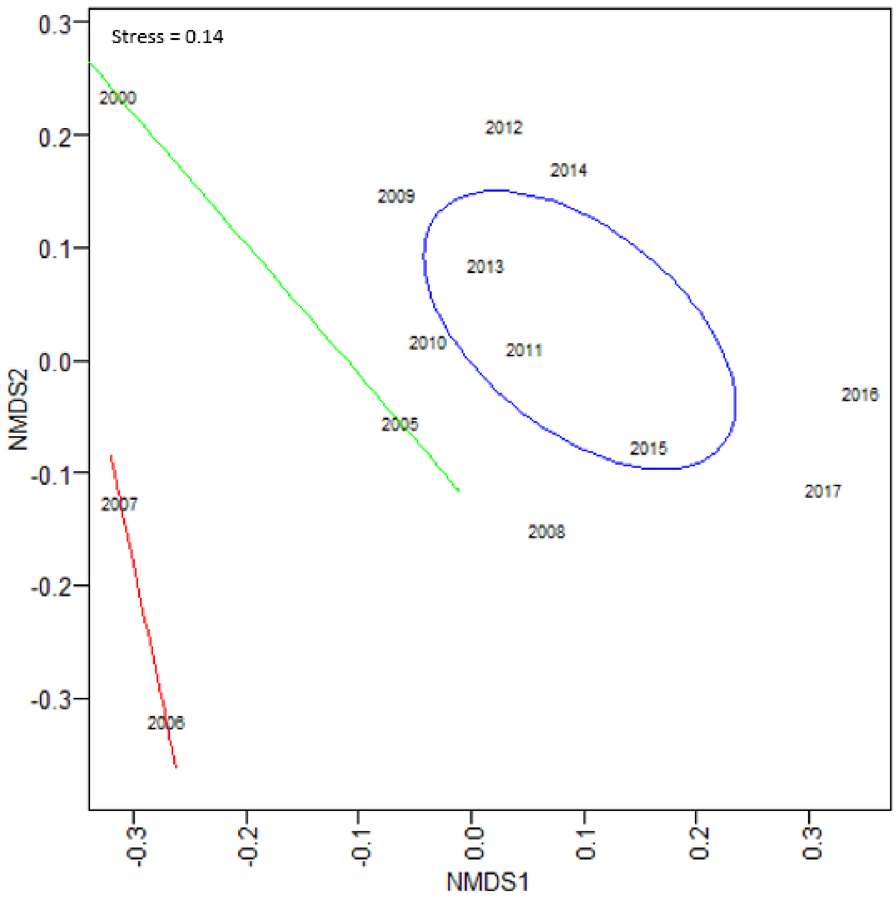

Figure 3.25. Non-metric multidimensional scaling ordination of macroinvertebrate community composition of a near perennial stream (located on the Mimram) over time with drought conditions indicated by lines/ellipses: pre-drought (green), during drought (red) and post (blue).

At the partially intermittent site, community composition differed between drought states (PERMANOVA: $R^2 = 0.33$, $F = 3.25$, df = 2, $P = 0.001$), with communities moving along NMDS1 over time as conditions changed from pre (1999-2001; n = 3) to post-drought (2009-2017; n = 8; Figure 3.26). Difference between pre and post-drought communities accounted for the most variation (pairwise PERMANOVA: $R^2 = 0.32$, $F = 5.27$, df = 1, $P = 0.001$), influenced by abundance increases in three caddis species and *G. pulex/fossarum* (SIMPER, Table A1.14) and decreases in 17 taxa, 10 of which were abundant before the drought (SIMPER, Table A1.14). Pre and during-drought (2006-2008; n = 3; pairwise PERMANOVA: $R^2 = 0.23$, $F = 1.49$, df = 1, $P = 0.023$), and during and post-drought communities (pairwise PERMANOVA: $R^2 = 0.17$, $F = 2.12$, df = 1, $P = 0.013$) also differed, with *Gyraulus albus, Dendrocoelum lacteum* and *Caenis luctosa/macura,* along with several other taxa, increasing in abundance from pre to during-drought conditions, but decreasing from during to post-drought conditions (SIMPER, Table A1.14).

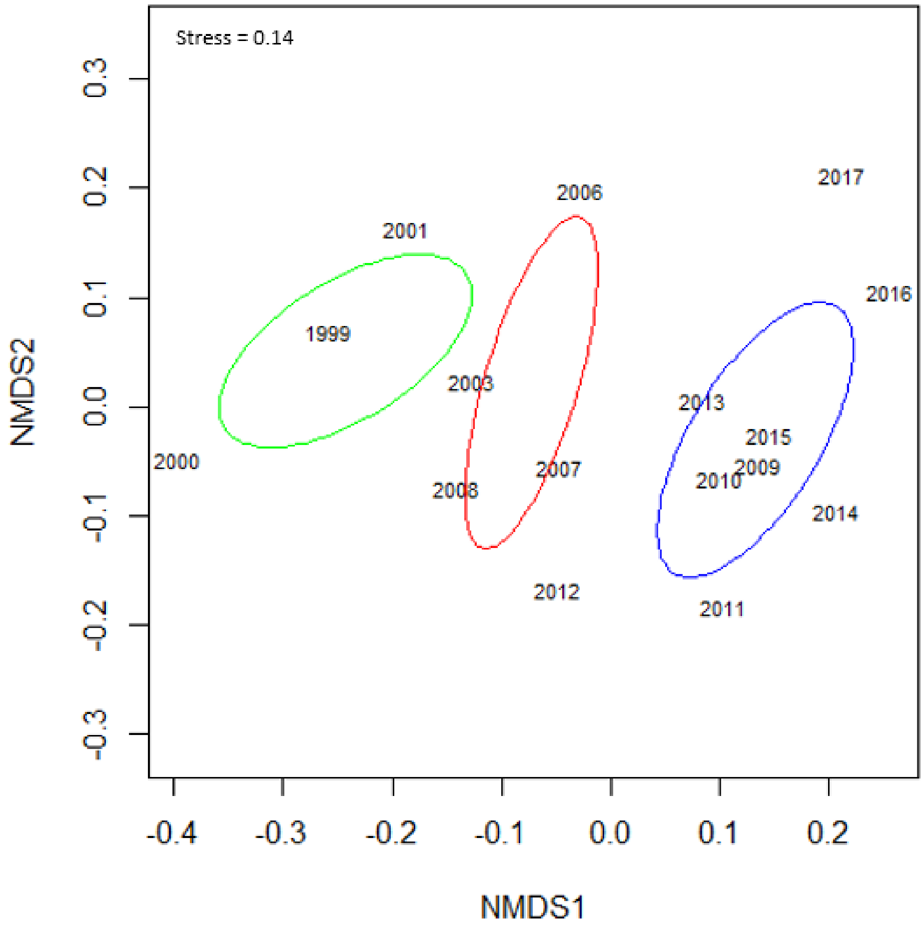

Figure 3.26. Non-metric multidimensional scaling ordination of macroinvertebrate community composition of a partially intermittent stream (located on the Beane) over time with drought conditions indicated by lines/ellipses: pre-drought (green), during drought (red) and post (blue).

Finally, the intermittent stream community composition changed over time overall (PERMANOVA: $R^2 = 0.28$, F = 1.96, df = 2, P = 0.014, Figure 3.27). Pre-drought communities (1999 and 2005, n = 2), varied, although 2007 and 2008 communities did appear to differ from most post-drought (2009-2017; n = 8) communities across NMDS2, this axis only explained 20%, compared to NMDS1 which explained more of the variation (23%). Only one taxon (*Stagnicola palustris/fuscus/corvus*) contributed to differences between pre and during drought communities, increasing in abundance. Two taxa decreased, and one increased, in abundance from the during drought state to the post-drought state, and between pre and post-drought states (SIMPER; Table A1.15).

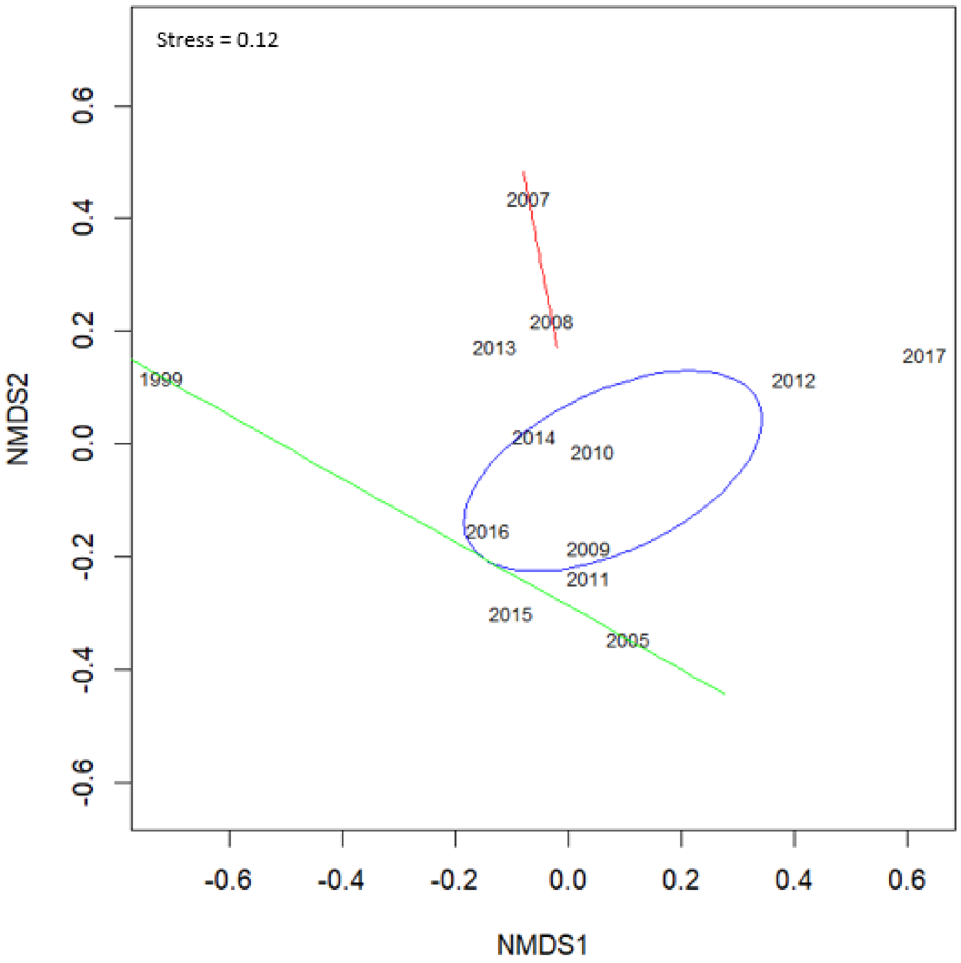

Figure 3.27. Non-metric multidimensional scaling macroinvertebrate community composition of an intermittent stream (located on the Beane) over time with drought conditions indicated by lines/ellipses: pre-drought (1999), during drought (red) and post (blue).

3.4 Discussion

Aquatic macroinvertebrate community responses to habitat changes influenced by three key factors, flow, sediment and vegetation, have been well-characterised individually and in tandem (Rempel et al., 2000; Blöcher et al., 2020). However, their concurrent independent and interactive effects remain poorly understood (Beermann et al., 2018). Additionally, whilst community responses to hydrological variability are increasingly well-understood in streams with contrasting permanence regimes (Rempel et al., 2000; Stubbington et al., 2017), relatively few studies distinguish regime-specific responses beyond the three major categories of perennial, intermittent and ephemeral flow (but see e.g. Sarremejane et al., 2019; 2020; 2021) or include consideration of morphological quality. To address these knowledge gaps, I characterised macroinvertebrate community responses to flow and morphological condition (sediment and vegetation) in streams with flow regimes ranging from perennial to seasonally intermittent (and encompassing near-perennial and partially intermittent), undertaking analysis for all regimes and then separately for communities at sites with perennial and intermittent regimes.

Flow was a major influence on communities in the all-regime analysis (H1), whereas sediment and vegetation were mostly influential within interactions with each other and/or flow (H2 and 3). In addition, perennial and intermittent results community composition responses differed in general, and in their responses to flow, sediment and vegetation. However, perennial and intermittent community metrics (which indicated either an increase in richness or were indicative of unimpacted conditions relating to humans and/or drought) responded similarly to each other, in contrast to H4. Vegetation was a major influence on both perennial and intermittent communities: whereas vegetation at its interactions with sediment largely influenced the former, vegetation and flow influenced the latter. Overall, flow, sediment and vegetation explained more variation in intermittent than perennial communities.

Biological data spanned 23 years, which enabled characterisation of temporal changes in macroinvertebrate communities. Communities became compositionally different and more variable since 2014 compared to earlier years (1998–2014), largely due to changes in the abundance of common taxa. Perennial and near-perennial communities shifted compositionally during drought years with indication of some recovery post-drought to pre-drought composition. Partially intermittent communities shifted completely during and post drought, and intermittent communities showed limited response to drought, with the fewest taxa significantly differing between drought states, although there was low level of replication in pre and drought communities (H5).

The results of this research highlight that considering flow, sediment and vegetation simultaneously can enhance the understanding of their independent and interactive effects upon macroinvertebrate communities. Additionally, the reduced hydrological influence and increased influence of vegetation in the individual perennial and intermittent analyses highlights the importance of considering communities separately in management plans to fully understand influences beyond flow type.

3.4.1 Community responses to flow, vegetation, sediment

An increase in flow complexity at a site (as represented here as the highest energy flow type) potentially provides a greater variety of low-to-high-velocity hydraulic habitats, dependent on channel morphology (Stanley et al., 1997; Reid & Thoms, 2008; Rosenfeld, 2017; Kärnä et al., 2018), and an increase in flow velocity provides taxa with well-oxygenated habitats and potential refuge during low flows (Negishi et al., 2002). This is reflected by increases in some taxonomic metrics, indicating a higher richness and abundance of rheophilic taxa, with higher energy flow types. However, whilst for some metrics, scores were higher at sites with unbroken and broken waves in comparison to those with lower energy flows e.g. NPF (no perceptible flow) and smooth, there was no difference between free fall, though this is limited by the low replication of free fall sites, or sometimes broken waves, and NPF. This pattern could reflect the exclusion of all but highly adapted specialist taxa, such as *Simulium* spp. and *Agapetus* spp., from the highest energy flow types (Baker et al., 2011; Clayton et al., 2016).

Taxa at reaches with intermittent flow regimes are often adapted to flow variability or slower flow velocities, or can be generalist in nature (Stubbington et al., 2017). Therefore, the similar taxonomic metric responses to flow between perennial and intermittent communities may reflect community adaptation to their respective flow regimes. However, community composition responses differed between perennial and intermittent sites, with flow explaining less variation in in perennial community composition, due to the sites having stable flow. At intermittent sites, the compositional differences between sites with different highest energy velocity types were driven largely by lower abundances of generalist taxa at higher energy sites (e.g. Chironomidae and Oligochaeta), which include species that inhabit lentic habitats and tolerate associated abiotic conditions such as increased silt, and low oxygen concentrations (Duan et al., 2009; Beerman et al., 2018).

Vegetation influences macroinvertebrate communities through providing habitat, food and shelter from predation (Duan et al., 2009; Warfe & Barmuta, 2004) and indirectly by altering both flow variability and sediment composition (Gurnell, 2014). In this study, vegetation had a strong influence on perennial and intermittent community metrics, both responding positively to an increase in emergent broadleaf vegetation from no to moderate cover and an increase in the number of vegetation morphotypes. The increase in vegetation morphotypes represents an increase in structural habitat complexity (Ferreiro et al., 2011, Walker et al., 2013), with different macrophyte structures such as emergent broadleaf (e.g. *Rorippa nasturtium-aquaticum*) and submerged fine leaf (e.g. *Ranunculus* spp.) supporting macroinvertebrates with differing habitat preferences (Taniguichi et al., 2003; Wolters et al., 2017). Additionally, compositional responses were variable in response to vegetation, with dissimilarities between sites with absent and extensive emergent broadleaved cover driven by increases in taxa that use vegetation as habitat (e.g. *Pisidium* spp. and *Stagnicola palustris/fuscus/corvus*), and decreases in generalist taxa such as *Gammarus* spp. Such vegetation influences flow at a microhabitat-scale, with differing morphotypes decreasing velocity at differing rates (Clarke, 2002), with the resultant hydraulic habitat heterogeneity allowing a greater range of taxa to inhabit sites (Walker et al., 2013; Wolters et al., 2017). However, extensive vegetation cover reduced some taxonomic and functional metrics across all-regimes, intermittent and perennial communities. Extensive cover can clog the channel, negatively affecting macroinvertebrates by increasing silt accumulation, reducing velocities and the cover of other vegetation types, and reducing the spaces between macrophyte structures (Gurnell, 2014; Wolters et al., 2017). Thus, extensive vegetation may create a more uniform habitat supporting fewer macroinvertebrate taxa.

Sediment was the least influential of the three key factors, explaining little variation in both the composition of communities at perennial and intermittent sites and related biological metrics. Perennial communities typically responded to sediment as part of an interaction, whereas intermittent communities responded only to sediment or responded independently to sediment and flow or vegetation. The greater influence at communities at intermittent sites could be due these sites characterised by slower flows and higher silt cover (Wright, 1992; Dewson et al., 2007). For all flow regimes, taxa richness increased with sediment complexity (as indicated by the number of sediment types), likely because, as with flow and vegetation, each additional sediment type increased the availability of habitats for taxa with different preferences. An increase in sediment complexity also reflects the higher hydraulic variability and the influence of plants at a microhabitat scale. The differences in community composition in response to sediment were driven by generalist taxa occurring at sites with fewer sediment types, and those with more specific habitat preferences which co-occurred at sites with higher sediment complexity (Duan et al., 2009; Beermann et al., 2018). At intermittent sites, silt cover influenced communities more than the number of sediment types. Silt has detrimental impacts on macroinvertebrates, causing smothering (as silt particles can accumulate in organs, including gills), and burial due to the instability of fine particles (Armitage et al., 1999; Wood et al., 2005; Jones et al., 2012; McKenzie et al., 2020). As such, these intermittent community responses indicate that the negative effects of silt may override any effects of increasing sediment complexity, or the silt may cover any sediment complexity present, particularly in slow flowing streams where silt is deposited more readily over the whole bed (Gurnell, 2014). Silt also has the potential to reduce habitat and refuge availability (Jones et al., 2012), which may have increased importance in intermittent streams if taxa are prevented from accessing dry-phase refuges, such as the hyporheic zone (Stubbington, 2012).

Taxonomic diversity, one of the only two metrics influenced by taxa abundance, did not respond to flow, sediment or vegetation in all-regime and intermittent analyses. Whilst characterisation of variability in abundance was beyond the scope of this study, taxon replacements may have had a stabilising influence on abundance, with no overall loss in abundance. WHPT ASPT and EPT richness did not respond to any environmental variables at perennial sites, suggesting that these streams are less influenced by human impacts and water quality issues, whereas intermittent sites (where the metrics did respond) may be more variable in their conditions (Stubbington et al., 2017). At perennial sites, EPSI increased in response to the highest energy flow type and decreased in response to both flow and sediment interactions with vegetation. However, the top EPSI models did not identify an independent response to silt cover, which may indicate flow as a ‘master’ variable (Poff et al., 1997) that alters community responses to sediment (Turley et al., 2016). Functional metrics were also relatively unresponsive in comparison to their taxonomic counterparts. The limited response could be due to taxa filling the same functional niche and therefore, there would be limited changes between sites if communities support different taxa with the same traits. Additionally, there is a lack of trait data at species level for dipterans and chironomids, which may underrepresent the functional diversity of these taxonomic groups (Hamilton et al., 2019).

3.4.2 Interactions between flow, vegetation and sediment and their influence on macroinvertebrate communities

The interaction between flow and sediment influenced biological metrics in both all-regime and intermittent analyses. Concurrent declines occurred in taxa richness in response to the interaction of the highest energy flow type and the extent of silt on the bed. Taxa that inhabit streams with faster flowing water are likely to have more specific preferences for well-oxygenated, coarse-grained habitats, and therefore less likely to occur in both slow-flowing and silt-impacted streams, such as those conditions found typically in intermittent streams (Dunbar et al., 2010; Turley et al., 2014). However, taxonomic richness in sites with lower energy flows (e.g. smooth flow) had either a positive relationship with increasing silt or decreased more slowly than at higher energy flow sites. Chalk streams have typically low-energy flows (Berrie, 1992), increasing silt deposition within the channel, and have additionally been impacted by humans in terms of water abstraction and increasing silt from agricultural practices (Wright, 1992; Mainstone, 1999; Rangley-Wilson, 2021). Therefore, communities in slow-flowing sites may be accustomed to silt exposure and its impacts (Mainstone, 1999; Bradford, 2002). In the all-regime analysis, at sites with rippled flows, EPSI (an index of community sensitivity to silt; Turley et al., 2015) barely increased as the number of sediment types increased, which was unexpected as more sediment types typically would be reflective of sites with higher proportions of gravels and cobbles and less silt. This was likely due to the influence of vegetation. At sites with extensive vegetation, there was a very low increase in EPSI as the number of sediment types at sites with extensive vegetation, which may have trapped silt. Therefore, even when the number of sediment types increased silt may still have influenced communities, whilst at other sites with lower vegetation cover EPSI increased, as the faster flows could move the silt away.

Intermittent sites saw interactions between flow and the number of vegetation morphotypes, reflecting an increase in EPT richness. At intermittent sites with NPF, EPT richness declined with an increase in vegetation morphotypes, indicating the negative effects of extensive vegetation when flow is already reduced. Vegetation can slow flows and thus facilitate silt accumulation (Clarke, 2002; Wolters et al., 2017), and an increase in the vegetation at sites which already have low/no flows may negatively impact EPT taxa which require faster flowing conditions and prefer sites with no silt (Jones et al., 2011; Beerman et al., 2018).

Both perennial and intermittent communities were influenced by interactions between sediment and vegetation. At intermittent sites, moderate vegetation cover supported a higher taxonomic richness which increased with increasing sediment complexity, which provided additional habitat (Luhar et al., 2008). In contrast, at perennial sites, where vegetation was extensive, again, there was potential silt accumulation, reducing sediment complexity.

3.4.3 Community composition responses to time and drought

Temporal changes had the largest influence on communities of all regimes. Post-2014 communities had lower abundances in common taxa in later years, and an increase in infrequently occurring taxa than communities pre-2014. Sampling changes, both in the field and identification, at the Environment Agency may have contributed to these temporal changes. Additionally, improvements in water quality over the last twenty years (Vaughan & Gotelli, 2019), invasive species (e.g. signal crayfish) and long term climatic changes may have contributed towards this variability (Watts et al., 2015; Kakouei et al., 2018). It is unlikely these compositional changes are due to variability in habitat conditions over time, as informed by expert opinion (Pers.Comm.).

The responses of the communities from the different flow regimes (perennial, near perennial, partially intermittent and intermittent) to drought could reflect their ability to be able to resist and recover from climate change impacts, which is predicted to increase the occurrence of extreme conditions of drought, drying and flooding (Masson-Delmotte et al., 2021). Communities at some perennial sites responded strongly to drought years (2005-2007; Marsh, 2007), with community composition changing strongly in these years, as aquatic habitat availability and connectivity between habitats decreased (Lake, 2003). Perennial communities then shifted to an alternative post-drought state in which the abundance of some but not all taxa recovered to pre-drought levels (Wright et al., 2002), with individuals potentially recolonising from drought refuges (Boulton, 2003; Sarremejane et al., 2021; Figure 3.28a).

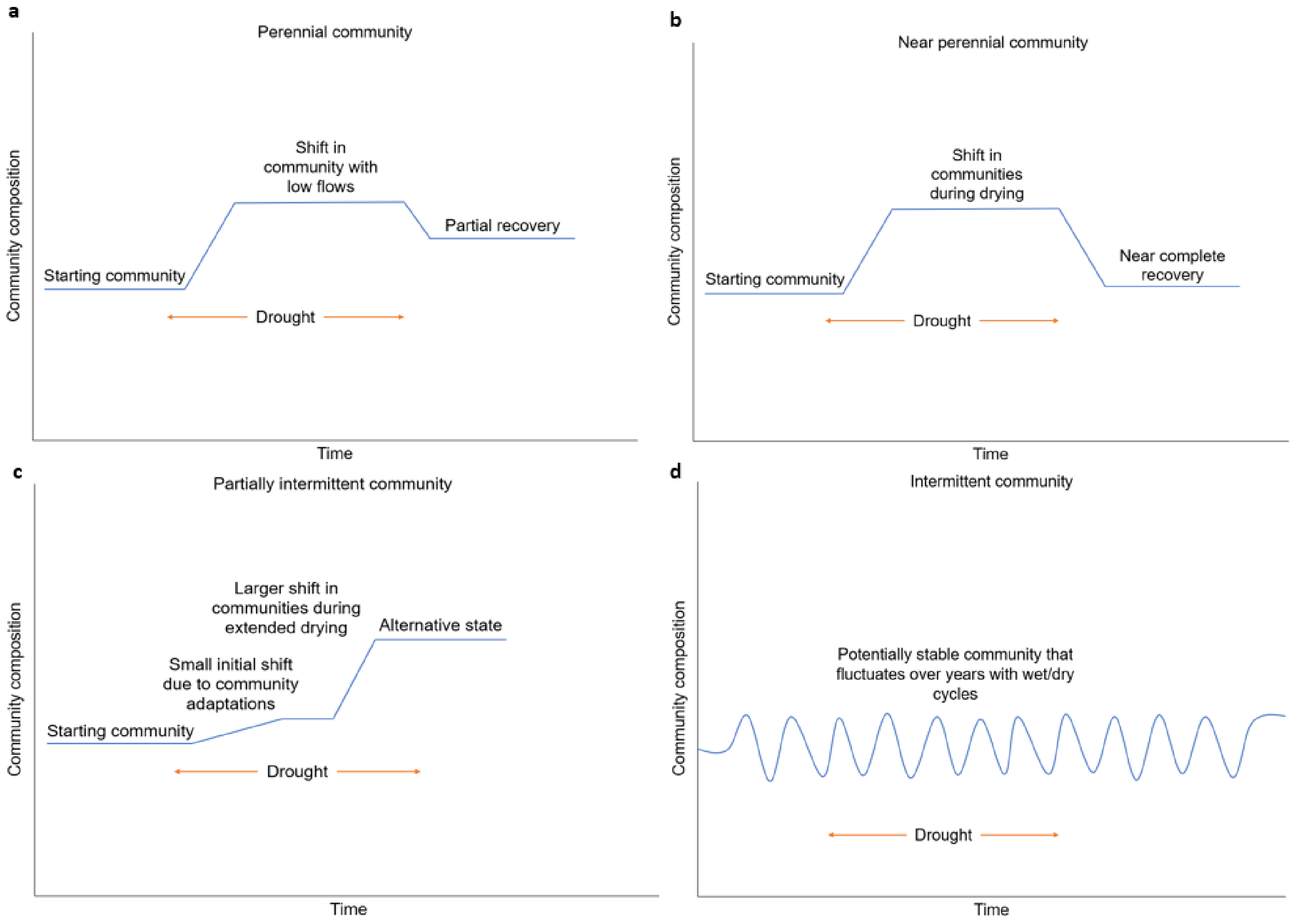

Figure 3.28. Conceptual models of the macroinvertebrate community compositional changes (arbitrarily defined) over time and during a drought period at a) perennial, b) near perennial, c) partially intermittent (unpredictably dries) and d) intermittent sites.

The community at the near perennial site showed similar responses to the those at the perennial site, changing in composition during drought years. However, the near perennial community recovered more readily than the perennial one returning to a baseline (although not completely to pre-drought composition) following drought (Figure 3.28b). The responses of the perennial and near perennial site communities is almost the reverse of what was hypothesised in the conceptual model (Figure 3.1), with near perennial site recovering nearly completely and the perennial site only partially recovering (Figure 3.28). The difference in the amount of recovery seen between perennial and near perennial site could reflect site-specific habitat difference. The fastest flow velocities at the perennial site was rippled flow and the near perennial was unbroken waves. Therefore, the near perennial site supported a greater variation in flow microhabitats and potentially creating more refuges for communities. This indicates that the presence of faster flow habitats play an essential role in the resilience of invertebrate communities to the effects of drought (Ledger et al., 2012).

The partially intermittent site changed the most in composition between pre and post-drought communities, with the most significant difference seen between drought and post-drought conditions (Figure 3.28c). At this site, flow and vegetation complexity were low, and there were only three sediment types. This lack of variation in microhabitats could have meant limited refuges for macroinvertebrate communities, in the change in composition after the drought with different species recolonising the site or similar species in lower abundances. This suggests that the site had lack of resistance to drought and reduced resilience following the drought, similar to patterns observed in Sarremejane et al. (2020).

The intermittent site community, whilst sometimes responding to changes over time, was the least affected by potential drought of the four regimes. The limited response to drought could be linked to higher beta diversity, as intermittent community composition varied more within than between years (Bogan et al., 2017), which would promote resilience amongst communities, and instead intermittent communities fluctuate between wet and dry cycles (Sarremejane et al., 2020; Figure 3.28d). Additionally, the intermittent site had five sediment types, the coarsest of which was cobble. This variation in sediment conditions may have allowed some macroinvertebrates to take refuge in the hyporheic zone, thus promoting resistance within the community (Wood et al., 2010; Stubbington, 2011).

Intermittent communities showed no seasonal responses (spring and autumn), in comparison to their perennial counterparts, contrary to what has previously been found (e.g. Bonada et al., 2007; Giam et al., 2017). Intermittent macroinvertebrate communities typically comprise generalist taxa which are adapted to low flows and potential drying to tolerate these conditions, resulting in a stable community of a select group of taxa (Storey & Quinn, 2008; Mathers et al., 2019). In contrast, perennial communities typically encompass a greater range of taxa with a variety of flow habitat preferences which results in a higher turnover of taxa as conditions change with season (Bêche et al., 2006).

3.4.4 Management Implications

Application of the study results can inform restoration practices and subsequent monitoring but should be interpreted considering the study limitations. MoRPh variables capture macroscale environmental conditions, and therefore, may not characterise community responses to microscale variability in flow, sediment and vegetation changes (Clarke et al., 2002; Gurnell, 2014). Additionally, MoRPh data were collected once and in different years, thus overlooking any seasonal and long-term variability in the morphological conditions, such as plant growth.

Study results indicate that restoration measures traditionally applied to perennial streams can also potentially benefit macroinvertebrate communities in intermittent streams. For both flow and vegetation, there is a ‘goldilocks’ zone which provides suitable habitat for diverse macroinvertebrate communities across all flow regimes (Katz et al., 2012). Therefore, restoration schemes should try to restore the natural processes that promote appropriate microhabitat conditions both at reach scale and throughout the river network to improve the effectiveness of restoration and promote network-scale community resilience (Negishi et al., 2002; Verdonschot et al., 2016). This would restore relatively high energy flows (unbroken waves and broken waves) and supporting macrophyte communities with moderate cover. In turn this restoration of diverse flow habitats and vegetation should facilitate the development of sediment complexity, restricting surface silt cover to the channel margins, and thus also supporting diverse macroinvertebrate communities (Barnes et al., 2013). In perennial reaches, restoration should consider the interactions between sediment and vegetation, with too little or too much vegetation cover causing negative impacts on invertebrate communities, even at sites with high sediment complexity (Sand-Jensen & Mebus, 1996). Restoration of intermittent reaches should promote the mobilisation of silt following flow resumption, to remove any that accumulates in the centre of the channel bed, in particular in low-energy chalk streams (Wright, 1992; Mainstone, 1999). Riparian and catchment actions to reduce fine sediment inputs may be particularly valuable in their intermittent reaches (Gurnell & Grabowski, 2016) such as catchment sensitive farming, which can reduce the risk of fine sediment from agriculture (Naura et al., 2016).

Finally, the results of this chapter highlighted that the analysis of biological metrics and community compositional data, and that considers both the individual environmental parameters and their interactions, are important to make an informed design and implement effective restoration methods. The top models, which included all three environmental variables (flow, sediment, and vegetation), typically explained more variation in the response metrics than those composed of one or two variables. Also, whilst, univariate metrics are used by managers and researchers to track taxonomic responses to environmental parameters in stream ecosystems (Extence et al., 1999; Turley et al., 2016), compositional responses differed to those summarised by community metrics.

To conclude, the results of this chapter indicated that whilst flow complexity was the overriding variable, vegetation and sediment complexity were also important influences on macroinvertebrate communities, and an increase in all three of these variables generally had positive effects on communities. Additionally, these environmental variables aid in providing functioning habitats and refugia during drought periods, increasing community resilience. Also, this chapter demonstrated the value of incorporating interactions to fully assess the impacts of flow, sediment and vegetation on communities, and that community composition responses may reveal additional information such as specific changes in specialist taxa not gathered by metrics, particularly in intermittent streams.

Chapter Four: Dry-phase plant communities and their potential as biomonitors

4.1 Introduction

Temporary streams, which sometimes stop flowing at a point in space or time and often dry, dominate global river networks (Messager et al., 2021) and support diverse communities of both aquatic and terrestrial taxa (Katz et al., 2012; Corti & Datry, 2016; Bunting et al., 2021). A major threat to these ecosystems and biological communities is eutrophication: excessive inorganic nutrient (in particular nitrogen and phosphorus) input through human pressures such as agriculture, wastewater, and urban runoff (Schindler, 2006; Conley et al., 2009; Hautier et al., 2009). Temporary streams are also under threat from other human impacts such as climate change, groundwater abstraction, and land-use change. Both climate change and over-abstraction can increase the duration of the dry phase and increase its spatial extent (Döll & Schmied, 2012). Land-use change, including increasing agriculture and urbanisation, can increase fine sediment inputs into streams, increase abstraction pressures, and modify channel morphologies (Wood & Armitage, 1997; Nikolaidis et al., 2013; Addy et al., 2016).

It is important that we protect our watercourses from the influence of human impact and effectively manage them to achieve good ecological health and meet statutory requirements (e.g. the EU Water Framework Directive 2000/60/EC (WFD), the Australian National Water Initiative and the US Clean Water Act). To monitor the ecological health of a water body, biological metrics are used to measure changes in taxonomic values in response to a stressor gradient (Karr & Chu, 1999). Metrics belong to one of four groups (Hering et al., 2006): compositional (e.g. proportion of a taxonomic group), taxonomic richness/diversity (e.g. Shannon H diversity), a measure of known tolerance to stressors, such as Ellenberg indices (Ellenberg et al., 1992; Hill et al., 1999), and functional (e.g. representing biological traits such as body size, life cycles). In addition to individual metrics, multimetric indices (which include several metrics) are frequently used to assess ecosystem health in freshwaters, to improve the accuracy of responses to environmental variables including those representing human impacts (Barbour et al., 1995; Hering et al., 2006).

To effectively monitor responses of temporary stream communities to human impacts, the aquatic and terrestrial biota present during flowing, ponded and dry phases should be considered (Corti & Datry, 2016; Stubbington et al., 2018). Despite this, dry-phase monitoring remains limited, with current biomonitoring focusing almost exclusively on the flowing phase, because the knowledge of aquatic taxa and biomonitoring methods used in perennial rivers can be easily applied to flowing-phase communities. Research has explored dry-phase invertebrate communities that include both aquatic and terrestrial taxa, and has established their potential as biomonitors of ecological status (Steward et al., 2018; Stubbington et al., 2019; Bunting et al., 2021). However, dry-phase plant communities remain poorly characterised, with terrestrial taxa often grouped as terrestrial grasses or terrestrial herbs (Holmes, 1999; Sabater et al., 2017; Westwood et al., 2021). In contrast, plants have been used for monitoring in many ecosystems, including aquatic taxa in perennial rivers (in the UK, Mean Trophic Rank; Holmes et al., 1999; LEAFPACS; WFD-TAG, 2014; Ellenberg; Ellenberg et al., 1991; Hill et al., 1999), and may prove particularly useful for dry-phase biomonitoring in cooler, wetter temperate climates where in-channel communities retain cover during dry-phases.

The ecological impacts of eutrophication are widely monitored using aquatic plant communities in perennial rivers and other freshwater and terrestrial ecosystems (Holmes et al., 1999; Hill et al., 1999; Birk et al., 2012; Stromberg & Merritt, 2016). This is due to the strong links between phosphorus and inorganic nitrogen and both plant growth and cover (Bieleski, 1973; Smith et al., 1999; Vance et al., 2003), and community composition (Schindler, 2006). Whilst very low nutrient concentrations can limit plant growth and diversity (Grime et al., 1997; Smith et al., 1999), high concentrations in soils and sediments can cause shifts in composition (Hautier et al., 2009; Kneitel & Lessin, 2010), increases in invasive species (Chase & Knight, 2006) and decreases in overall richness. These changes can lead to morphologically uniform communities due to the dominance of competitive species (Grime, 1979; Cleland & Harpole, 2010) or families such as grasses (Poaceae spp.; Critchley et al., 2002; Stubbington et al., 2019). There are also well-established links between phosphorus and nitrogen: low concentrations of either nutrient can limit plant growth, even if the other nutrient is highly available (Hood, 2001; Critchley et al., 2002).

Additionally, shading (which can also reflect land-use impacts) influences in-channel plant communities (Devkota et al., 1997; Dodd et al., 2005). Historically, riparian trees were removed to accommodate increasing urbanisation and agriculture and to improve access to the channel for dredging (Dawson & Haslam, 1983). Shading alters plant communities (Dawson & Kern-Hansen, 1979; Köhler et al., 2010), by reducing in-channel temperatures (Kalny et al., 2017) and limiting the abundance of dominant species by reducing light availability (Dawson & Kern-Hansen, 1979).

Some other habitat characteristics represent direct human impacts, such as channel modification, and trampling, by both humans and livestock, and can influence plant morphology and reduce diversity (Sun & Liddle, 1993; Santoro et al., 2012). During flowing phases, interactions between the channel, flow and vegetation (Gurnell, 2014; Beermann et al., 2018) may indirectly influence dry-phase communities, through shaping the habitat the dry-phase communities persist in or colonise. In contrast, excessive fine sediments (reflected in sediment diversity) deposited on the substrate, shading, nutrient concentrations and road proximity (which influences the potential for urban runoff) represent indirect human impacts and can influence composition through species-specific tolerances and preferences (Stubbington et al., 2019). Plant communities also respond to other habitat characteristics that may reflect conditions less influenced by human impact, for example sediment moisture influences community composition due to species-specific preferences (Holmes, 1999; Hood, 2001; Sabater et al., 2017), and sediment organic content, which can influence plant growth (Barko & Smart, 1983). The concurrent responses of plants to both ‘natural’ variation (e.g. in sediment moisture and organic matter) and human impacts (e.g. trampling and fine sediments) may complicate their use as biomonitors.

I evaluated the capacity of plants to act as dry-phase biomonitors of eutrophication and general environmental degradation. This chapter aims to 1. characterise the dry-phase plant communities, including both aquatic and terrestrial taxa, and their responses to natural and anthropogenic variability in habitat conditions (i.e. sediment moisture, organic matter and diversity; phosphorus, nitrate-nitrogen and shading); 2. investigate the responses of specific biological metrics representing dry-phase plant communities to in-channel nutrient concentrations, and general human impact, represented by channel modification, trampling, road proximity, nutrient concentrations, shading and fine sediment. I hypothesised that:

- (H1) dry-phase plant communities responded to differing in-channel habitat conditions, including more natural conditions (i.e. sediment moisture and organic matter).
- (H2) community diversity and plant morphological complexity decrease whilst Ellenberg N, dominance, and competitive group richness and cover (%) increase with increasing phosphorus and nitrate-nitrogen concentrations.
- (H3) community diversity and plant morphological complexity decrease with increasing human impact levels whilst competitive taxa cover, dominance and Ellenberg N increase.

- (H4) was that a multimetric index would have a stronger response to nutrient concentrations than those found in individual metrics.

4.2 Methods

4.2.1 Site selection

An initial visit to 20 sites in March (spring) 2019 informed site selection. Four sites were discounted due to the uncertainty of channel drying during the survey period and two were excluded due to access issues. The remaining 14 sites were selected to reflect variability in a range of environmental conditions: sediment composition, nutrient concentrations and moisture, shade, trampling, road proximity and channel morphology (summarised in Table A.2.1), allowing comparisons among sites and among differing levels of human impact. All sites dried partly or completely during the study, ranging from a two-month to a multi-year dry phase.

4.2.2 Study sites

The 14 study sites were located across four streams (Ver, Gade, Bulbourne and Misbourne) in the Colne catchment in Hertfordshire and Buckinghamshire, southeast England (Figure 4.1; Figures 4.2–4.5). All four streams have underlying chalk geology meaning that streams are well connected to the aquifer and their flow is groundwater dominated due to the porous nature of the chalk (Westlake et al., 1972; Mainstone, 1999). The four stream catchments are dominated by agricultural land use (36–51% of total land cover), with urban and semi-natural grassland forming the other major land uses (National Flow Archive, 2022a-c). The area has historic human influence, with many river channels being modified to accommodate urban and agricultural (e.g. watercress farms, arable, livestock) land uses.

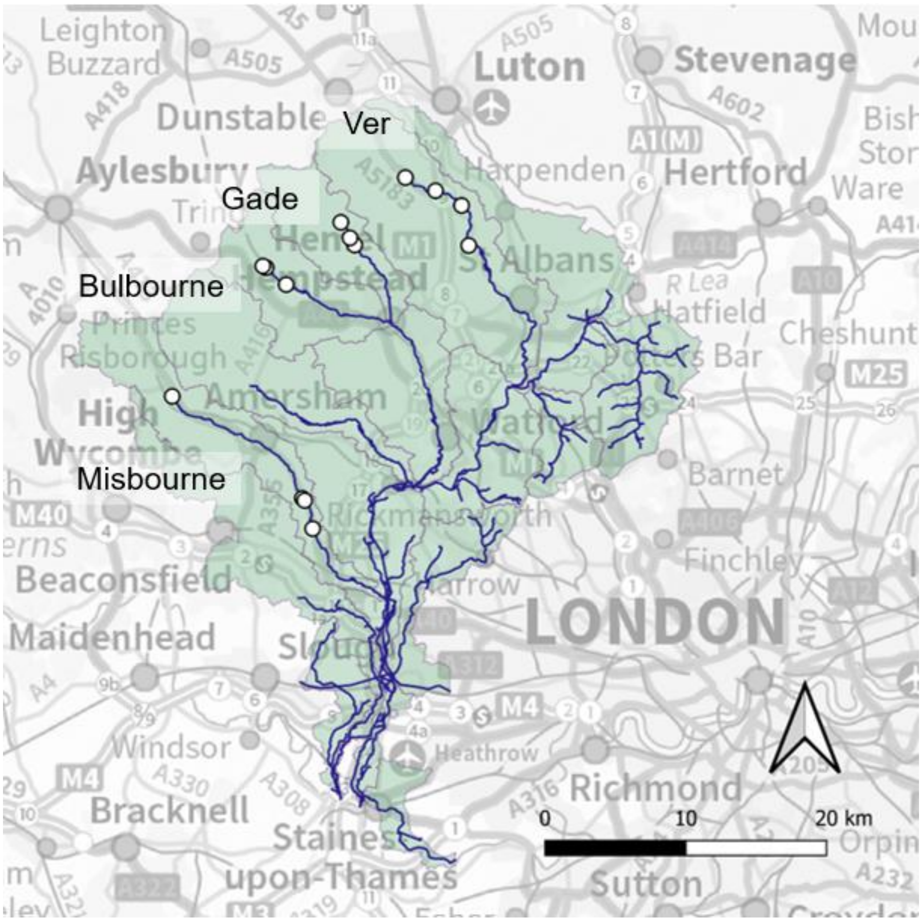

Figure 4.1. The Colne catchment (shaded area) and its watercourses (dark blue lines), indicating the study rivers (Ver, Gade, Bulbourne and Misbourne) and sites (white dots).

Figure 4.2. The River Ver study sites from upstream to downstream. Site locations are shown on Figure 4.1.

Figure 4.3. The River Gade study sites from upstream to downstream. Site locations are shown on Figure 4.1.

Figure 4.4. The River Bulbourne study sites from upstream to downstream. Site locations are shown on Figure 4.1.

Figure 4.5. The River Misbourne study sites from upstream to downstream. Site locations are shown on Figure 4.1.

4.2.3 Plant surveys

Plant communities were surveyed monthly between March (spring) and October (autumn) 2019, based on the protocol for LEAFPACS2 (WFD-UK TAG, 2014), but modified to include both terrestrial and aquatic plants. At each site a 100-m survey reach was defined to represent in-channel conditions. Each plant taxon was identified mostly to species level however, where mowing had occurred or flowering parts were missing, taxa were recorded to as low a taxonomic resolution as possible (i.e. family or genus). The percentage cover of each taxon was estimated by walking across the channel from bank to bank in a zigzag formation, as per Holmes et al. (1999). Estimated percentages were also converted into abundance categories: 1 = <0.1%; 2 = 0.1–1%; 3 = >1–2.5%; 4 = >2.5–5%; 5 = >5–10%; 6 = >10–25%; 7 = >25–50%; 8 = >50–75%; and 9 = >75% (Holmes et al., 1999; WFD-UK TAG, 2014).

4.2.4 Environmental sampling

Environmental data were collected using three different methods: visual assessments, Modular River Surveys (MoRPh; Shuker et al., 2017) and sediment samples. Visual assessments were made during each survey to document shading (percentage of the channel shaded), trampling occurrence/intensity (both human and livestock), road proximity (as distance categories), dominant land use and sediment composition (percentage cobble, pebble/gravel, sand, silt and soil). Other environmental variables representing channel dimensions, sediment types, vegetation morphotypes and channel modifications were characterised using MoRPh for the channel, banks and riparian zone (10 m from the bank top). MoRPh survey lengths were 10 m for sites with channel widths of <5 m and 20 m where channel widths were 5–10 m, the survey section selected to be representative of the entire 100 m plant survey length.

Sediment analysis methods are described in Appendix 2. In brief, sediment samples were collected during three surveys to characterise conditions during spring (April), summer (July) and autumn (October). Sediment moisture was measured both in the field, using a soil probe, and in the laboratory, by weighing approximately 100 g of wet sediment, air drying the sample, weighing the sample again once dry and then calculating the difference between wet and dry weights. To analyse the soil/sediment pH, 20-g samples were stirred in 50 ml of distilled water and a FieldScoutSoilStik meter used to give a pH reading. Sediment phosphorus concentrations were determined from 10-g of air-dried sieved (<2 mm) soil samples using the Olsen's extraction method and a spectrometer. To measure nitrate-nitrogen in the sediment samples, a 2M KCl extractant solution was used and concentrations measured using a Nitrachek colourimeter. These values were then converted to nitrate-nitrogen. To assess sediment organic matter (SOM) levels, samples were heated in a furnace at 550°C for 3 hrs as per Hoogsteen et al. (2015). All sediment variables were measured in triplicate. Sediment diversity was assessed through grain size analysis using sieves at 64 mm, 4 mm, 2 mm, 1 mm, 500 μm, 250 μm, 150 μm and 63 μm, calculating the percentage proportion each grain size contributes to the total sample, and then calculating diversity in R using the 'vegan' package (Oksanen et al., 2007).

4.2.4 Data analysis

4.2.4.1 Community composition, data exploration and preliminary analysis

Seven environmental variables were selected for preliminary analysis to explore plant community composition responses to environmental variables comprising land use, shade and those collected from the sediment samples: sediment moisture, phosphorus, nitrate-nitrogen, sediment diversity, SOM and pH. Non-metric multi-dimensional scaling (NMDS) analysis ('vegan' package; Oksanen et al., 2007) using Bray-Curtis similarity coefficients was conducted (999 iterations) and an ordination plot was produced to visualise variability in community composition. The vegan 'envfit' function was used to fit a vector for each environmental variable to the NMDS ordination, and thus, to visualise community composition in relation to these predictors. IndVal scores were calculated, using the 'multipatt' function (De Cáceres et al., 2010), to identify individual taxa indicative of the different land use, as described in section 2.4.5.1.

Random forests (RF) quantified the contribution of each environmental variable to the variability in community composition, and alongside a visual assessment of the envfit ordination, were used to inform selection of environmental predictors for further analysis. Variables with a contributing value > 0.01 in the RF, supported by the strength of response in the envfit analysis (Figure 4.8), were selected and as such SOM, sediment diversity, sediment moisture, phosphorus and shade were selected. For these five variables, permutational analysis of variance (PERMANOVA; Anderson, 2014) was conducted to relate variability in community composition to environmental variables. TITAN (Threshold Indicator Taxa Analysis) was used to identify changes in taxa distributions along a gradient representing each continuous environmental variable (TITAN2 package; Baker and King, 2010).

4.2.4.2 Calculating environmental variables and biological metrics

Seven environmental variables were selected to represent site-specific impact levels: channel modification, trampling (by both humans and animals), road proximity, phosphorus concentration categories, nitrate-nitrogen concentration categories, fine sediment (< 63 μm) and shading. Sediment moisture and SOM were excluded because human impacts could not be distinguished from natural variability. Sediment diversity was discounted in favour of fine sediment because both sediment variables were collinear and fine sediment is more indicative of human impact (Wood and Armitage, 1997; Jones et al., 2012). Each environmental variable was split into five categories from 0 to 4 to represent least impacted or very low impact levels to most impacted or very high impact levels (Table 4.1). The scores for each variable were then combined to create an overall impact score for each site (0–28).

Table 4.1. The impact categories assigned to each environmental variable to represent impact levels (0–4) and the total number of sites for each category in parentheses (see Tables A2.2 and A2.3 for category ranges).

Environmental variables	Categories				
	0	1	2	3	4
Phosphorus concentrations	Very low (5)	Low (30)	Medium (20)	High (15)	Very high (0)
Nitrate-nitrogen concentrations	Very low (20)	Low (20)	Medium (15)	High (10)	Very high (5)
Shading	Heavy (20)	High (0)	Moderate (20)	Low (15)	None (15)
Channel modification	Least impact (10)	Low (15)	Medium (10)	High (20)	Most impact (15)
Trampling	None (35)	Low (15)	Medium (5)	High (10)	Most impact (5)
Road proximity	Very far (20)	Far (10)	Medium (15)	Close (15)	Very close (10)
Fine sediment	Least impact (10)	Low (35)	Medium (5)	High (15)	Most impact (5)

Phosphorus categories were assigned according to ranges based on the DEFRA index scale (AHDB, 2010), its two ‘very high’ phosphorus categories combined to allow for a 0–4 scale (Table A.2.2). Channel modification, trampling and road proximity were assigned categories using the visual assessments, supplemented by expert opinion, as described in Table A.2.3. Nitrate-nitrogen and shading were split into five equal categories, supplemented by expert opinion (Table **A.2.3** A.2.3). Phosphorus and shading had missing categories (very high and high respectively) because no sites experienced these values (Table 4.1).

Eight metrics were calculated to represent the plant communities: taxonomic richness (*richness*); Shannon-H diversity (*diversity*); Poaceae (i.e. grass) richness (*PoaRich*), Poaceae cover (*Poa%*); herb richness (*HerbRich*), Berger-Parker dominance (*dominance*); Ellenberg nitrogen (*Ellenberg N*), which is an index to measure general sediment fertility (Hill et al., 1999); and the number of plant morphotypes with > 30% cover (*NumMorph*; as per MoRPh, Shuker et al., 2017).

4.2.4.3 Metric responses to environmental variables

Several models were created for each metric to investigate their responses to the overall impact scores, phosphorus, nitrate-nitrogen and shading categories. Selections were made due to replication issues in trampling and road proximity, and whilst channel morphology and fine sediment contribute to general site degradation, they were unlikely to influence plant metrics as individual variables (see Introduction 4.1). Mixed models were initially conducted with the river, survey month and sediment moisture as random factors. If a random factor had limited influence on the response of the metric to the environmental variable (as indicated by a 'singular fit') it was removed from the model. April (spring) surveys were removed due to the likely influence of the growing season on plant communities: metrics were significantly lower in April (spring) surveys than those between May (spring) and September (autumn) which resulted in inaccurate values for sites (Table A.2.4). For the metric models testing the influence of phosphorus, the Community Centre surveys were removed due to having unusually high HerbRich and diversity (Figure 4.6) and being the only site in the very low phosphorus category, providing insufficient replication to assess this category. Similarly, for the nitrate-nitrogen analysis, the Mandelyns surveys were removed as they were the sole representation for the very high category but had unusually high values for HerbRich and diversity and unusually low values for dominance (Figure 4.7).

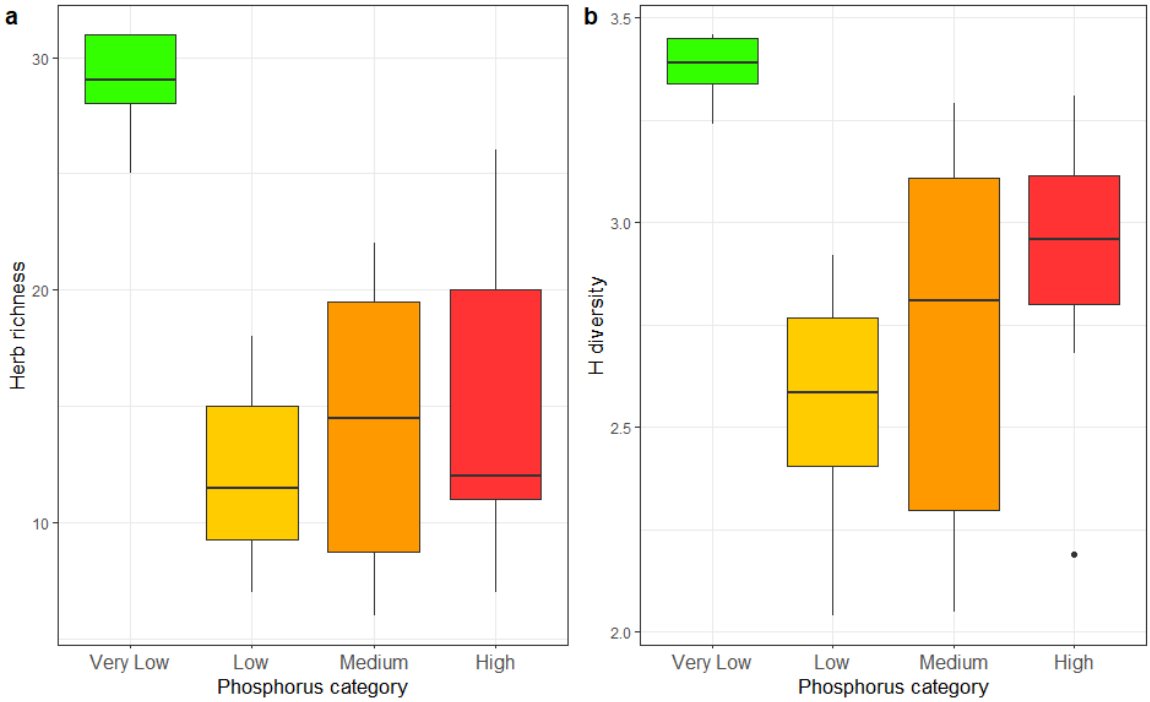

Figure 4.6. The median, interquartile range and 95% confidence intervals for a) herb richness and b) H diversity in different phosphorus concentration categories, with the Community Centre surveys being the only site occurring in the very low phosphorus concentration category. Big dots are outliers.

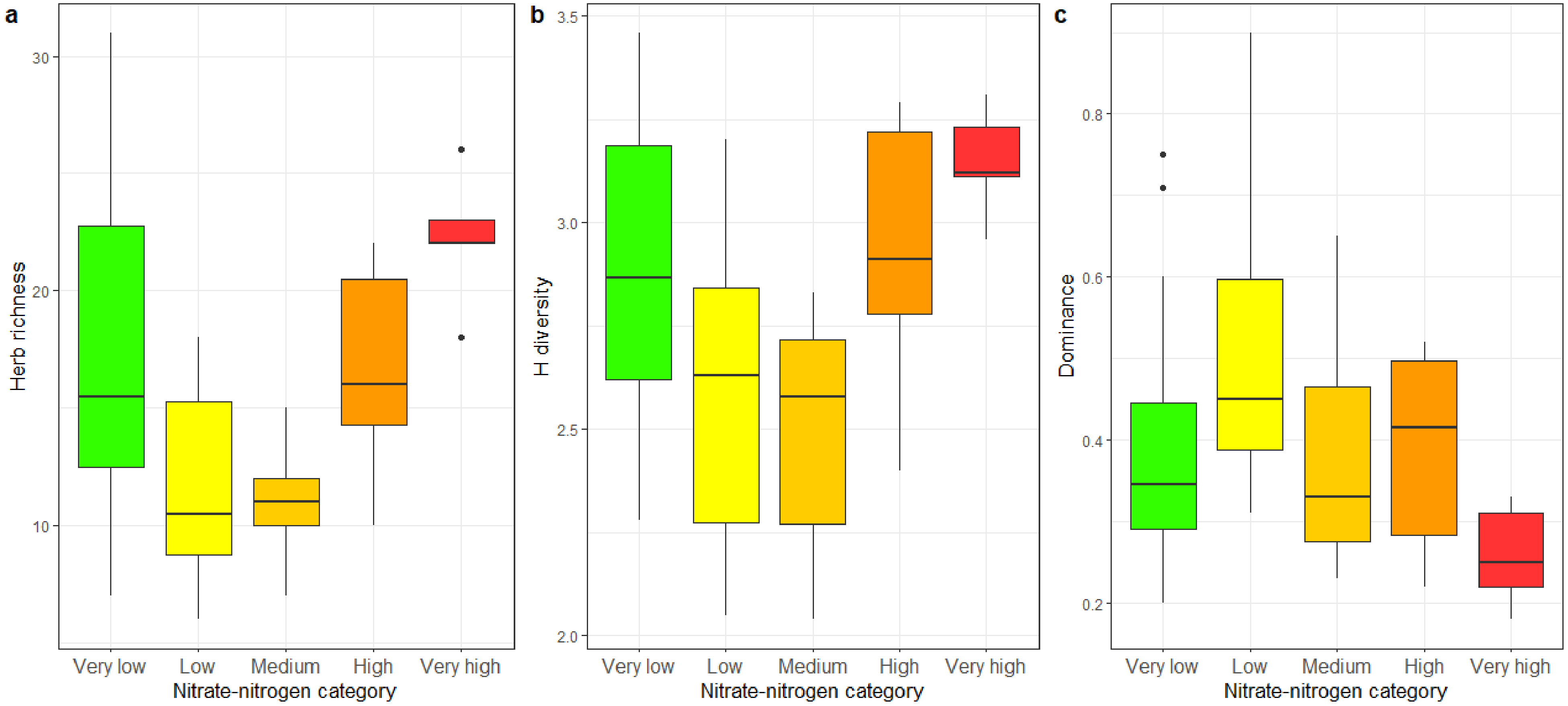

Figure 4.7. The median, interquartile range and 95% confidence intervals for a) Herb richness, b) Shannon H diversity, and c) Berger-Parker dominance in different nitrate-nitrogen categories. Big dots are outliers.

Linear mixed models (LMMs; see section 2.4.2-4) were used to assess the responses of metrics with a Gaussian distribution (diversity and Ellenberg N) to the environmental variables. If metrics did not conform to a Gaussian distribution a generalised linear mixed model (GLMM) was used. GLMMs were used to assess the responses in richness (using a Poisson family distribution with a log link function), PoaRich (zero-inflated Poisson with a square-root link due to zero-inflation) and NumMorph (Poisson with a square-root link). Dominance was initially modelled using a GLMM, but due to unequal variances in the model residuals, was arcsine square-root transformed, and a LMM was used. Poa% was arcsine square-root transformed due to non-normal residuals, and a linear model (LM) was applied because all random factors created a model with a singular fit, except for modelling Poa% responses to shading in which river and sediment moisture were included as random factors. GLMMs, LMMs and LMs were created using the “glmmTMB” (Brooks et al., 2017) and “lme4” (Bates et al., 2015) packages. The “performance” package (Lüdecke et al., 2021) was used to calculate marginal and conditional R^2, to quantify the proportion of response variation explained by the fixed factors and the fixed and random factors, respectively.

4.2.4.4 Multimetric index responses

Metrics that responded significantly to the individual impact variables (diversity, PoaRich, HerbRich, Poa%, Ellenberg N and dominance) were selected from to create a multimetric index with the potential to have a stronger response to nutrient concentrations. Diversity, HerbRich, Poa% and PoaRich had similar responses to phosphorus, and to avoid including redundant metrics only HerbRich, dominance and Ellenberg N were selected to develop the multimetric index (Hering et al., 2006). Similarly, for nitrate-nitrogen, only HerbRich, PoaRich and Ellenberg N were used. For each selected metric, a lower and upper anchor were calculated to reflect the lowest and highest potential metric value, respectively. A multimetric index value was calculated to convert the metric into an indicator of ecological health (ranging between 0 and 1, with higher values indicating low human impact levels) using the equations below, depending on whether the metric decreased or increased with impact.

$$Decreasing\ multimetric\ value = \frac{Metric\ value - Lower\ anchor}{Upper\ anchor - Lower\ anchor}$$

$$Increasing\ multimetric\ value = 1 - \frac{Metric\ value - Lower\ nchor}{Upper\ anchor - Lower\ anchor}$$

An overall multimetric index was then calculated for each survey by averaging each metric’s multimetric index value. A GLMM (beta distribution) was used to analyse the multimetric index responses to only phosphorus and nitrate-nitrogen categories. These two environmental variables were selected due to the limited responses seen in shading and total impact scores (detailed in 4.3.4).

All data analyses were conducted in R version 4.1.1 (R Core Team, 2021).

4.3 Results

4.3.1 Environmental conditions

At the beginning of the survey period (April; spring), the number of months since water was present in-channel at each site (since flow, no perceptible flow and/or ponded conditions) varied from 0–57 months (mean ± SE: 20.93 ± 6.07 months). Over the survey period, all 14 sites dried or were dry before surveying began, with in-channel dry phase durations lasting from 1–6 months (4.57 ± 0.50 months). The flowing/drying regimes are fully detailed in Table A.2.5). The dominant land use at sites included urban (18 surveys; 3 sites), agriculture (18; 3), recreational (18; 3), fen (12; 2) and wooded (12; 2). Site-specific channel modification levels ranged from heavily modified (n = 4) to unmodified (n = 1), and very low modifications were the most widespread (n = 5). Sites varied from having heavy shading (95 % shaded) to open (0 % shaded), with heavy (95 % shaded) and moderate shading (40–60 % shaded) being the most widespread (24 surveys: sites each). Soil pH ranged from 6.78–7.68 (mean: 7.33 ± 0.02), site phosphorus concentrations from 4.93–33.75 mg/kg (18.58 ± 0.89 mg/kg) and site nitrate-nitrogen concentrations from 19.25–95.88 mg/kg (33.67 ± 2.13 mg/kg). Sediment organic matter (SOM) at each site ranged from 3.6–24.0 % (11.77 ± 0.62 %), sediment (H) diversity from 1.26–1.98 (1.72 ± 0.02) and sediment moisture (as % by weight) from 2.24–71.35 % (31.63 ± 2.08 %).

4.3.2 Community characterisation

The dry-phase plant communities comprised 126 species from 33 families, and supported species classified as aquatic (e.g. fools watercress; *Apium nodiflorum* and water mint; *Mentha aquatica*), terrestrial (e.g. Yorkshire fog; *Holcus lanatus* and field forget-me-not; *Myosotis arvensis*), and some semi-aquatic or marginal species (e.g. reed canary grass; *Phalaris arundinacea* and creeping bentgrass; *Agrostis stolonifera*). Taxonomic richness (*richness*) ranged from 6-35 taxa per survey (mean ± SE: 17.52 ± 7.18 taxa), H diversity (*diversity*) from 1.76-3.46 (2.68 ± 0.41), Poaceae cover between 0-80 % (23.32 ± 20.21 %), Poaceae richness (*PoaRich*) from 0-11 taxa (3.66 ± 2.59 taxa), Berger-Parker dominance (*dominance*) ranged between 0.18-0.90 (0.42 ± 0.17), the number of morphotypes (*NumMorph*) was between 0-4 (2.25 ± 1.18) and Ellenberg N values were between 5.30-7.38 (6.20 ± 0.48). Species from families Poaceae (31%), Urticaceae (13 %), Apiaceae (11 %), Brassicaceae (9 %) and Laminaceae (7 %) made up 71 % of total cover across all surveys. Communities were often dominated by 1-2 taxa; typically either *A. nodiflorum*, *M. aquatica* or watercress (*Nasturtium officinale*) at sites with shorter dry-phase durations, and Poaceae spp. or stinging nettle (*Urtica dioica*) at drier sites.

4.3.3 Community compositional responses to environmental variables

4.3.3.1 Individual environmental variables

SOM explained the most variation (12 %) in community composition (PERMANOVA: F = 13.22, df = 1, P = 0.001). Communities associated with higher SOM had higher NMDS1 and lower NMDS2 scores than other communities (Figure 4.8). Twenty taxa decreased and 23 taxa increased in cover with increasing SOM. Taxa including bird's-foot trefoil (*Lotus corniculatus*), timothy grass (*Phelum pratensis*) and crested dog's-tail (*Cynosurus cristatus*) had the highest magnitude increases as SOM increased (TITAN; Figure 4.9). Higher magnitude decreasers included *P. arundinacea*, *N. officinale* and water forget-me-not (*Myosotis scorpiodes*), which decreased as SOM increased (TITAN; Figure 4.9).

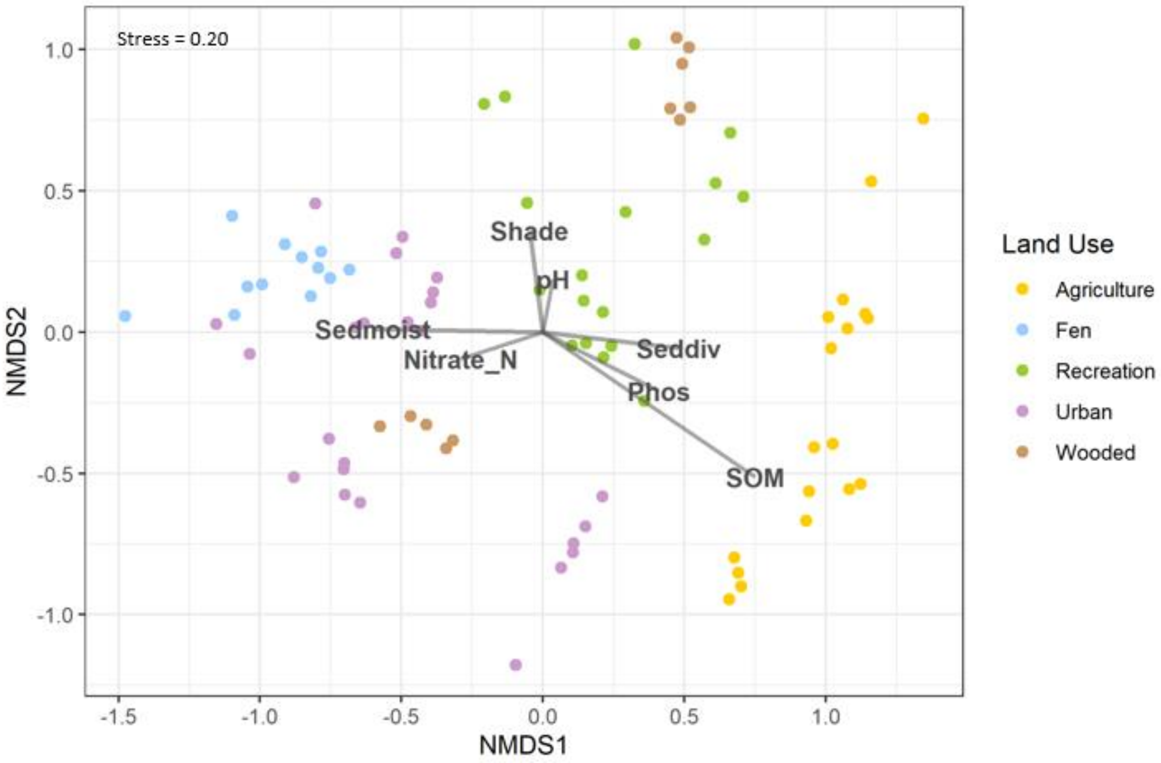

Figure 4.8. Non-metric multi-dimensional scaling ordination for dry-phase plant community composition at all surveys in relation to land use and continuous environmental variables/vectors. Each vector is represented by a line, the direction of the line from the origin indicates the general direction of increase in the variable, and the length of the line indicates the strength of the effect. Sedmoist = sediment moisture, Seddiv = sediment diversity, SOM = sediment organic matter, Nitrate_N = nitrate-nitrogen concentration, Phos = phosphorus concentration.

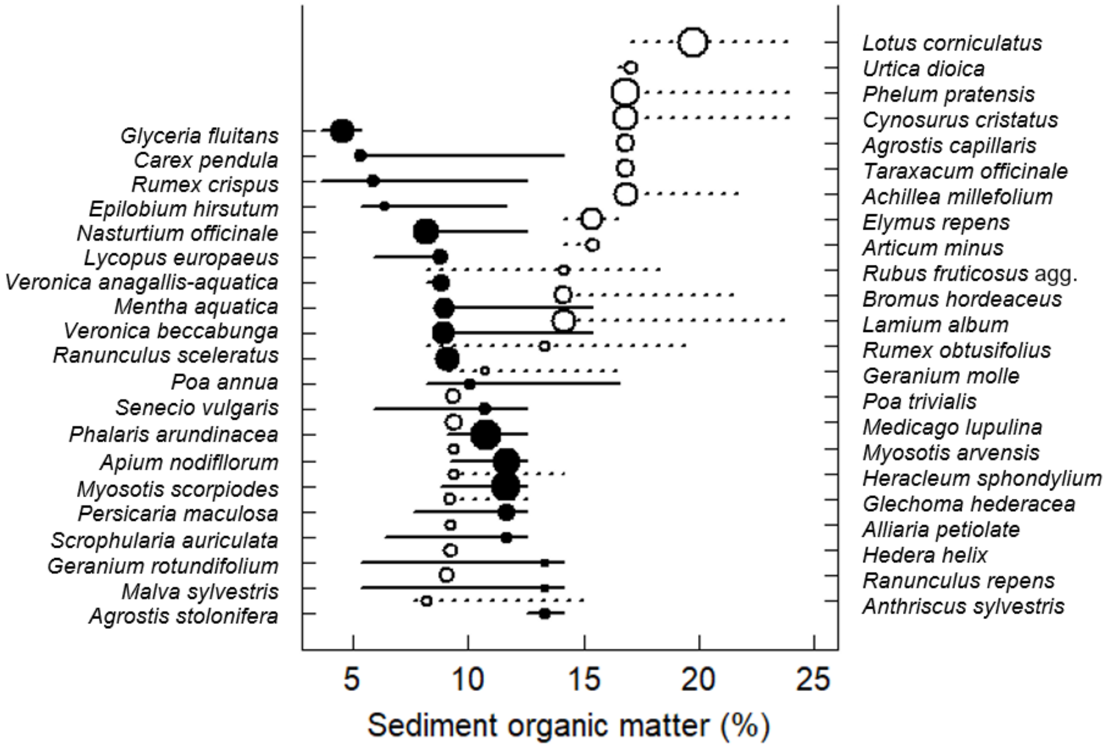

Figure 4.9. Threshold Indicator Taxa ANalysis (TITAN) plot for taxa which decreased (black circles) or increased (white circles) in cover in relation to sediment organic matter (%). The circle position indicates the mean change point for taxa cover, circle size represents the relative magnitude of the change in cover, and the lines represent the range of changes in 95% of bootstraps.

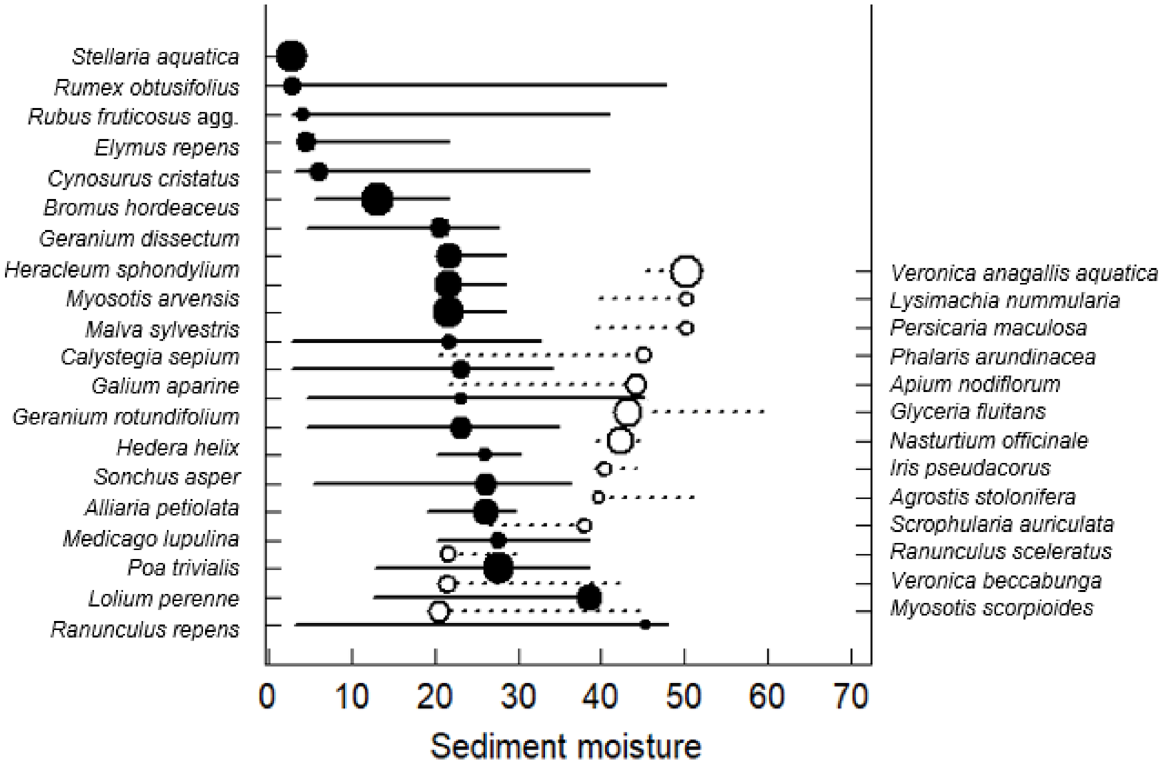

Figure 4.10. TITAN plot for taxa which decreased (black circles) or increased (white circles) in relation to sediment moisture. The circle position indicates the mean change point for taxa cover, circle size represents the relative magnitude of the change in cover, and the lines represent the range of changes in 95% of bootstraps.

Sediment moisture accounted for 11 % of the variation in community composition (PERMANOVA: F = 13.22, df = 1, P = 0.001). Communities associated with higher sediment moisture were those with lower NMDS1 scores (Figure 4.8). Twelve taxa increased with increasing sediment moisture, three of which increased at a high magnitude: blue/pink speedwell (*Veronica anagallis aquatica*), reed sweet grass (*Glyceria fluitans*) and *N. officinale* (Figure 4.10). Twenty taxa decreased with increasing sediment moisture, such as soft brome (*Bromus hordeaceus*), *M. arvensis* and rough meadow grass (*Poa trivialis;* Figure 4.10).

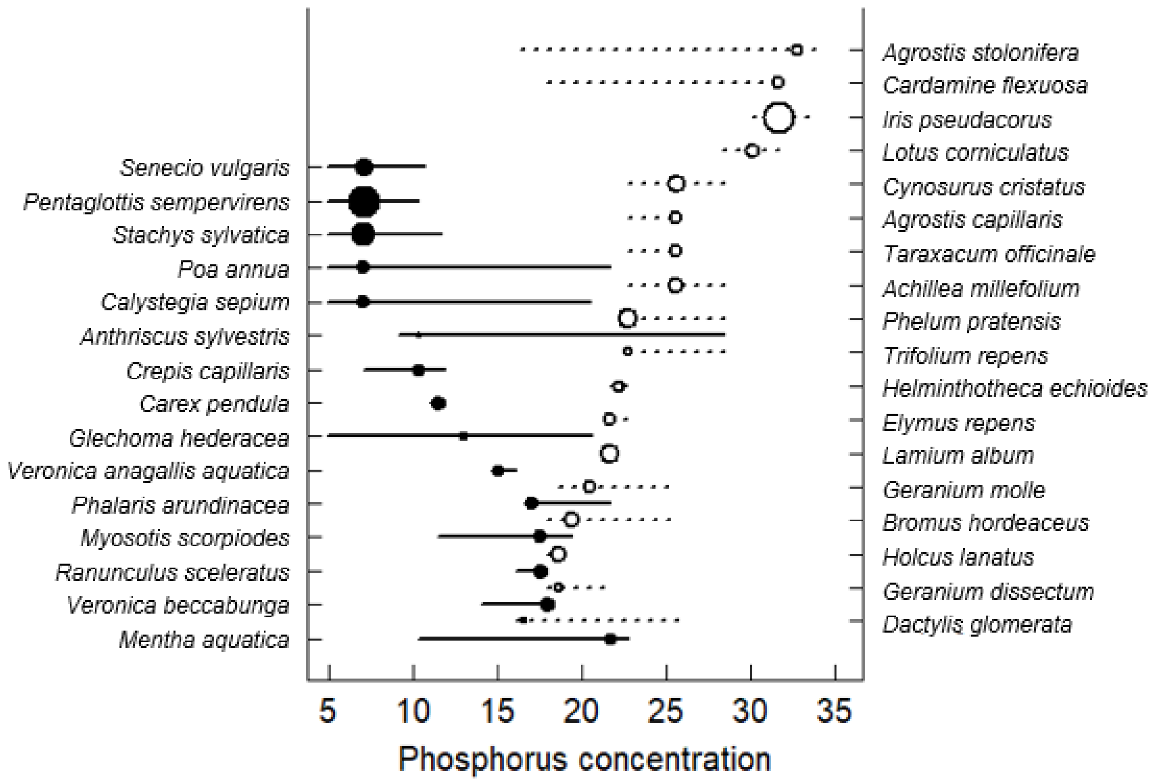

Figure 4.11. TITAN plot for taxa which decreased (black circles) or increased (white circles) in relation to soil phosphorus concentrations (mg/kg). The circle position indicates the mean change point for taxa cover, circle size represents the relative magnitude of the change in cover, and the lines represent the range of changes in 95% of bootstraps.

Phosphorus concentrations explained 4 % of variation in community composition (PERMANOVA: F = 4.93, df = 1, P = 0.001). Eighteen taxa increased in cover with increasing phosphorus concentrations, and 15 taxa decreased. There was only one high-magnitude increaser: flag iris (*Iris pseudacorus*), and taxa with moderate increases included white-dead nettle (*Lamium album*), timothy grass (*P. pratensis*), crested dog's-tail (*C. cristatus*) and yarrow (*Achillea millefolium*; TITAN; Figure 4.11). Green alkanet (*Pentaglottis sempervirens*) and hedge woundwort (*Stachys sylvatica*) had high-magnitude decreased as phosphorus concentrations increased (TITAN; Figure 4.11).

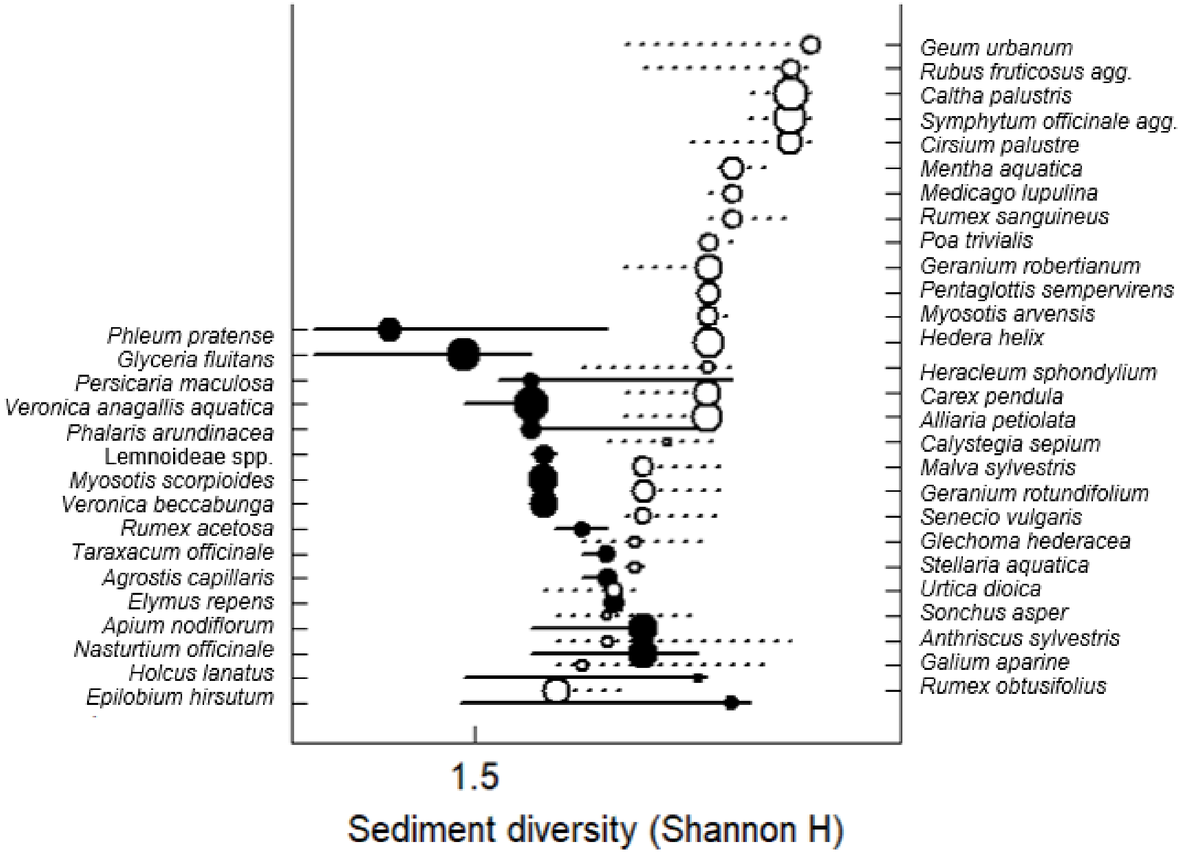

Figure 4.12. TITAN plot for taxa which decreased (black circles) or increased (white circles) in relation to sediment diversity. The circle position indicates the mean change point for taxa cover, circle size represents the relative magnitude of the change in cover, and the lines represent the range of changes in 95% of bootstraps.

Sediment diversity accounted for 5 % of variation in community composition (PERMANOVA: F = 5.90, df = 1, P = 0.001), and communities associated with higher sediment diversity had higher NMDS1 scores (Figure 4.8). Twenty-seven taxa increased with increasing sediment diversity including marsh marigold (*Caltha palustris*), pendulous sedge (*Carex pendula*) and garlic mustard (*Alliaria petiolata*), which were high-magnitude increasers. Whilst sixteen taxa decreased (Figure 4.12), those that decreased at a higher magnitude included reed sweet grass (*G. fluitans*), watercress (*N. officinale*) and blue/pink water speedwell (*V. anagallis aquatica*).

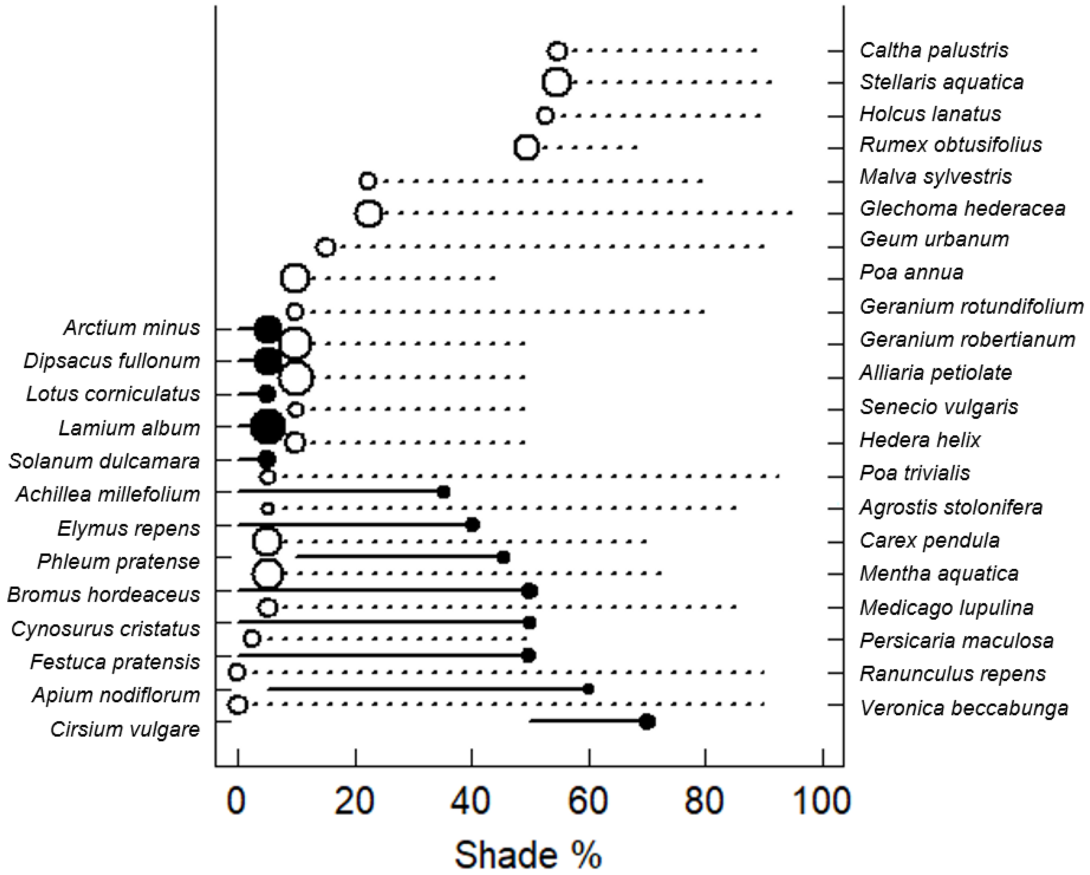

Figure 4.13. TITAN plot for taxa which decreased (black circle) or increased (white circle) in relation to shade %. The circle position indicates the mean change point for taxa cover, circle size represents the relative magnitude of the change in cover, and the lines represent the range of changes in 95% of bootstraps.

Shading explained 4 % of variation in community composition (PERMANOVA: $R^2 = 0.04$, F = 4.01, df = 1, P = 0.001). Communities associated with higher shading were those with higher NMDS2 scores (Figure 4.8). Twenty-one taxa increased with increasing shading, including herb robert (*Geranium robertianum*), garlic mustard (*A. petiolata*) and ground ivy (*Glechoma hederacea*), and 13 decreased with increasing shading such as white deadnettle (*L. album*), wild teasel (*Dipsacus fullonum*) and lesser burdock (*Arctium minus*; Figure 4.13).

4.3.3.2 Dominant land use

The dominant land use was often reflected by several environmental variables, for example, agricultural sites were associated with higher SOM, phosphorus, sediment diversity and, in general, lower sediment moisture (Figure 4.8). Dry-phase community composition varied according to land use (PERMANOVA: F = 12.55, df = 4, P = 0.001). Communities at sites with agricultural land use had high NMDS1 scores but had variable NMDS2 scores (Figure 4.8). Nineteen taxa were indicative of agricultural land use including seven aster (Asteraceae) and six grass (Poaceae) taxa (IndVal; Table A.2.6), 18 of which occurred exclusively at sites with agricultural land use. Seven taxa were indicative of fen land use (IndVal; Table A.2.6) – typically sites with higher sediment moisture, but lower sediment diversity and phosphorus (Figure 4.8) – all of which are considered either aquatic or marginal. Recreational land use – sites with higher shading and pH, and lower nitrate-nitrogen (Figure 4.8) – had 12 indicator species, nine of which were found only at sites with recreational land use, and three of which only occurred at one site overall (IndVal; Table A.2.6). Communities at sites with urban land use had low NMDS1 scores, associated largely with higher sediment moisture, and lower SOM and phosphorus (Figure 4.8). Two taxa were indicative or urban sites: *G. fluitans* and *I. pseudacorus* (IndVal, Table A.2.6). Communities at sites with wooded land use were split into two site specific clusters (Figure 4.8), one had composition similar to communities at sites with urban land use and the other similar to those with recreational land use. Only one species was indicative of wooded land use, *C. palustris*), but this only occurred at only one site (IndVal, Table A.2.6).

4.3.4 Metric responses to total impact scores

Total impact scores explained < 0.1–3.5% of the variation in each of the eight response metrics (Table 4.2). Only Poa% responded significantly, increasing as total impact scores increased (Table 4.2; Figure 4.14). A similar relationship was marginally non-significant for PoaRich ($P = 0.089$; Table 4.2; Figure 4.14), which may be due to high variability in richness at high impact scores (14–16).

Table 4.2. The models used (GLMM, LMM and LM) to test the influence of total impact scores on the response metrics representing dry-phase plant communities, with the associated R^2 values (R^2C and R^2M) and results of each model. The significant results and marginally non-significant (P = 0.05-0.10) results are in bold, with the exception of the intercept which reflects a deviation of the intercept from zero.

Metric (model)	**R^2C**	**R^2M**	**Total impact scores**	**Estimate**	**SE**	**P**
Taxonomic richness (GLMM)	0.41	0.02	Intercept	2.728	0.157	<0.001
			Total impact	0.014	0.010	0.185
H diversity (LMM)	0.26	<0.01	Intercept	2.674	0.193	<0.001
			Total impact	0.005	0.013	0.685
Poaceae richness (GLMM)	0.47	0.03	Intercept	1.498	0.341	<0.001
			Total impact	**0.037**	**0.021**	**0.089**
Poaceae cover (LMM)	0.46	0.04	Intercept	0.302	0.103	0.012
			Total impact	**0.013**	**0.006**	**0.047**
Herb richness (GLMM)	0.10	<0.01	Intercept	2.578	0.207	<0.001
			Total impact	0.007	0.017	0.654
Berger-Parker dominance (LMM)	0.29	<0.01	Intercept	0.632	0.063	<0.001
			Total impact	-0.000	0.004	0.957
Ellenberg N (LMM)	0.58	<0.01	Intercept	1.499	0.341	<0.001
			Total impact	-0.006	0.015	0.702
Number of morphotypes (GLMM)	0.24	0.01	Intercept	0.576	0.370	0.120
			Total impact	0.024	0.027	0.376

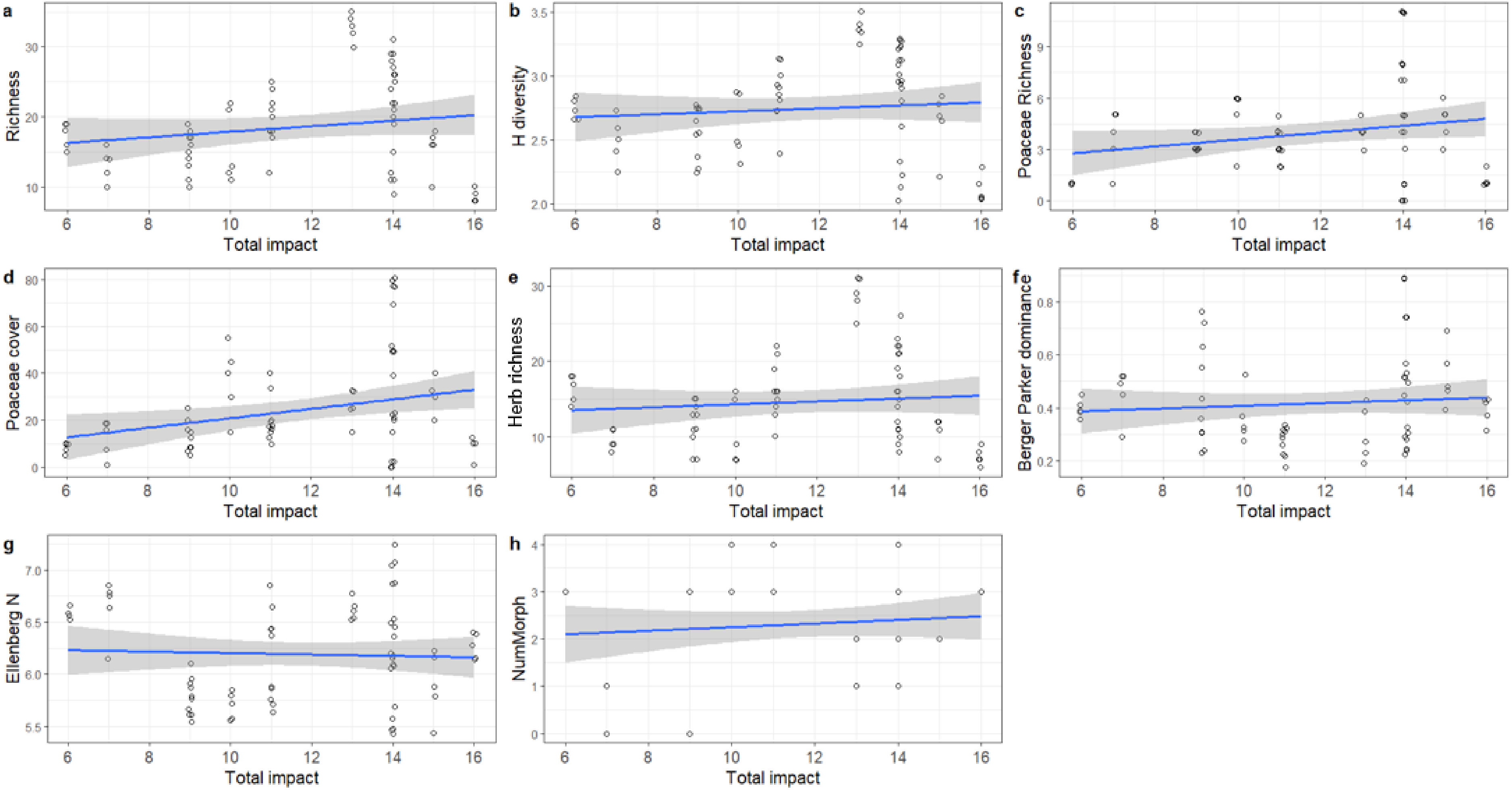

Figure 4.14. The plant community metric responses to the total impact score: a) taxonomic richness, b) H diversity, c) Poaceae richness, d) Poaceae cover, e) Herb richness, f) Berger-Parker dominance, g) Ellenberg N and h) the number of morphotypes. The shaded area represents 95% confidence intervals.

4.3.5 Metric responses to nutrients and shading categories

4.3.5.1 Phosphorus and nitrate-nitrogen

Seven out of the eight dry-phase plant metrics responded significantly to phosphorus concentration categories, explaining between 4–22% of variation in the metrics. Six metrics responded significantly to nitrate-nitrogen, which explained between 5–37% (Table 4.3 and 4.4). Of the two nutrients, phosphorus accounted for the most variation in Poa%, PoaRich and dominance, whilst nitrate-nitrogen account for the most variation in richness, diversity, HerbRich, richness and Ellenberg N (Table 4.3 and 4.4).

Richness, diversity, PoaRich, Poa% and HerbRich were higher at sites in the high compared to low phosphorus concentration categories (Figure 4.15a-e), whilst Ellenberg N was lower at sites with high phosphorus (Table 4.3, Figure 4.15g). Richness and HerbRich were also higher at sites with moderate phosphorus concentrations than those in the high category, although this was marginally non-significant possibly due to high variability in the medium category (Figure 4.15a and e; Table 4.3). The responses of richness, diversity, HerbRich and Ellenberg N were contrary to what was hypothesised (H2). Dominance was higher at sites with medium and high compared to the low phosphorus category, as hypothesised (H2; Table 4.3, Figure 4.15f). The number of morphotypes was comparable across all phosphorus concentrations, contrary to H2.

Table 4.3. The model used (GLMM, LMM and LM) to test the influence of phosphorus concentration categories on the response metrics representing dry-phase plant communities, with the associated R^2 values (R^{2}C and R^{2}M for mixed models and R^2 for linear models) and results of each model. The significant results and marginally non-significant (P = 0.05-0.10) results are in bold, with the exception of the intercept which reflects a deviation of the intercept from zero.

Metric (model)	**R^{2}C or R^2**	**R^{2}M**	**Phosphorus category**	**Estimate**	**SE**	**P**
Taxonomic richness (GLMM)	0.30	0.13	Intercept (Low)	2.736	0.070	<0.001
			Medium	**0.145**	**0.086**	**0.093**
			High	**0.300**	**0.081**	**<0.001**
H diversity (LMM)	0.19	0.12	Intercept (Low)	2.594	0.076	<0.001
			Medium	0.117	0.103	0.266
			High	**0.310**	**0.104**	**0.004**
Poaceae richness (GLMM)	0.51	0.09	Intercept (Low)	1.811	0.255	<0.001
			Medium	0.121	0.198	0.542
			High	**0.530**	**0.180**	**0.003**
Poaceae cover (LMM)	0.38	0.22	Intercept (Low)	0.392	0.054	0.005
			Medium	0.041	0.057	0.476
			High	**0.265**	**0.059**	**<0.001**
Herb richness (GLM)	0.112		Intercept (Low)	2.500	0.065	<0.001
			Medium	**0.165**	**0.100**	**0.099**
			High	**0.218**	**0.108**	**0.044**
Berger-Parker dominance (LMM)	0.70	0.09	Intercept (Low)	0.727	0.090	<0.001
			Medium	**-0116**	**0.043**	**0.008**
			High	**0.089**	**0.038**	**0.024**
Ellenberg N (LMM)	0.72	0.04	Intercept (Low)	6.137	0.229	<0.001
			Medium	-0.123	0.118	0.300
			High	**-0.271**	**0.104**	**0.012**
Number of morphotypes (GLMM)	0.26	<0.01	Intercept (Low)	1.502	0.179	<0.001
			Medium	0.064	0.195	0.741
			High	0.082	0.181	0.65

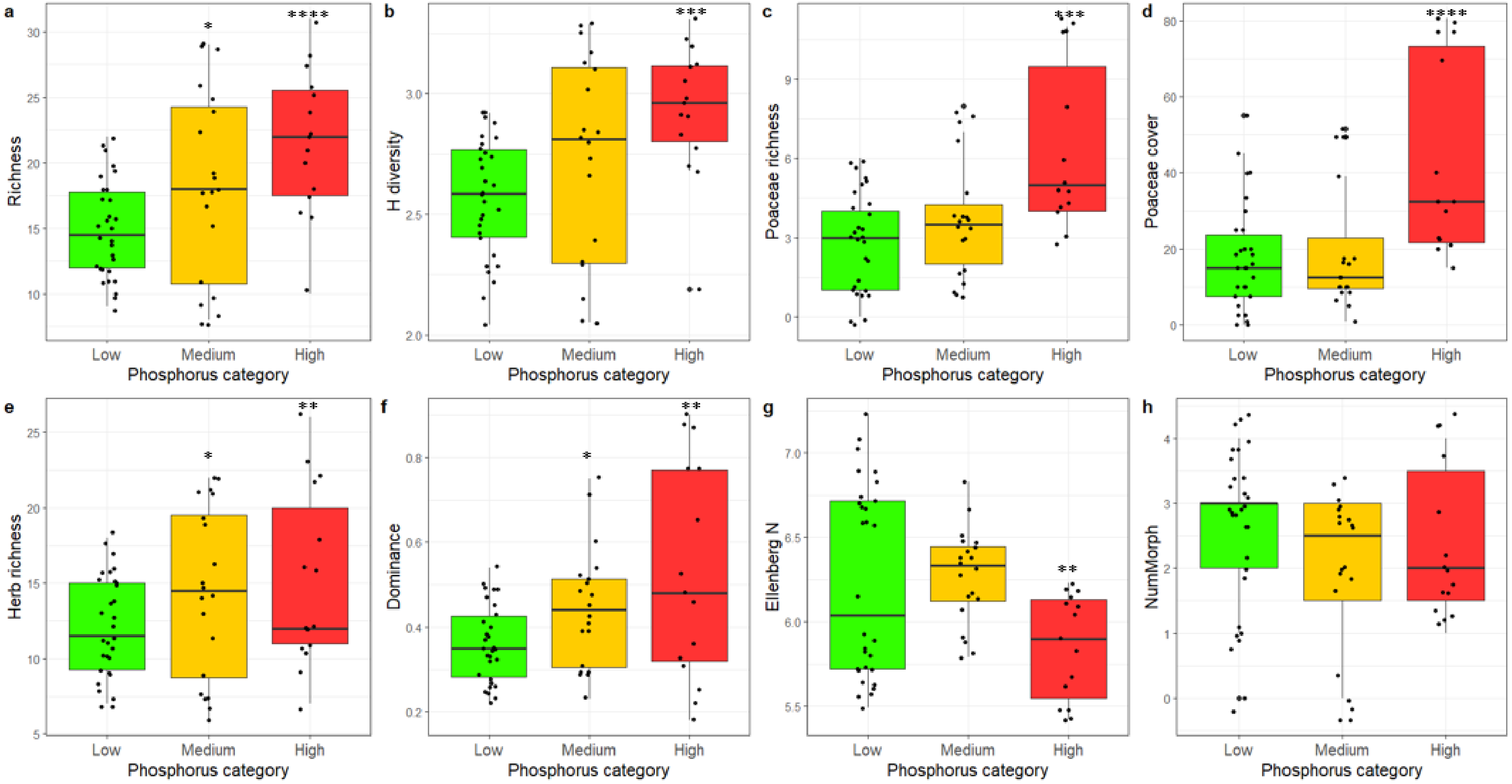

Figure 4.15. The median, interquartile range and 95% confidence intervals for a) taxonomic richness, b) H diversity, c) Poaceae richness, d) Poaceae cover, e) herb richness, f) Berger-Parker dominance, g) Ellenberg N and h) the number of morphotypes in low, medium and high phosphorus categories. Big dots represent outliers The significance for each category compared to the intercept (i.e. the low category) is highlighted as such: * = marginally non-significant: P < 0.1, ** = moderately significant: P < 0.05, *** = significant: P <0.01, **** = highly significant: P < 0.001.

Richness, diversity and HerbRich were lower, and dominance was higher, at sites in low and medium nitrate-nitrogen concentration categories in comparison to those in the very low category whilst the metric values at very low and high nitrate-nitrogen categories were comparable (Table 4.4; Figure 4.16a, b, e and f). Poa% was higher at sites with high nitrate-nitrogen concentrations compared to very low concentrations (Table 4.4; Figure 4.16d); it was also higher at low nitrate-nitrogen, likely due to the variability in Poa% with around half of all points occurring in 70–80% (Figure 4.16d). Poa% at very low and medium concentrations were comparable. Ellenberg N was higher at sites in both medium and high categories in comparison to sites in the low category, but the response at the medium concentration was only marginally non-significant (Table 4.4; Figure 4.16g). PoaRich was comparable across all nitrate-nitrogen concentrations except for at low concentrations where PoaRich was higher, but this was also marginally non-significant (Table 4.4; Figure 4.16c). NumMorph was comparable across all nitrate-nitrogen concentrations (Table 4.4; Figure 4.16h).

Table 4.4. The model used (GLMM and LMM) to test the influence of nitrate-nitrogen concentration categories on the response metrics representing dry-phase plant, with the associated R^2 values (R^2C and R^2M) and results of each model. The significant results and marginally non-significant (P = 0.05-0.10) results are in bold, with the exception of the intercept which reflects a deviation of the intercept from zero.

Metric (model)	**R^2C**	**R^2M**	**Nitrate-nitrogen category**	**Estimate**	**SE**	**P**
Taxonomic richness (GLMM)	0.55	0.25	Intercept (Very low)	2.97	0.111	<0.001
			Low	**-0.259**	**0.090**	**0.004**
			Medium	**-0.432**	**0.126**	**<0.001**
			High	0.009	0.099	0.925
H diversity (LMM)	0.56	0.22	Intercept (Very low)	2.83	0.136	<0.001
			Low	**-0.263**	**0.107**	**0.018**
			Medium	**-0.466**	**0.134**	**<0.001**
			High	0.039	0.127	0.759
Poaceae richness (GLMM)	0.61	0.08	Intercept (Very low)	1.86	0.307	<0.001
			Low	**0.353**	**0.209**	**0.092**
			Medium	-0.252	0.258	0.330
			High	0.183	0.245	0.456
Poaceae cover (LMM)	0.81	0.11	Intercept (Very low)	16.15	12.86	0.258
			Low	**25.20**	**5.63**	**<0.001**
			Medium	8.784	7.129	0.223

			High	**16.63**	**6.49**	**0.013**
Herb richness (GLMM)	0.70	0.10	Intercept (Very low)	2.799	0.109	<0.001
			Low	**-0.494**	**0.118**	**<0.001**
			Medium	**-0.538**	**0.139**	**<0.001**
			High	-0.043	0.111	0.697
Berger-Parker dominance (LMM)	0.70	0.27	Intercept (Very low)	0.601	0.077	<0.001
			Low	**0.262**	**0.045**	**<0.001**
			Medium	**0.148**	**0.059**	**0.015**
			High	0.002	0.055	0.965
Ellenberg N (LMM)	0.83	0.09	Intercept (Very low)	6.031	0.323	0.103
			Low	-0.209	0.126	0.103
			Medium	**0.285**	**0.162**	**0.084**
			High	**0.347**	**0.146**	**0.021**
Number of morphotypes (GLMM)	0.14	0.11	Intercept (Very low)	1.502	0.144	<0.001
			Low	-0.084	0.181	0.642
			Medium	0.046	0.184	0.803
			High	0.228	0.213	0.283

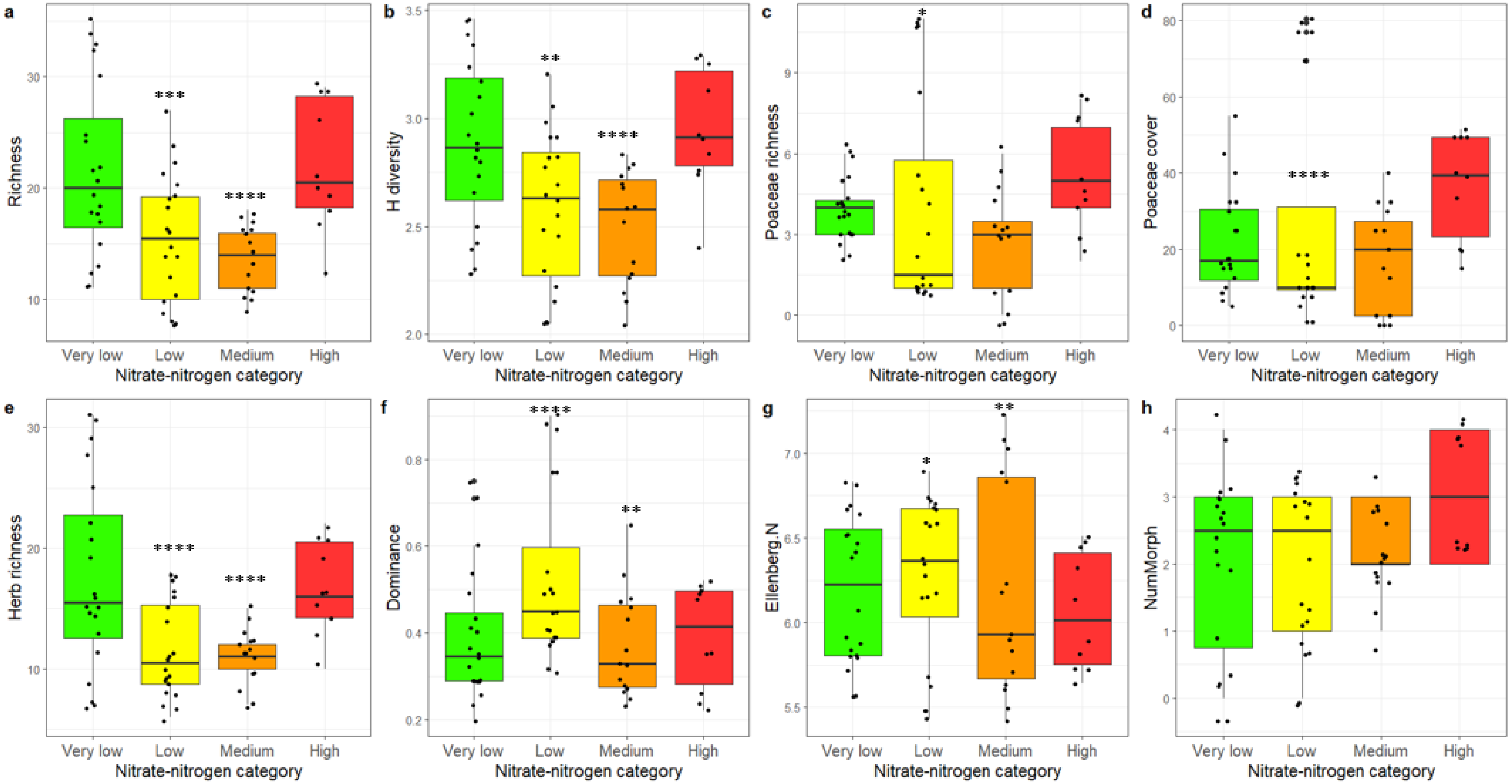

Figure 4.16. The median, interquartile range and 95% confidence intervals for a) taxonomic richness, b) H diversity, c) Poaceae richness, d) Poaceae cover, e) herb richness, f) Berger-Parker dominance, g) Ellenberg N and h) the number of morphotypes in very low, low, medium, and high nitrate-nitrogen categories. The significance for each category is highlighted as such: * = marginally non-significant: $P < 0.1$, ** = moderately significant: $P < 0.05$, *** = significant: $P < 0.01$, **** = highly significant: $P < 0.001$.

4.3.5.2 Shading

Shading explained between 3-28%, with seven out of the eight metrics responding significantly (Table 4.5). Poa% and PoaRich were higher at sites with low or no shading in comparison to those with heavy shading (Table 4.5; Figure 4.17). However, for PoaRich, visually those with no shading appear lower than sites with low shading, but this is due to the lower median value, whilst the mean remained higher at no shading (Figure 4.17c). Additionally, Poa% was higher at sites with moderate shading than at heavy shading but this was non-significant (Table 4.5; Figure 4.17d). Richness was higher at sites with moderate shading in comparison to those with heavy shading (Table 4.5; Figure 4.17a). HerbRich was lower at sites with low shading in comparison to sites with heavy shading. Ellenberg N was highest at sites with moderate shading and lowest at sites with low shading (Table 4.5; Figure 4.17). The NumMorph was marginally non-significantly higher at sites with moderate shading in comparison to those with heavy shading, however visual assessments of Figure 4.17 revealed no difference. Dominance was comparable across sites in different shading categories (Table 4.5; Figure 4.17)

Table 4.5. The model used (GLMM, LMM and LM) to test the influence of shading on the response metrics representing dry-phase plant communities, with the associated R^2 values (R^2C and R^2M for MM and R^2 for LM) and results of each model. The significant results and marginally non-significant (P = 0.05-0.10) results are in bold, except for the intercept which reflects a deviation of the intercept from zero.

Metric (model)	R^2C	R^2M	Shading category	Estimate	SE	P
Taxonomic richness (GLMM)	0.47	0.09	Intercept (Heavy)	2.830	0.114	<0.001
			Moderate	**0.198**	**0.082**	**0.015**
			Low	-0.051	0.084	0.546
			None	0.073	0.105	0.488
H diversity (LMM)	0.26	0.03	Intercept (Heavy)	2.702	0.131	<0.001
			Moderate	0.137	0.119	0.255
			Low	-0.038	0.121	0.751
			None	0.040	0.134	0.767
Poaceae richness (GLMM)	0.66	0.13	Intercept (Heavy)	1.669	0.289	<0.001
			Moderate	0.045	0.195	0.819
			Low	**0.512**	**0.186**	**0.006**
			None	**0.537**	**0.226**	**0.018**
Poaceae cover (LMM)	0.62	0.19	Intercept (Heavy)	3.256	0.817	0.017
			Moderate	**0.869**	**0.497**	**0.085**

			Low	**2.473**	**0.498**	**<0.001**
			None	**2.103**	**0.563**	**<0.001**
Herb richness (GLMM)	0.23	0.19	Intercept (Heavy)	2.697	0.094	<0.001
			Moderate	0.186	0.1171	0.113
			Low	**-0.278**	**0.130**	**0.033**
			None	-0.153	0.149	0.307
Berger-Parker dominance (LMM)	0.56	0.15	Intercept (Heavy)	2.702	0.131	<0.001
			Moderate	0.137	0.119	0.255
			Low	-0.038	0.121	0.751
			None	0.040	0.135	0.767
Ellenberg N (LMM)	0.84	0.28	Intercept (Heavy)	6.117	0.208	<0.001
			Moderate	**0.409**	**0.087**	**<0.001**
			Low	**-0.399**	**0.093**	**<0.001**
			None	-0.075	0.098	0.499
Number of morphotypes (GLMM)	0.63	0.08	Intercept (Heavy)	1.282	0.189	<0.001
			Moderate	**0.377**	**0.203**	**0.064**
			Low	0.323	0.202	0.110
			None	0.340	0.208	0.103

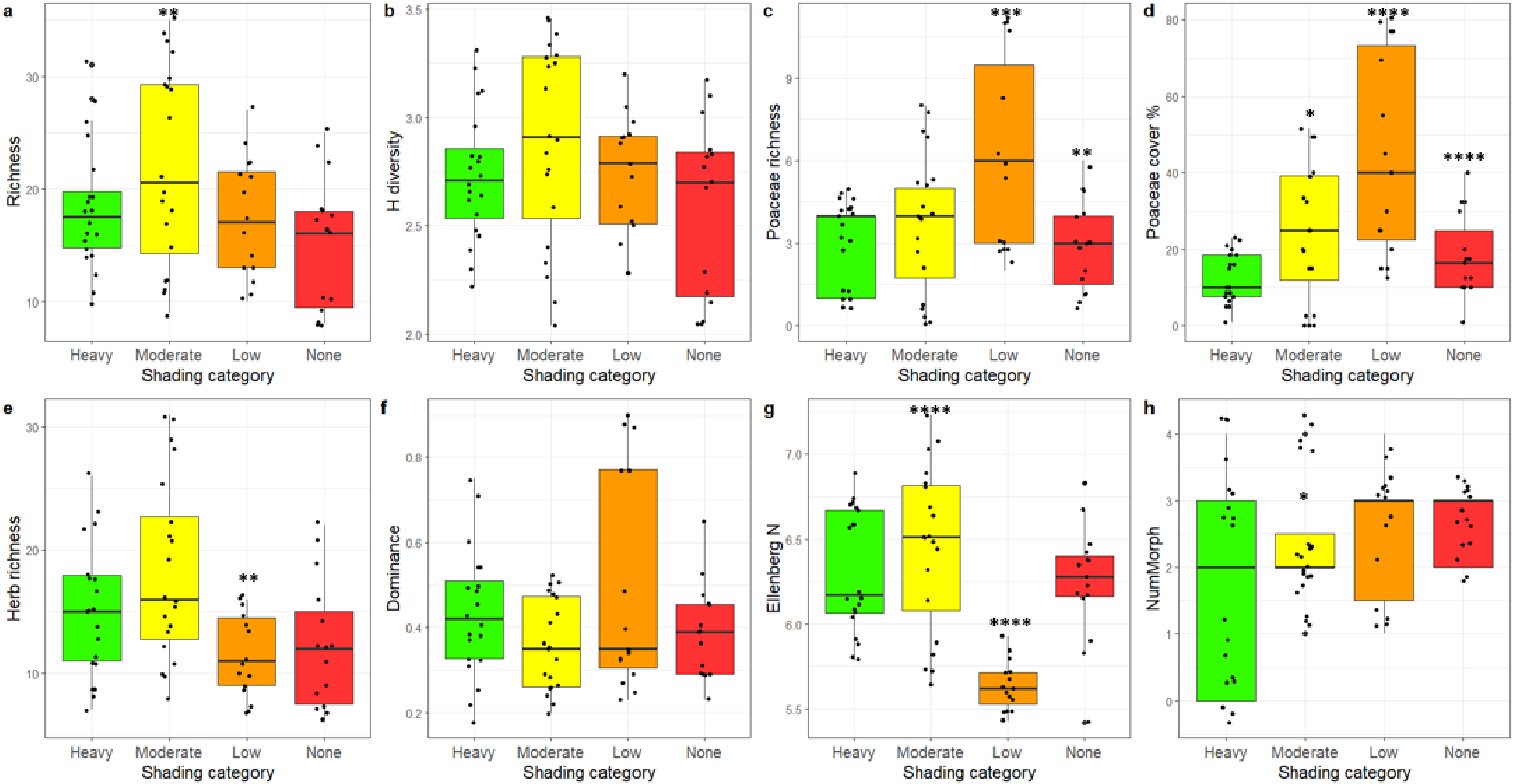

Figure 4.17. The median, interquartile range and 95% confidence intervals for a) taxonomic richness, b) H diversity, c) Poaceae richness, d) Poaceae cover, e) herb richness, f) Berger-Parker dominance, g) Ellenberg N and h) the number of morphotypes in heavy, moderate, low and none shading categories. The significance for each category is highlighted as such: * = marginally non-significant: $P < 0.1$, ** = moderately significant: $P < 0.05$, *** = significant: $P < 0.01$, **** = highly significant: $P < 0.001$.

4.3.6 Multimetric index responses

Nutrient concentrations explained more variation in the multimetric indices than the other metrics, with phosphorus explaining 29% of multimetric index variation and nitrate-nitrogen explaining 43%, supporting H4 (Table 4.6). For phosphorus, the multimetric was lower at sites with high compared to low concentrations (Table 4.6; Figure 4.18), however, both HerbRich and Ellenberg N, which contributed towards the multimetric index, responded in the opposite way than what was hypothesised (H2). For nitrate-nitrogen, the multimetric index was lower at sites with low and medium concentrations than those with very low nitrate-nitrogen concentrations (Table 4.6). However, Figure 4.19 shows considerable overlap between concentration categories.

Table 4.6. The results of the GLMMs used to test the influence of phosphorus and nitrate-nitrogen on the multimetrics of dry-phase plant communities, with the associated R^2 values (R^2C and R^2M for mixed models and R^2 for linear models). The significant results are in bold (including those marginally non-significant $P < 0.1$), except for the intercept which reflects a deviation of the intercept from zero.

Environmental variable (model)	**R^2C**	**R^2M**	**Impact category**	**Estimate**	**SE**	**P**
Phosphorus (GLMM beta)	0.92	0.29	Intercept (Low)	0.330	0.109	0.003
			Medium	0.005	0.073	0.947
			High	**-0.299**	**0.066**	**<0.001**
Nitrate-nitrogen (GLMM beta)	0.97	0.43	Intercept (Very low)	0.128	0.115	0.266
			Low	**-0.396**	**0.094**	**<0.001**
			Medium	**-0.297**	**0.129**	**0.021**
			High	-0.188	0.124	0.129

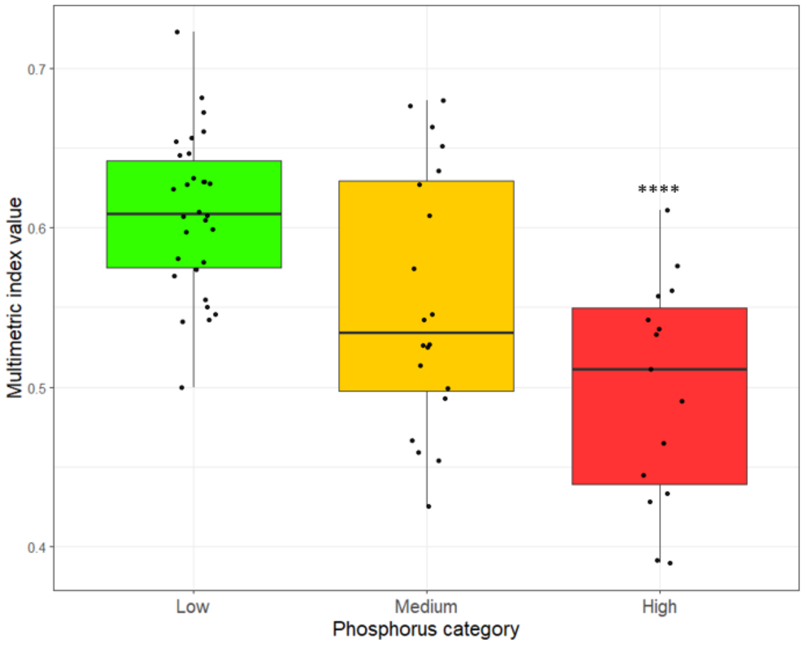

Figure 4.18. The median, interquartile range and 95% confidence intervals for the multimetric index values in low, medium and high phosphorus categories. The significance for each category is highlighted as such: * = marginally non-significant: P < 0.1, ** = moderately significant: P < 0.05, *** = significant: P <0.01, **** = highly significant: P < 0.001.

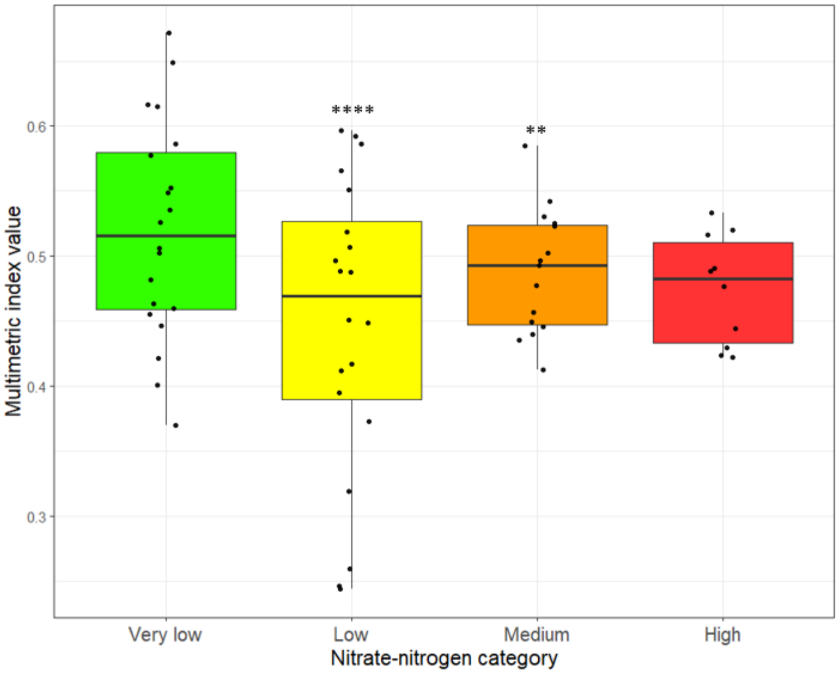

Figure 4.19. The median, interquartile range and 95% confidence intervals for the multimetric index values in very low, low, medium and high nitrate-nitrogen categories. The significance for each category is highlighted as such: * = marginally non-significant: P < 0.1, ** = moderately significant: P < 0.05, *** = significant: P <0.01, **** = highly significant: P < 0.001.

4.4 Discussion

The monitoring of temporary stream ecosystem health has previously been limited by the lack of research into dry-phase plant communities, and their responses to environmental change. These dry-phase plants have potential as biomonitors in cooler temperate climates where in-channel communities are extensive, unlike those in hotter, drier climates. I identified biological metrics, such as Poaceae richness and dominance, which responded to inorganic nutrient concentrations indicative of different human impact levels, supporting H2. These metrics were responsive despite sediment moisture and sediment organic matter (SOM) having the most influence on community composition (H1) and despite biological metrics not responding to total impact scores, meaning the data did not support H3.

4.4.1 Temporal influences on plant communities

The survey month had no influence on community composition but did influence metrics: values were lower in April (spring) than other months, and these surveys were thus excluded from metric analyses. The lower metric values in April are likely due to the influence of the temperature on plant growth (Woodward, 1988), with some species potentially still in the ground as seeds or bulbs in April (spring). The lack of compositional response could indicate that dominant taxa had established by the start of the surveying, meaning composition would remain largely similar even if some smaller species had not established.

The year prior to surveying was a particularly dry year, with some sites not rewetting overwinter. The dry-phase duration is an important influence on in-channel plant communities (Katz et al., 2012; Leigh & Datry, 2017; Westwood et al., 2021), and therefore, may have influenced some observed responses. Later observations of some of the drier sites in 2021 – a much wetter year – indicating differences in moisture conditions between years, with some sites which were dry in September 2019, flowing in September 2021. These differences resulted in visual differences in plant communities between years. Some sites had reduced grass and vegetation cover in 2021 (Figure 4.20b-c) or no vegetation cover (Figure 4.20a) whilst others had increased overall cover and, potentially, richness (Figure 4.21a-b). The observed growth differences could reflect that plant communities are adapted to a seasonal flowing and drying regime, meaning a longer dry phase may have put communities, particularly the aquatic and marginal species, under more stressful drying conditions that they are not adapted to. This indicates that more than one year of monitoring is needed to characterise interannual variability in dry-phase communities and their potential as indicators.

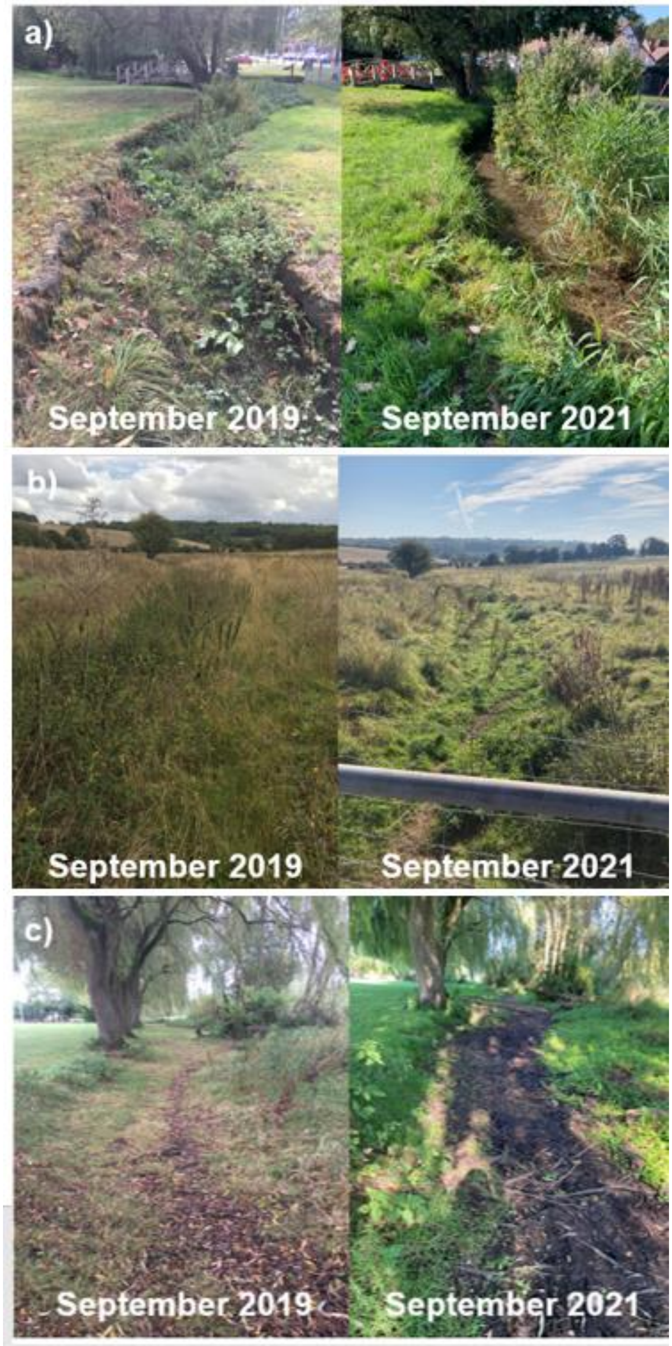

Figure 4.20. Photos from September 2019 (the survey year) and September 2021 of plant communities at a) Chalfont Playground, b) Four Ways Farm and c) Northchurch, showing the extent of plant growth in-channel.

Figure 4.21. Photos from September 2019 (the survey year) and September 2021 of plant communities at a) the Community centre and b) Luton Lane, showing the extent of plant growth in-channel.

4.4.2 Plant community composition responded to land use, sediment moisture and sediment organic matter

Dry-phase plant community composition was mostly influenced by the surrounding land use, an overarching parameter influencing several environmental variables and thus supporting communities with different habitat preferences. Sites surrounded by agricultural land use (which had lower moisture, higher phosphorus and SOM than other land uses) were often associated with species including white dead nettle (*Lamium album*), common couch grass (*Elymus repens*) and smooth meadow grass (*Poa pratensis*), which prefer well drained, highly fertile soils and, the latter of which can withstand trampling (BSBI & BRC, 2021; CABI, 2021). Species with preferences for damp or ponded conditions such as blue/pink water speedwell (*Veronica anagallis-aquatica* × *catenata*) and duckweed (Lemnoideae spp.) were indicative of fen land use, whilst those indicative of recreational land use were associated with waste/disturbed ground (e.g. groundsel: *Senecio vulgaris*, hedge bindweed: *Calystegia sepium;* BSBI & BRC, 2021) or shading, which was typically provided by planted riparian trees (e.g. ground-ivy: *Glechoma hederacea*, tufted hair-grass: *Deschampsia cespitosa,* BSBI & BRC, 2021).

Sediment moisture and SOM were the main influences of the specific environmental variables on community composition. The hypothesised influence of sediment moisture (H1) reflects is importance for plant communities (Tilman & Lehman, 2001; Bunn et al., 2006), in terms of growth (Veihmeyer & Hendrickson, 1927) and the moisture preferences of aquatic, semi-aquatic and terrestrial plants. Sites had differing drying regimes, whilst all sites had inputs of moisture during the survey period, some had inputs sufficient to cause rewetting briefly. Therefore, influencing variation in composition seen between sites, potentially through stressing terrestrial species, such as *M. arvensis*, *P. trivialis* and *Ranunculus repens* (creeping buttercup), which decreased with increasing moisture. SOM was also hypothesised (H1) to influence communities due to its impact on soil health and structure, promoting nutrient retention and increasing their availability within the soil (Halvin et al., 2005; Milić et al., 2019). Plant communities may also have influenced the SOM, as plant roots can play an important role in SOM decomposition, with some plants, such as crop species (wheat and barley), supressing the amount of SOM decomposition (Cheng et al., 2003). Contrary to previous studies (Walczack et al., 2002; Sabater et al., 2017), in which sediments with high organic matter retained more moisture, in this study SOM and sediment moisture had opposing influences on community composition. Site-specific drying durations meant some soils or subsurface sediments were wetter for longer, and thus had moister soils regardless of SOM. Additionally, finer sediments and SOM may have been transferred downstream at sites with longer flow periods, which also had higher sediment moisture content (Larned et al., 2010).

4.4.3 Metrics did not respond to total human impact score

Contrary to my hypothesis (H3), the total impact score either had no influence on plant metrics or its influence accounted for very little variation. The study catchment is heavily influenced by human activities, both historically and currently, in terms of channel morphology, hydrology and land use change (River Colne Catchment Action Network, 2021; Ver Valley Society, 2021). The lack of response to total impact scores may thus reflect the limited human impact gradient across in this study (Feld et al., 2016). Also, unimodal responses were seen in the results, unlike the hypothesised linear relationship, which, could also be due to the sites being subjected to multiple human impacts, and for a long time. Therefore, plant communities may be adapted to certain levels of human impact, and thrive under intermediate disturbance, acting as a ‘Goldilocks zone’ (Townsend et al., 2003). Future research should represent a full impact gradient, from sites of best available quality to most impacted to identify potential reference conditions for chalk streams (one of the requirements for the Water Framework Directive, European Commission, 2000).

4.4.4 Plant metrics as potential indicators of sediment nutrient concentrations

Despite not responding to overall impact scores (H3), all metrics except for the number of morphotypes (*NumMorph*) and the nitrate-nitrogen multimetric index, responded to either phosphorus or nitrate-nitrogen concentrations, or to both (H2). Taxonomic richness (*richness*)*,* H diversity (*diversity*), Poaceae richness (*PoaRich*), Poaceae cover (*Poa%*), herb richness (*HerbRich*) and Berger-Parker dominance (*dominance*) all increased with increasing phosphorus. Low phosphorous concentrations often lead to low biodiversity due to nutrients limiting growth (Dodson et al., 2000; Mittelbach et al., 2001), and richness can also decline at high concentrations (Willems, 1980), contrasting with the observed increases in all three richness metrics. However, the phosphorus concentration range observed herein, with very low and very high concentrations missing, may only reflect one part of the relationship, and a decrease may be eventually seen at higher concentrations. Also, light availability can be a key cause of a reduction in richness at nutrient-enriched sites (Hautier et al., 2009; Cleland & Harpole, 2010). Although a reduction in light availability (shading) was seen at sites with a dominant species with broad-leaved morphology such as stinging nettles, for sites with dominant species with linear morphology such as grass, light availability at a microhabitat scale could still be sufficient for other species may be able to survive. Additionally, Critchley et al. (2002) showed increases in phosphorus led to a shift from herbs to grasses in wet grassland, and whilst HerbRich did increase in our study, PoaRich contributed more to the higher richness values in the high phosphorus category.

Phosphorus concentrations explained more of the variation in the PoaRich, Poa% and dominance, and nitrate-nitrogen explained more of the variation in richness, HerbRich, diversity and Ellenberg N. The responses of these plant metrics demonstrates that the principles underpinning flowing/wet phase methods (Mean Trophic Rank: Holmes et al., 1999; LEAFPACS: WFD-UK TAG, 2014) also would work during the dry phase, supported by work in Stubbington et al. (2019).

High phosphorus concentrations have been associated with an increase in competitive species (Grime, 1979; Critchley et al., 2002), which can outcompete other species and become dominant. These species can then limit light availability and promote their own dominance (Hautier et al., 2009), unless they have a linear morphotype. The higher richness, HerbRich and diversity values seen at the high phosphorus concentrations indicated that whilst the dominance of one taxon may increase at high phosphorus concentrations, there was also an increase in taxa present at low % cover, suggesting that nutrient availability can support increasing richness and HerbRich regardless of the cover of the dominant taxa/taxon.

Ellenberg Ns decreased with increasing phosphorus concentrations, which contrasts H2, which was formulated to reflect the metric's indication of both nitrogen and overall soil fertility (Hill et al., 1999). However, Ellenberg indicators can be highly variable due to climatic and geographic differences (Hedwall et al., 2019) or in ecosystems that are in earlier successional stages (Dzwonko, 2001), such as temporary streams which are in a highly variable environment transitioning between aquatic and terrestrial conditions.

The multimetric index (comprising HerbRich, dominance and Ellenberg N) decreased with increasing phosphorus concentrations which, although is the response hypothesised, is likely due to Ellenberg N and HerbRich which responded in opposite ways to the hypothesis (H2). Due to the method needed to calculate the multimetric index, higher multimetric values were given to Ellenberg N (an increasing multimetric), since Ellenberg N decreased with increasing phosphorus, contrary to H2. These responses means that the multimetric index may not transfer to other chalk stream systems, where potentially HerbRich could decrease at the highest of phosphorus concentrations, and Ellenberg N would increase as expected (Grime, 1979). Further data collection across a full impact gradient should encompass the breath of phosphorus concentrations that occur in temporary chalk streams.

Richness, diversity and HerbRich decreased as nitrate-nitrogen increased from very low to low and moderate concentrations. Elevated nitrate-nitrogen conditions reduce in plant biodiversity by allowing fast-growing species to outcompete slower-growing species (Al-Mufti et al., 1977; Stevens et al., 2006; Hautier et al., 2009). The metrics were comparable across sites with high and very low nitrate-nitrogen concentrations. Additionally, the nitrate-nitrogen multimetric index (comprised of HerbRich, PoaRich and Ellenberg N) decreased only slightly with increasing nitrate-nitrogen concentrations, which could reflect site-specific phosphorus concentrations. These responses to nitrate-nitrogen could be due to the composition of the plant communities which may comprise taxa which tolerate the very low and high availability of nitrate-nitrogen through increased root growth and leaf area respectively (van der Werf et al., 1993). Thus, very low and high nitrate-nitrogen concentration sites had similar richness. Additionally, phosphorus can be the limiting factor for plant growth, regardless of nitrate-nitrogen concentrations. This is particularly the case in calcareous grasslands and freshwater ecosystems, where phosphorus concentrations can prevent nitrogen uptake (Critchley et al., 2002; Cleland & Harpole, 2010). At medium nitrate-nitrogen concentrations, two of the sites had low phosphorus concentrations, potentially limiting herb growth. Plant nutrient uptake can also be influenced by water availability (Güsewell et al., 2003), and differences in drying duration between sites. In this study, some sites had been dry since the previous summer, whereas others experienced brief occurrences of rewetting, which may have caused variation in responses to nitrate-nitrogen.

The lack of response to either nutrient by NumMorph is likely due to the turnover of species with the same morphotypes but contrasting nutrient preferences. Plant morphotypes may also be influenced strongly by flow and sedimentation processes occurring during the flowing phase (Clarke, 2002; Gurnell, 2014), overriding any response to nutrient concentrations.

4.4.5 Metric responses to shading can help inform restoration

The metric responses to shading indicate the influence of shading on plants in bioassessment. Moderate shaded sites had the highest richness and NumMorph than other categories, perhaps reflecting ‘goldilocks’ conditions at these sites. At heavy shaded sites, the limited light availability may only enable photosynthesis by shade-adapted taxa, reducing taxa richness (Wood et al., 2012). At sites with low or no shading, temperatures and light intensity may be too high for some species to tolerate (Barber & Anderson, 1992) or faster-growing species may outcompete slower-growing species (Hautier et al., 2009). Contrastingly, PoaRich and Poa% were higher sites with low or no shading, likely due to grasses tolerating high intensity light conditions (Devkota et al., 1997). It was hypothesised (H4) that Poaceae metrics would be highest at unshaded sites, as grasses are often competitive in open habitats, but values were lower than those found at low shading. This apparent relationship could be an artifact of open sites having higher phosphorus concentrations, allowing other species with broader leaves and higher above-ground biomass such as stinging nettle (*Urtica dioica*) and fool’s watercress (*Apium nodiflorum*) to outcompete the grass species, effectively creating their own shading to stop other species growth (Al-Mufti et al., 1977; Cleland & Harpole, 2010). Therefore, the responses seen could imply that to help maintain or improve plant biodiversity, a moderate amount of shading/riparian vegetation is required. This is an important observation that could inform climate change adaptation measures i.e. tree planning for shading to reduce temperatures (Rutherford et al., 1997).

Generally, these responses to shading corresponded with those of aquatic plant communities found in perennial streams or flowing phases (Dawson & Haslam, 1983).

Given that LEAFPACS (WFD-UK TAG, 2014) metrics are influenced by heavy shading, shading may influence the dry-phase metrics in identified in this research when applied to other chalk streams. However, results from this research suggested changes in nutrients concentrations are still distinguishable under differing shade conditions.

4.4.6 Implications for future biomonitoring

Dry-phase plant metrics responded significantly to differing nutrient concentrations, with dominance and PoaRich demonstrating the most potential for detecting phosphorus concentrations. This research has demonstrated the potential of dry-phase taxa (both terrestrial and aquatic) to monitor eutrophication in temporary streams, despite the influences of flow regime, sediment moisture and shade. The temporal differences in the biological metrics indicate that biomonitoring surveys can be conducted between May (spring) and September (autumn), similar to LEAFPACS2 (June; spring–September; autumn; WFD-UK TAG, 2014), with little seasonal influence on plant growth in these months. Additionally, although there did appear to be some influence of dry-phase duration on plant communities, this did not hinder the ability to detect changes in nutrient concentrations, meaning dry-phase plant metrics can be used for biomonitoring across a range of wet and dry conditions. For example, at sites with higher phosphorus the dominance of one taxon was high, but the dry-phase duration influenced the species (i.e. fool’s watercress for sites with shorter dry phases, and stinging nettles for sites with longer dry phases). Future research should be conducted to expand into other drying chalk streams – the priority in the UK due to their conservation status and biodiversity – and cover the full range of human impact levels.

Chapter Five: Dry-phase invertebrate communities and their potential as biomonitors

5.1 Introduction

The drying of a riverbed is a typical part of the natural flow regime for many temporary streams. The change from flowing to dry conditions causes a general shift in physical habitat and biotic conditions from aquatic to terrestrial. With the increase of impacts such as climate change and over-abstraction, the dry phase will potentially increase in both duration and occurrence (Palmer et al., 2008; Tramblay et al., 2020). The understanding of temporary stream ecosystems is growing (e.g. Larned et al., 2010; Corti & Datry, 2016; Stubbington et al., 2017) but there are limitations in our knowledge of the in-channel communities, especially those present during the dry phase (Stubbington et al., 2019; Steward et al., 2022). The dry phase provides suitable habitat, food and refuge to biological communities, is of cultural significance, and provides potential water resources and flood regulation to humans (Steward et al., 2012; Acuña et al., 2014; Stubbington et al., 2019). Therefore, our understanding of these ecosystems, including both their wet and dry phases, is important to understand their ecological health and to protect and manage them and the services they provide.

In addition to climate change and over-abstraction, temporary streams, as with all river systems, face threats from land use change and pollution (both point source and diffuse; Buttle et al., 2012; Acuña et al., 2014; Smeti et al., 2019). Increasing urbanisation and agricultural intensification can impact the habitat within temporary streams through influencing vegetation and sediments. Urban sources of pollution and agricultural practices can lead to increased nutrients in-channel influencing vegetation, causing dominance of competitive species (Willems, 1980) and changes in community composition from herbs to grasses (Critchley et al., 2002). Increased fine sediment inputs into streams can also be associated with agricultural practices (Wood & Armitage, 1997; Soulsby et al., 2001; Naden et al., 2016), and reduce sediment heterogeneity and infilling interstitial spaces.

Despite these ongoing impacts, temporary stream monitoring is lacking in comparison to their perennial counterparts (Stubbington et al., 2018) and without fully understanding these systems, they cannot be protected or restored. Current monitoring practices often focus solely on aquatic taxa or lack the means to sample/survey the dry phase (Stubbington et al., 2018). Tools to monitor community responses to human impacts, despite intermittence, are being developed to incorporate persisting aquatic and colonising terrestrial dry-phase communities in the Mediterranean basin (Sánchez-Montoya et al., 2020), California (Mazor et al., 2014) and in arid parts of Australia (Acuña et al., 2017; Steward et al., 2018). However, these developments have not been seen for temporary streams found in temperate conditions (i.e. cooler, wetter climates), although the value and potential of dry-phase invertebrates as biomonitors to intermittence has been highlighted in Bunting et al. (2021) and Stubbington et al. (2019).

Dry-phase invertebrates form an important part of temporary stream communities, providing food for other biota during the dry phase and aquatic organisms when flow resumes (Nakano et al., 1999; Wishart, 2000; Eberle & Stanford, 2010), processing organic matter (Clarke & Grant, 1968; Wishart, 2000; Steward et al., 2017) and pollinating in-channel and riparian vegetation (Boulton et al., 2008). Dry-phase invertebrate communities are often diverse (Steward et al., 2011; Sánchez-Montoya et al., 2020), supporting taxa such as ants, woodlice, carabid beetles and spiders. Carabids play an important role in ecosystem functioning, alongside spiders, aiding in pest control (Lövei & Sunderland 1996; Pearce & Venier, 2006; Zieche & Roth, 2008).

Invertebrates, both aquatic and terrestrial, are effective biomonitors and have been used in other habitats (Niemelä et al., 1993; Boscaini et al., 2000; Eyre & Luff, 2002), and temporary streams in other climates (Mazor et al., 2014; Steward et al., 2018; Sánchez-Montoya et al., 2020). Invertebrate communities, in particular carabids (Carabidae: ground beetles) and spiders (Araneae), are abundant, are easy and cost-effective to sample, responsive to environmental conditions and, for many invertebrate taxonomic groups, the taxonomy and ecology are well understood (Niemelä et al., 2000; Rainio & Niemelä, 2003; Borchard et al., 2014). Most importantly, they are responsive to environmental variability, due to their beneficial average population turnover in comparison to other organisms, and their ability to colonise habitats matching their environmental preferences through active dispersal (Hodkinson & Jackson, 2005; Gerlach et al., 2013), making them useful biomonitors.

Vegetation provides habitat, shelter (from both predation and harsh abiotic conditions) and food for invertebrates (Adis & Junk, 2002; Crist et al., 2005), and thus the structure, morphotype and taxonomic richness of plant communities influences the invertebrate community composition and diversity (Siemann et al., 1998; Crist et al., 2005). Typically, complex vegetation morphotypes (e.g. water mint: *Mentha aquatica* and garlic mustard: *Alliaria petiolata*) or plant communities comprised of multiple morphotypes, and sites with high vegetation richness support rich, diverse invertebrate communities (Boscaini et al., 2000; Cole et al., 2008; Schirmel et al., 2016). In-channel organic matter (OM), including leaf litter, also provides similar ecosystem roles for invertebrates: habitat, food and shelter (Bultman & Uetz, 1984; Uetz, 1991; Adis & Junk, 2002). In the dry phase, OM can accumulate in large amounts due to the lower decomposition rates than flowing phases, and the lack of flow to move the OM downstream (Dahm et al., 2003; Langhans & Tockner, 2006; von Schiller et al., 2015), potentially increasing its importance.

Sediment impacts invertebrate communities through providing refuge and habitat, and influencing water availability (Lambeets et al., 2005). In exposed riverine sediments – a similar aquatic-terrestrial environment to the dry phase – sediment composition influences ground beetle communities (Eyre & Luff, 2002), with larger gravels providing a wider range of interstitial spaces, which are also shaded from the sun and thus cooler (Lambeets et al., 2005; Steward et al., 2022). Water availability, through sediment moisture, is an important influence on community composition (Butterfield et al., 1995; Eyre & Luff, 2002) through differing species tolerances (Thiele et al., 1977), availability of aquatic prey that may persist during the dry phase (Ramey & Richardson, 2017) and its influence on humidity (Antvogel & Bonn, 2001).

Site-level and microscale shading influences temperature, with shading causing cooler conditions, and species temperature preferences can thus influence community composition (Antvogel & Bonn, 2001; Feld et al., 2018). Additionally, trees, which are the main source of shading, can provide an escape from inundation for more mobile species, and therefore an indirect impact of increased shading (Adis & Junk, 2002; Corti & Datry, 2012).

The research in this chapter aims to characterise these communities and their responses (including community composition and metrics such as taxa richness and abundance) to spatial variability in sediment, vegetation, leaf litter and shading conditions. The results will improve understanding of dry-phase invertebrate communities in temperate climates with cooler, wetter conditions. I hypothesised that (H1) dry-phase community composition (including carabids and spiders) vary and (H2) taxa richness will increase and activity densities (hereafter *abundance*) will decrease, in response to increasing plant richness, greater vegetation structure complexity, greater sediment complexity and increasing sediment moisture.

5.2 Methods

5.2.1 Site selection and description

An initial site visit in March (spring) 2019 and plant surveys conducted in April (spring) 2019 (see Chapter 4) informed site selection. From the 14 study sites described in

Chapter 4 (see section 4.2.1-2), six sites were selected to represent variation in the habitat conditions whilst maintaining sufficient replication and ensuring sites had a high probability of being, and remaining, dry throughout the sampling period (May: spring–July: summer and September: autumn). Additionally, because all sites had public access, sites were selected to reduce to possibility of traps being disturbed by the general public. The six study sites (Chequers Pub, Luton Lane, Gade Cottages, Mandelyns, Chalfont Playground and Chalfont Church) were located across the Rivers Ver (n = 2), Gade (n = 1), Bulbourne (n = 2) and Misbourne (n = 1) in the Colne catchment (see section 4.2.2; Figure 4.1–4.6).

5.2.2 Pitfall traps

The dry-phase invertebrate communities were sampled using pitfall traps set and emptied every two weeks (14 days ± 5 hours) between 30th May (spring) and 18th July 2019 (summer; n = 4), and in September 2019 (autumn; n = 1). These two time periods ensured that communities were sampled during the peak activity period to capture almost all major taxa (May–July) and to sample taxa with different activity periods (September). Pitfall trapping is frequently used to study ground-dwelling invertebrates such as Araneae and Carabidae, the focus of this study (Spence & Niemelä, 1994; Wishart, 2000; Ellis et al., 2001). Pitfall traps provide advantages compared to other methods (e.g. ground searching, netting and sticky traps). Sampling occurs over longer periods of time (days to weeks as opposed to minutes to hours) and collects taxa active during the day and the night, meaning pitfall traps can sample taxa that may be missed by other methods (Wishart, 2000; Gobbi et al., 2018). This is particularly true for dry riverbeds which may experience higher temperatures during the day, potentially promoting nocturnal and crepuscular activity (Corti et al., 2013). However, a limitation of pitfall traps is that they characterise activity densities rather than absolute abundance and are biased towards the capture of large, mobile taxa (Luff, 1975; Corti et al., 2013; Engel et al., 2017).

At all sites eight pitfall traps were set 1-m intervals in a diagonal transect across the channel with the transect trajectory modified as necessary to ensure representation of all microhabitats. The eight collected pitfall traps were pooled to produce a single in-channel sample for each site. Despite taking measures to avoid disturbance by the public, in total 20 traps at two sites were removed or damaged over the sampling period, and one sample was removed due to the loss of six traps. Each pitfall trap consisted of two plastic cups (10 cm diameter), set into the ground so that the rim was flush with the sediment surface. The inner cup was then ⅓-filled with a 50:50 ethylene glycol/water preservative, with an additional 1% formaldehyde to enhance preservation, a drop of detergent to break surface tension and prevent invertebrates escaping (Webb et al., 2017), and a drop of

Bittrex to deter consumption by vertebrates. This preservative is potentially attractive to some invertebrates (i.e. Carabidae and Araneae; Skvarla et al., 2014). A wooden lid was placed 1 cm above the rim of the cup to prevent entrance of rain and small mammals, whilst still allowing invertebrates to fall into the cup.

Invertebrates were identified with a microscope (magnification 40x) and standard taxonomic keys, and preserved in 70% industrial methylated spirits in the laboratory. Taxa were identified to a mixed taxonomic level: all Carabidae, Araneae, Dermaptera, Hymenoptera, Isopoda, Limnephilidae, Planariidae were identified to species where possible (i.e. juvenile Carabidae and Araneae were recorded to family level), Formicidae to subfamily, and other Coleoptera adults were identified to genus/species level. Acari, Diptera, Gastropoda, Collembola, Lumbricina, Julida, Opiliones, Orthoptera, Polydesmida and Siphonaptera were identified as such. Four datasets were produced for analyses: one with family-level taxonomic resolution, one with mixed-level taxonomic resolution, one comprising all spider taxa and one of all carabid taxa.

Environmental parameters were characterised to reflect the habitat conditions, including those indicative of human impact: sediment moisture and composition, in-channel vegetation morphology and richness, shading, and in-channel organic matter. A mixture of visual assessments and MoRPh (Modular River Physical survey; Shuker et al., 2017) was used to characterise these environmental conditions, with sediment samples taken for analysis in the laboratory for moisture, organic matter content and grain size distribution (see section 4.2.4) for further details).

5.2.3 Data analysis

5.2.3.1 Environmental variables

Following data exploration and previous research (see section 5.1), two continuous variables: sediment moisture (*SedMoist*) and vegetation richness (*VegRich*), and four categorical variables: gravel proportion (*GravelProp*: to represent sediment complexity), vegetation morphology (*VegMorph*), shading, and in-channel leaf litter cover (*LeafLitter*) were selected from the environmental variables collected/sampled. VegMorph, VegRich and GravelProp represented the influence of agricultural land use on communities, reflecting the inputs of nutrients and fine sediments, whilst LeafLitter and shading reflect the removal of riparian vegetation. Although SedMoist does not reflect human impact, it included due to the known influence of this natural variable and to enable its influence to be distinguished from the effects of human impact. GravelProp and shading had two categories, low (< 50%) and high (> 50%). VegMorph was also split into two categories: simple and complex. Sites with simple VegMorph had linear-structured in-channel vegetation (i.e. predominantly grass), whilst sites with complex VegMorph had in-channel plants with branched structures or had multiple layers of branched and linear-structured plants. LeafLitter categories comprised the absent, present and extensive MoRPH cover categories (see Chapter 2). After data exploration, shading was removed from further analysis due to collinearity (GVIF > 3; see Chapter 2) between shading and GravelProp: all but one sample that had low GravelProp was in the high shading category and all samples with high GravelProp had low shading. Therefore, GravelProp can be considered indicative of both Gravel proportions and shading.

5.2.3.2 Community composition

To characterise variability in community composition in relation to the environmental predictors (H1), separate non-metric multidimensional scaling (NMDS) analyses ('vegan' package; Okansen et al., 2007) with Bray-Curtis similarity coefficients (999 iterations) were conducted for family-level (which did include some higher taxonomic resolutions i.e. order), mixed-level, spider and carabid communities. To visualise variability in community composition, corresponding ordination plots were produced with environmental variables represented by colour-coding communities according to the category levels. Permutational analysis of variance (PERMANOVA; 'vegan' package; Oksanen et al., 2007; Anderson, 2014) was conducted to test the significance of compositional differences in response to the environmental variables. Indicator taxa were identified for each categorical environmental variable using the function multipatt from the 'indicspecies' package (De Caceres et al., 2016), and indicative changes in taxa in responses to the continuous environmental variables were analysed using TITAN (Baker and King, 2010; see section 2.4.5.1). Collembola dominated abundances at all sites, and analyses conducted to test their influence on the characterisation of community responses (see Appendix 3.1), indicated that their inclusion masked the responses of other taxa. Collembola were thus excluded from the calculation of abundance metrics (section 5.2.3.3; Barbour et al., 2009).

5.2.3.3 Metrics

Seven metrics were calculated to represent invertebrate communities (H2): family-level (which did include some higher taxonomic resolutions i.e. order) taxonomic richness (*FamRich*), mixed-level taxonomic richness (*richness*), activity densities (*abundance*), spider richness (*SpiderRich*), spider abundance (*SpiderAbund*), carabid richness (*CarabidRich*) and carabid abundance (*CarabidAbund*). Because all metrics followed a Poisson distribution, several generalised mixed models (GLMM) were initially created to test each metric's response to the environmental variables (section 2.4; lme4; Bates et al., 2014). Model residuals were over-dispersed in the abundance GLMM and thus, a negative binomial GLMM was used ('glmmTMB' package, Brooks et al., 2017).

SpiderAbund and CarabidAbund were square root transformed to meet the assumption of normality for the model residuals, and thus a LMM was instead used. Due to the small dataset size (n = 29), each environmental variable was included in individual models separately, without interactions, to avoid overfitting models. River and sampling date were used as random factors for all models, unless the models had a singular fit, after which random factors were removed.

Through identifying and processing samples, I observed that samples for the simple VegMorph category comprised of largely the same species in high abundances, whilst at complex VegMorph sites there were lower abundances of differing species. Based on these observations, I hypothesised that betadiversity would differ between VegMorph categories and thus calculated the Sørensen dissimilarity index (β_{SOR}), and its nestedness and turnover components for each VegMorph category, to represent beta diversity, using the ‘betapart’ package (Baselga and Orme, 2012; see Chapter 2 and 4). To visualise the beta diversity of invertebrate communities, the percentage of total abundance accounted for by simple and complex VegMorph was plotted.

All data analyses were conducted in R version 4.1.1 (R Core Team, 2021).

5.3 Results

5.3.1 Environmental description

All sites dried during the sampling period, although two sites (Chequers Pub and Mandelyns; Figure 4.1) had disconnected in-channel pools in June and September 2019. The site-specific SedMoist (as % weight) ranged from 2.29–53.75 % (mean ± SE: 26.20 ± 3.68 %) and GravelProp was either low (n = 15) or high (n = 12). VegMorph was either simple (n = 10) or complex (n = 17) with VegRich ranging between 11 and 30 taxa (20.15 ± 1.09) and LeafLitter was either absent (n = 10), present (n = 8) or extensive (n = 9).

5.3.2 Community description

A total of 25,091 invertebrates were recorded from 164 pitfall traps taken from the dry channel of six sites on five sampling dates between May-July (spring-summer) and September (autumn). The family-level dataset comprised 55 taxa and the mixed-level dataset comprised 139 taxa. The carabid and spider datasets included 27 and 35 taxa respectively. Taxa included aquatic organisms e.g. water scorpion (*Nepa cinerea*) and common water measurer (*Hydrometra stagnorum*), and terrestrial taxa e.g. woodlice (Oniscidea), spiders (Araneae) and ground beetles (Carabidae/carabids). Collembola made up 67 % of all invertebrate abundance. Excluding Collembola, Isopoda and Hymenoptera contributed to 52 % and 27 %, respectively, of all invertebrates with spiders and carabids each accounting for 4 %. Dominant spider taxa included *Pirata piracticus* (37 % of total spider abundance)*, Pardosa palustris* (9 %) and *Pardosa prativaga* (9 %). *Pterostichus madidus* and *Nebria brevicolis* made up 45 % and 24 % of total carabid abundance respectively.

Including Collembola, taxonomic richness ranged from 6–36 taxa (mean ± SE: 20 ± 1.53 taxa) per sample, family richness (*FamRich*) from 6–23 taxa (15.19 ± 0.94 taxa) per sample and activity densities (*abundance*) from 29–4248 individuals (930.74 ± 195.62 individuals) per sample. Without Collembola, richness ranged from 5–35 taxa (18.59 ± 1.59 taxa) per sample, FamRich from 5–22 taxa (14.19 ± taxa) per sample and abundance from 18–910 individuals (246.11 ± 52.59 individuals) per sample. Carabid richness (*CarabidRich*) ranged from 0–5 taxa (2.81 ± 0.28 taxa) per sample, carabid abundance (*CarabidAbund*) from 0–73 individuals (13.22 ± 2.84 individuals) per sample, spider richness (*SpiderRich*) from 0–13 taxa (4.44 ± 0.72 taxa) per sample and spider abundance (*SpiderAbund*) from 0–101 individuals (15.90 ± 4.77 individuals) per sample.

5.3.3 Responses to vegetation

5.3.3.1 Community responses

Family-level and mixed-level invertebrate community composition responded similarly to site-specific vegetation morphology (*VegMorph*), and only family-level community composition responded to vegetation richness (*VegRich*). Therefore, only family-level responses are presented (mixed-level responses are available in Appendix 3.5). The two vegetation variables accounted for 23 % of family-level compositional variation, with VegMorph accounting for more variation than any other environmental variable (PERMANOVA, VegMorph: $R^2 = 0.17$; VegRich: $R^2 = 0.08$).

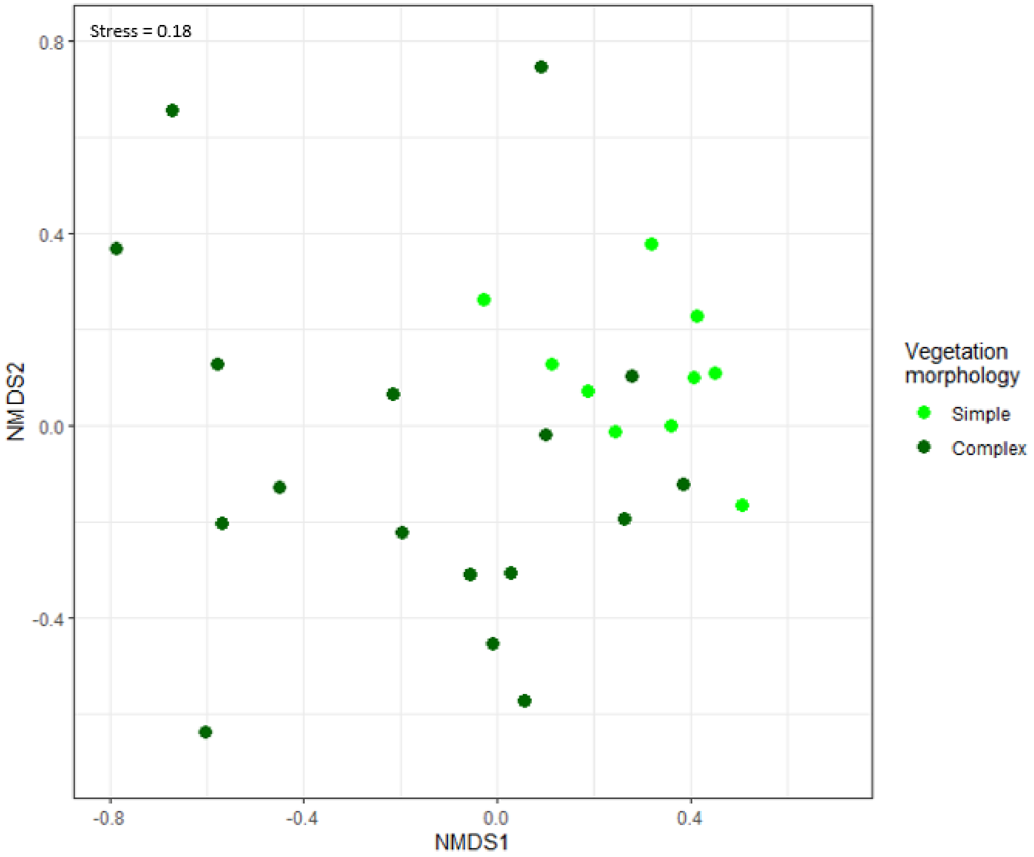

Figure 5.1. Non-metric multidimensional scaling (NMDS) ordination of invertebrate community composition according to vegetation morphology (simple or complex).

Communities at sites with simple VegMorph differed from those at sites with complex VegMorph (PERMANOVA, VegMorph: F = 7.45, df = 1, P = 0.001). Those at simple VegMorph sites had positive NMDS1 scores and are plotted as a small cluster on the periphery of a highly dispersed complex VegMorph group (Figure 5.1). Families indicative of sites with simple VegMorph included an ant sub-family (Myrmicinae), two woodlice families (Armadillidae, Phiiloscidae), earwigs (Forficulidae), Polydesmida (millipedes) and pill beetles (Byrrhidae), with Myrmicinae, Armadillidae and Phiiloscidae occurring exclusively at these sites (Table 5.1). Sites with complex VegMorph had no indicative taxa.

Table 5.1. Families (and sub-families) indicative of sites with simple VegMorph, displaying the IndVal statistic, specificity, fidelity and P value. Specificity and fidelity represent the probability (0–1) of the taxon occurring only at sites with simple VegMorph and occurring at all sites with simple VegMorph, respectively. P values are stated according to standard precision thresholds (De Cáceres et al., 2010).

Taxa	**IndVal**	**Specificity**	**Fidelity**	**P**
Myrmicinae	0.95	0.90	1.00	0.01
Armadillidae	0.88	0.78	1.00	0.01
Phiiloscidae	0.88	0.77	1.00	0.01
Forficulidae	0.71	0.84	0.60	0.02
Polydesmida	0.60	0.89	0.40	0.05
Byrrhidae	0.55	1.00	0.30	0.03

Communities at sites with simple (β_{SOR} = 0.78) and complex (β_{SOR} = 0.88) had a high spatial beta diversity based on the Sørensen dissimilarity index. The dissimilarity between communities at complex VegMorph sites was almost entirely explained by turnover (92%) rather than nestedness (7%), and whilst dissimilarity at sites with simple *VegMorph* was also explained mostly by turnover (85%), nestedness (15%) accounted for more variation than for complex communities. More invertebrate families occurred at sites with complex VegMorph in comparison to sites with simple VegMorph (Figure 5.2).

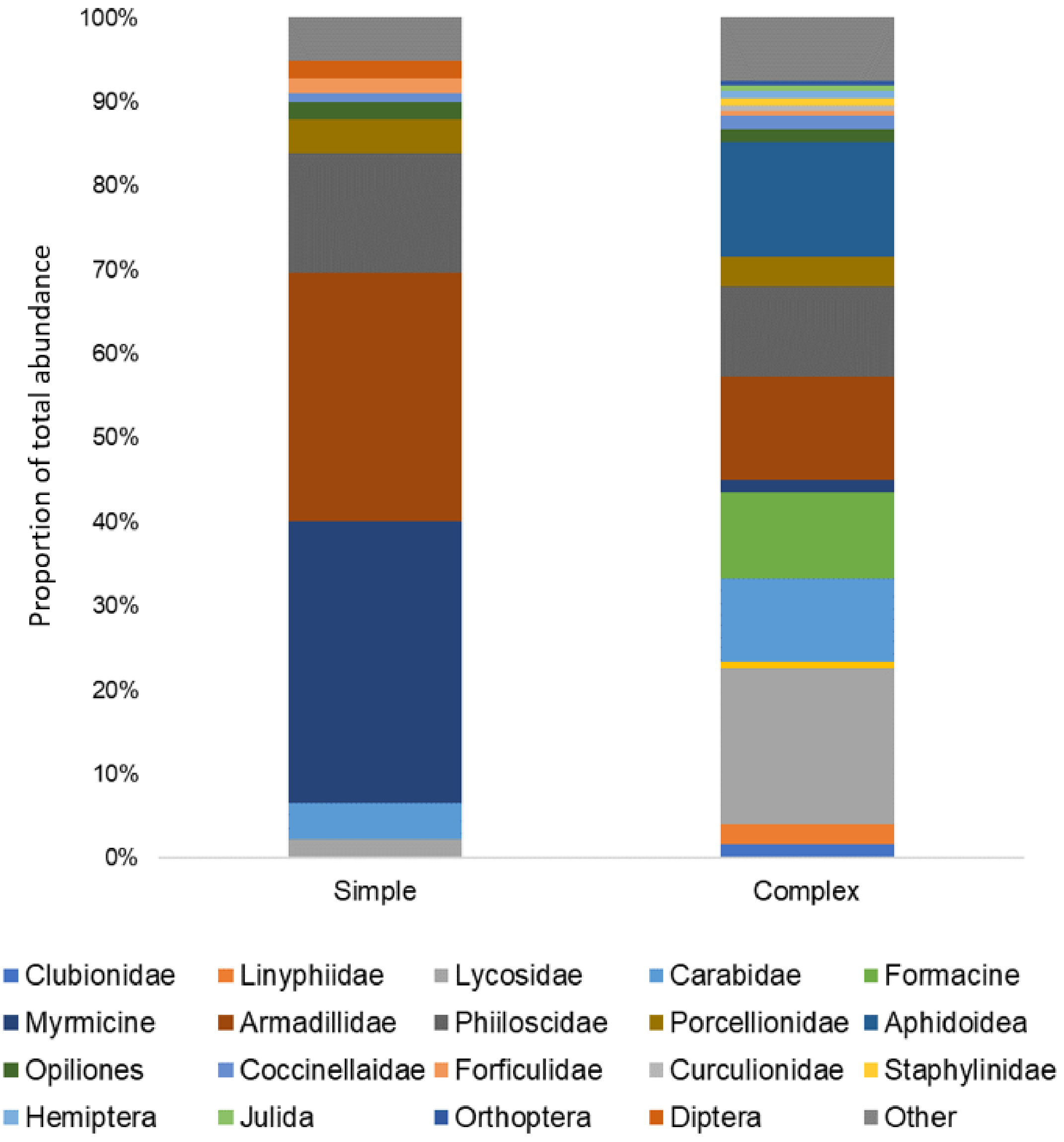

Figure 5.2. The percentage of the total abundance accounted for by invertebrate taxa (excluding Collembola) represented at sites with simple and complex vegetation morphotypes.

Communities also responded to VegRich (PERMANOVA, VegRich: F = 3.53, df = 1, P = 0.003) those at sites with higher VegRich occurred at higher NMDS1 scores and lower NMDS2 scores, with taxa spread evenly across the gradient (Figure 5.3). Families and orders associated with these communities included Gnaphosidae, Elateridae, Formacine, Hemiptera, Coccinellidae and Chrysomelidae (Figure 5.3). Communities at sites with the lowest VegRich occurred at low NMDS1 scores and central NMDS2 scores with taxa such as Diptera, Staphylinidae, Silphidae and Linyphiidae (Figure 5.3). Only Gastropoda significantly increased with increasing vegetation richness (TITAN).

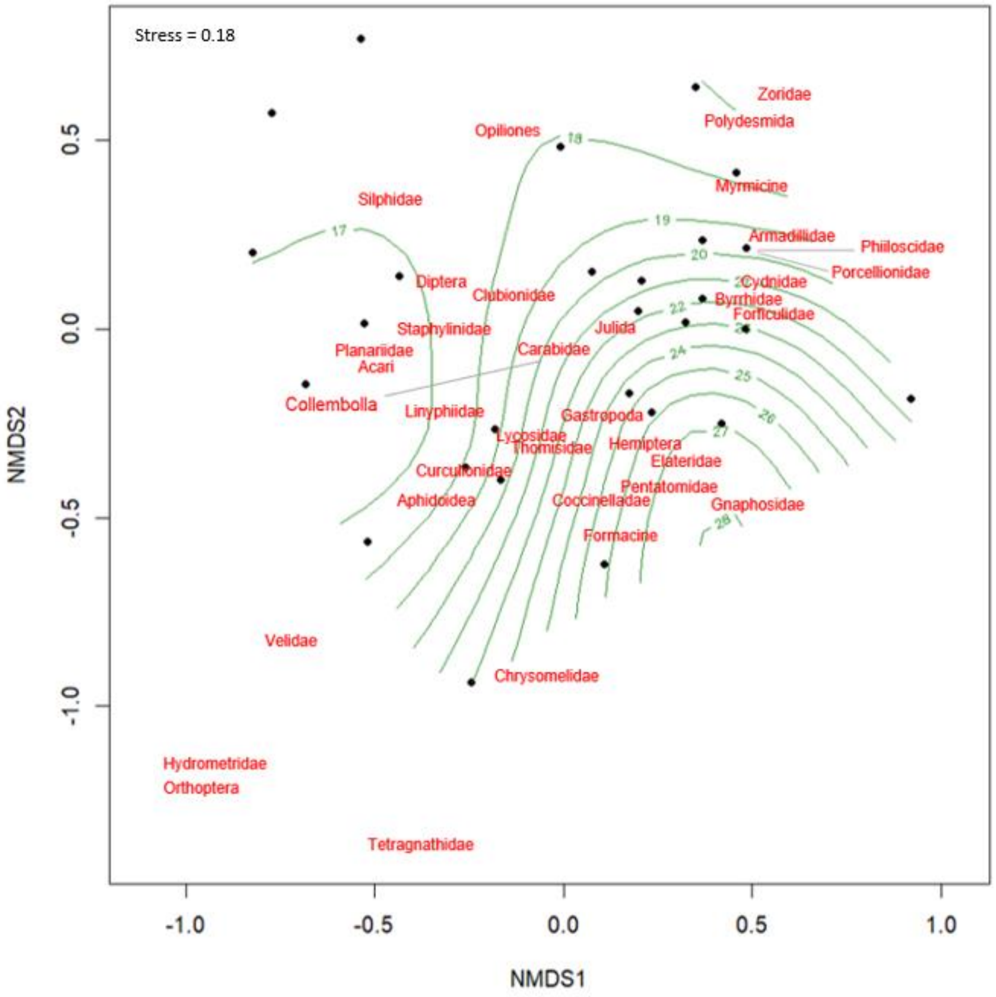

Figure 5.3. Non-metric multidimensional scaling (NMDS) ordination of invertebrate community composition (black points), mostly to family-level, with vegetation richness represented by contours, the number of each contour denoting the richness, and individual taxon labels to indicate associations with vegetation richness values.

Carabid community composition varied according to VegMorph (PERMANOVA, $R^2 = 0.09$, F = 3.66, df = 1, P = 0.005) but not VegRich (PERMANOVA, F = 5.89, df = 1, P = 0.593). Spider community composition showed no response to vegetation (PERMANOVA, VegMorph: F = 2.02, df = 1, P = 0.130; VegRich: F = 1.29, df = 1, P = 0.332). Carabid communities associated with simple VegMorph had high NMDS1 scores and all but two had low NMDS2 scores and were closer in composition, whilst those associated with complex VegMorph spread out along both dimensions (Figure 5.4). Only *Pterostichus rhaeticus/nigrita* was indicative of complex VegMorph (IndVal, Specificity = 1.00, Fidelity = 0.40, stat = 0.63, P = 0.035) and no carabid taxa were indicative of simple VegMorph.

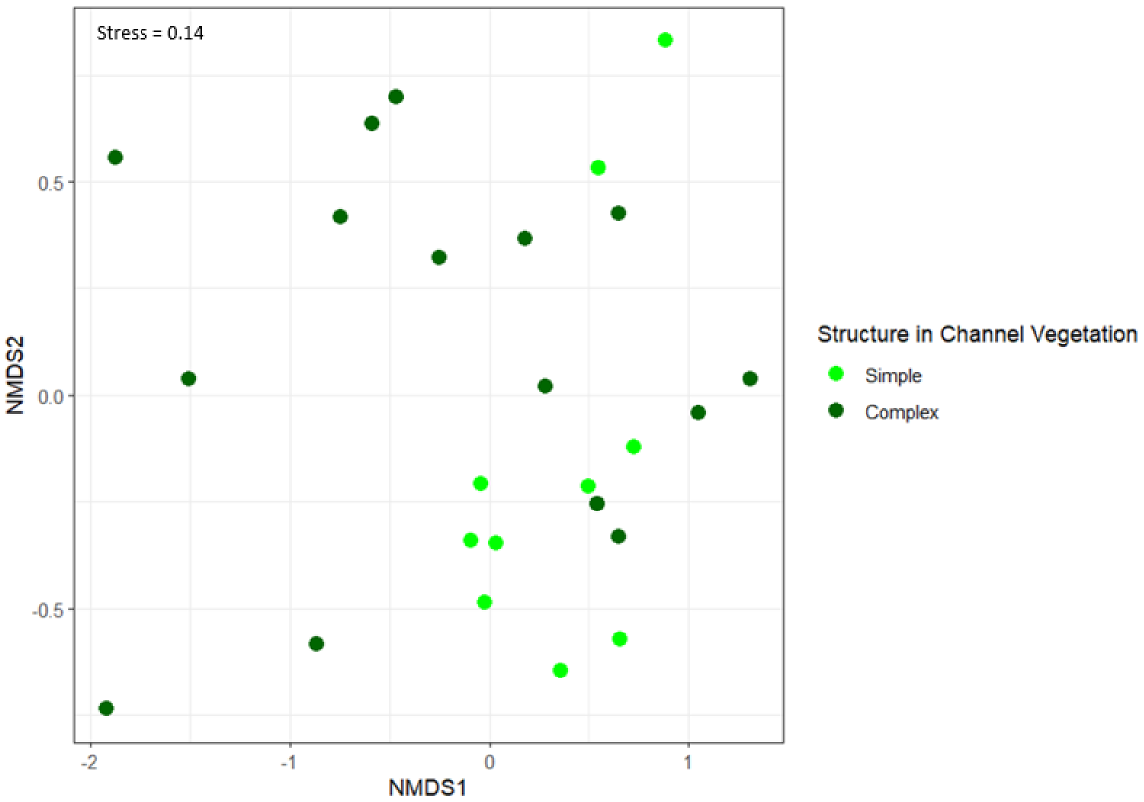

Figure 5.4. NMDS ordination of carabid community composition according to the vegetation morphology (simple or complex).

5.3.3.2 Metric responses

Taxonomic abundance and SpiderRich were the only metrics to respond to VegMorph and VegRich, respectively (Table 5.2; Table 5.3). VegMorph explained 50% of the variance in abundance and VegRich explained 12% of SpiderRich variance. Abundance was lower and less variable (Table 5.2) at sites with complex VegMorph compared to sites with simple VegMorph (Figure 5.5). SpiderRich increased with increasing VegRich (Figure 5.6). Although FamRich and richness increased with increasing VegRich (Figure 5.6), this was not significant (Table 5.3).

Table 5.2. The model used (Generalised Linear Mixed Model, Linear Mixed Models and Generalised Linear Model) to characterise the influence of vegetation morphology categories on the family-level and mixed-level taxonomic richness and abundance, spider richness and abundance, and carabid richness and abundance of dry-phase invertebrate communities, with the associated R^2 values (R^2C and R^2M for mixed models and R^2 for generalised linear models) and results of each model. The significant results are in bold, except for the intercept which reflects a deviation of the intercept from zero.

Metric (model)	**R^2C**	**R^2M or R^2**	**Intercept (Simple)**			**VegMorph (Complex)**		
			Estimate	**SE**	**P**	**Estimate**	**SE**	**P**
Taxonomic family richness (GLMM)	0.45	0.05	2.79	0.15	<0.001	-0.16	0.17	0.340
Taxa richness (GLMM)	0.70	0.05	3.02	0.21	<0.001	-0.16	0.22	0.460
Taxonomic abundance (GLMM)	0.73	0.50	6.10	0.36	<0.001	**-1.55**	**0.40**	**<0.001**
Spider richness (GLMM)	0.77	0.18	1.32	0.56	0.019	-0.28	0.64	0.665
Spider abundance (LMM)	0.70	0.01	1.67	0.86	0.053	0.32	1.01	0.750
Carabid richness (GLM)		0.03	1.13	0.18	<0.001	-0.16	0.23	0.499
Carabid abundance (GLM)		0.11	3.93	0.55	<0.001	-1.21	0.70	0.097

Table 5.3. The model used (Generalised Linear Mixed Model, Linear Mixed Models and Generalised Linear Model) to test the influence of vegetation richness on the taxonomic family richness, taxonomic richness and abundance, spider richness and abundance, and carabid richness and abundance of dry-phase invertebrate communities, with the associated R2 values (R2C and R2M for mixed models and R2 for generalised linear models) and results of each model. The significant results are in bold, except for the intercept which reflects a deviation of the intercept from zero.

Metric (model)	**R^2C**	**R^2M or R^2**	**Intercept**			**VegRich**		
			Estimate	SE	P	Estimate	SE	P
Taxonomic family richness (GLMM)	0.41	0.02	2.68	0.11	<0.001	0.04	0.07	0.547
Taxa richness (GLMM)	0.69	0.03	2.91	0.15	<0.001	0.07	0.07	0.325
Taxonomic abundance (GLMM)	0.71	<0.001	5.04	0.41	<0.001	0.02	0.21	0.934
Spider richness (GLMM)	0.74	0.12	1.10	0.36	0.003	**0.35**	**0.17**	**0.044**
Spider abundance (LMM)	0.71	0.003	2.85	1.05	0.031	-0.16	0.50	0.754
Carabid richness (GLM)		0.002	1.03	0.11	<0.001	-0.02	0.12	0.849
Carabid abundance (GLM)		0.08	2.55	0.19	<0.001	-0.26	0.19	0.175

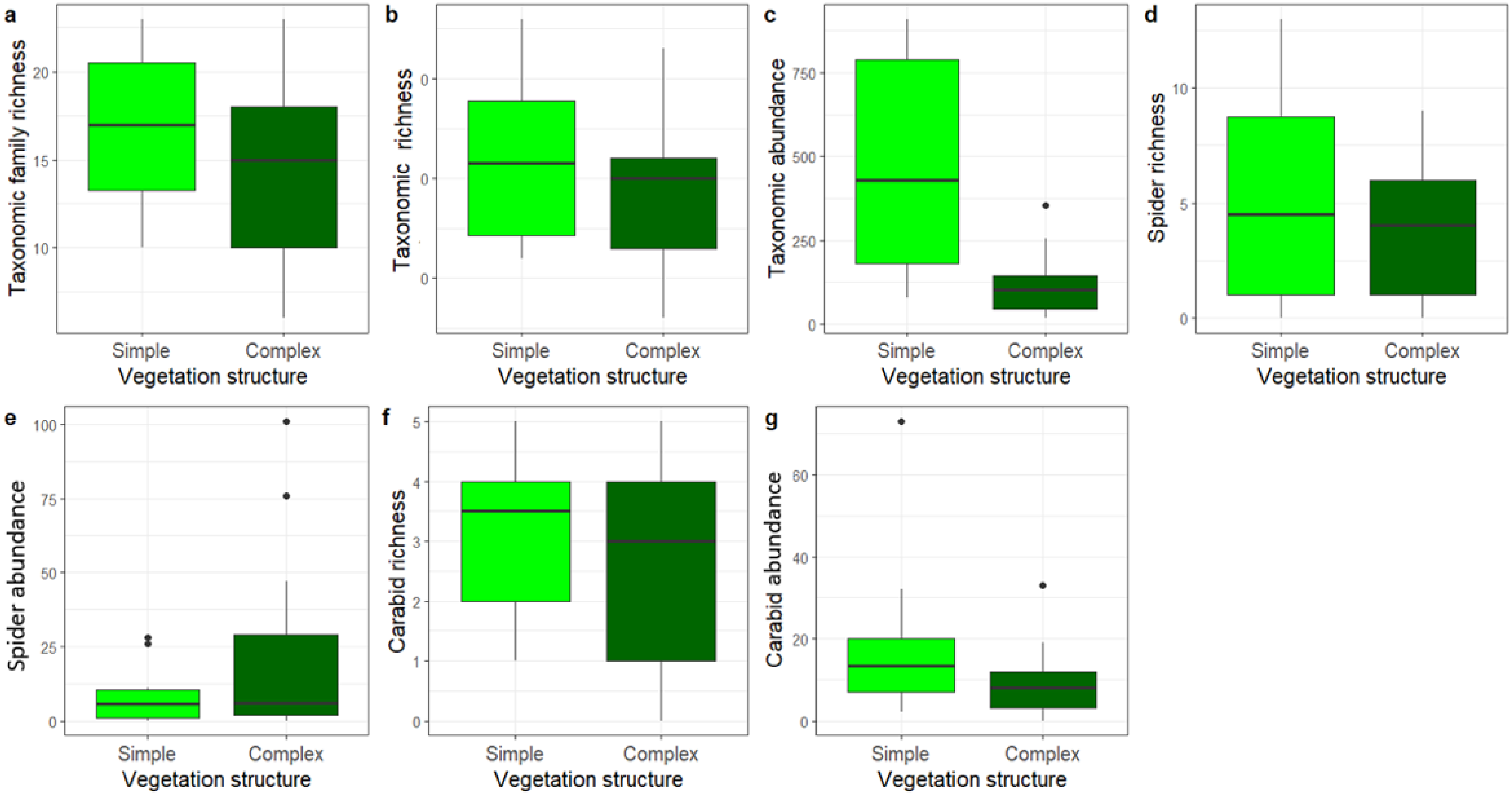

Figure 5.5. The median, interquartile range and 95% confidence intervals for invertebrate community metrics at simple and complex vegetation morphotype categories: a) taxonomic family richness, b) taxa richness, c) abundance, d) spider richness, e) spider abundance, f) carabid richness and g) carabid abundance. Big dots represent outliers.

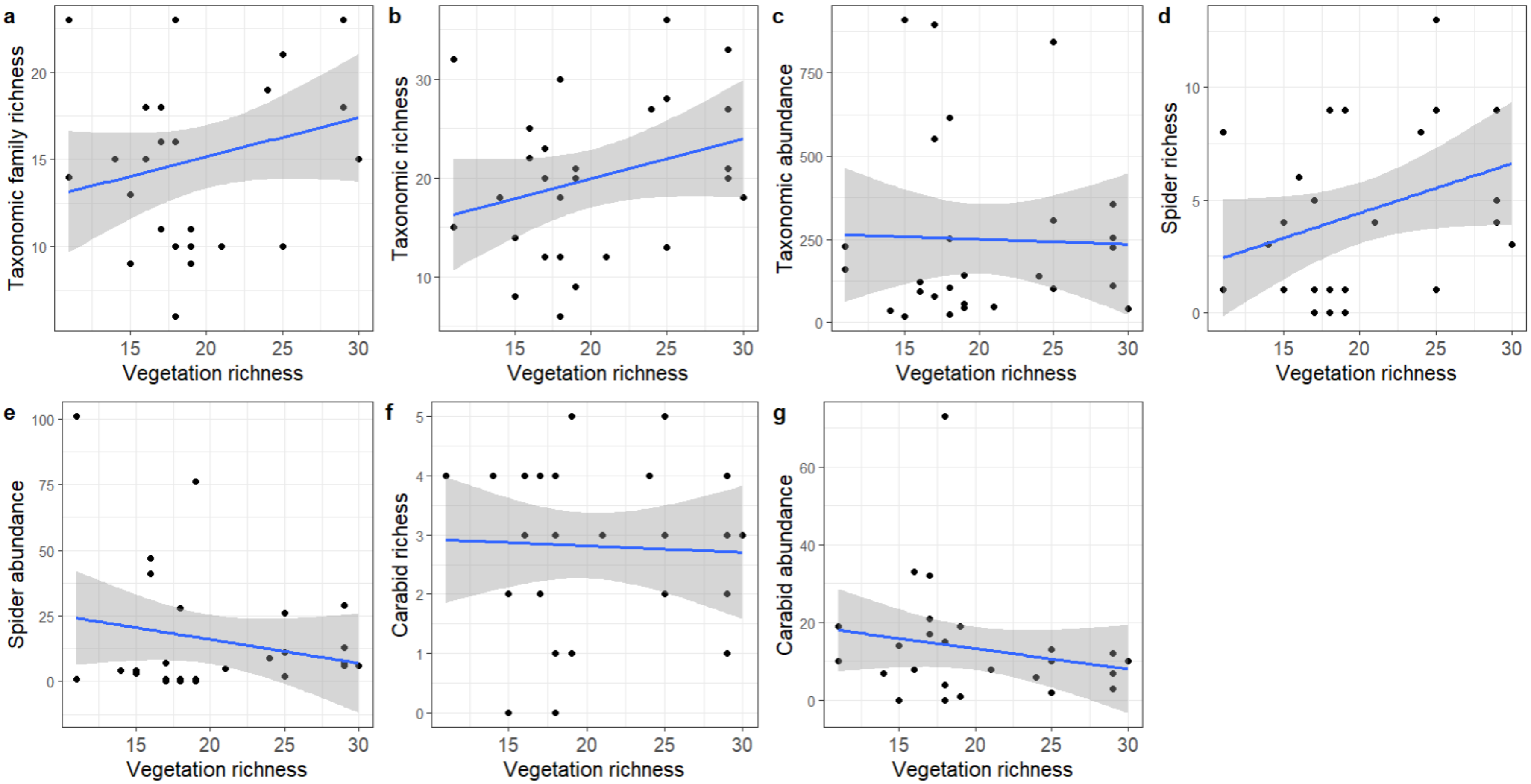

Figure 5.6. Invertebrate community metric responses to vegetation richness for: a) Taxonomic family richness, b) taxa richness, c) taxonomic abundance, d) spider richness, e) spider abundance, f) carabid richness and g) carabid abundance. The shaded area represents the 95 % confidence intervals.

5.3.4 Responses to sediment

5.3.4.1 Compositional responses

Family-level and mixed-level community composition showed similar responses to sediment. Therefore family-level responses are reported for SedMoist and mixed-level responses in Appendix 3.2, whilst mixed-level are reported for GravelProp here to give more detail of the community responses seen. SedMoist and GravelProp accounted a small amount of the community composition variance (PERMANOVA, GravelProp: R^2 = 0.09, SedMoist: R^2 = 0.07). An increase in SedMoist occurred from high to low NMDS1 and NMDS2 scores (Figure 5.7) with community composition varying along this gradient (PERMANOVA, F = 3.11, df = 1, P = 0.006). Taxa associated with low SedMoist included Armadillidae, Philosciidae, Cydnidae, Byrhidae and Myrmicinae, whilst Velidae, Aphidoidea, Curculionidae, Chrysomelidae and Linyphiidae were associated with high SedMoist. Five taxa decreased in abundance with increasing sediment moisture: Porcellionidae, Forficulidae, Armadillidae, Philosciidae and Myrmicinae (TITAN; Figure 5.8). There were no taxa which increased with increasing sediment moisture.

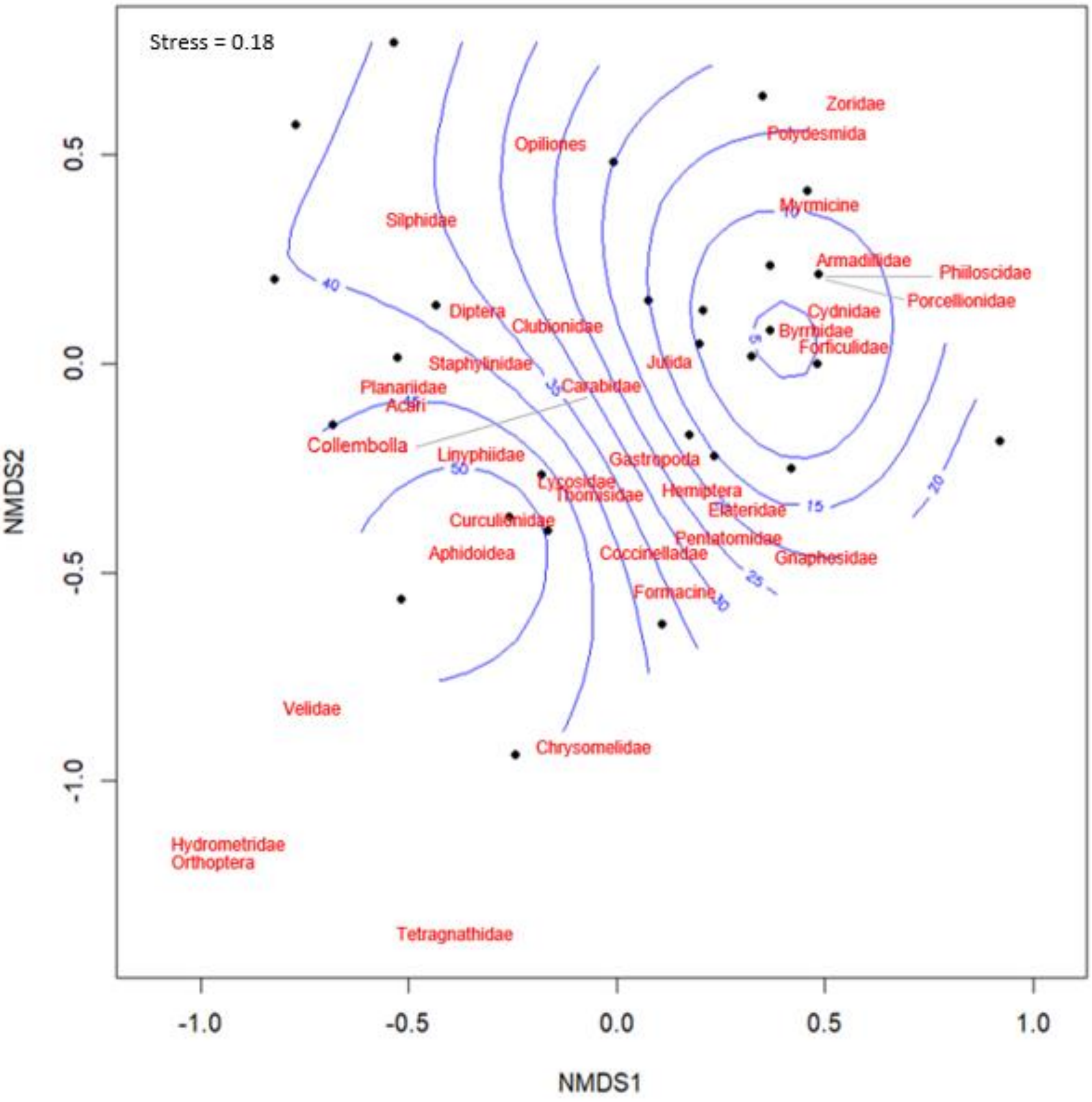

Figure 5.7. Non-metric multidimensional scaling (NMDS) ordination of invertebrate community composition, mostly to family-level, according to the SedMoist. Each point represents a community and SedMoist represented by contours, the number of each contour denote the value, and taxon labels indicate associations with SedMoist.

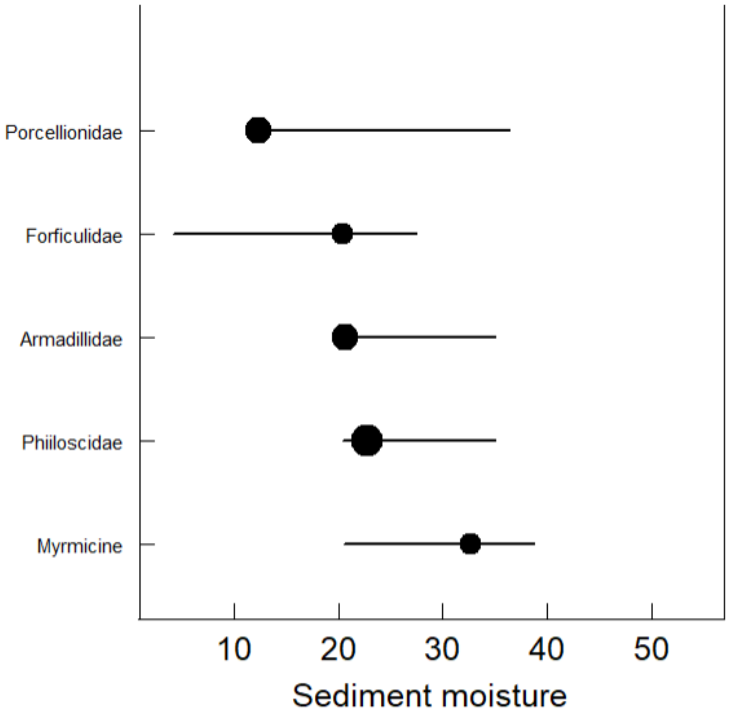

Figure 5.8. Threshold Indicator Taxa ANalysis (TITAN) plot for taxa which decreased (black circles) in abundance in relation to sediment moisture (%). The circle position indicates the mean change point for taxa abundance, circle size represents the relative magnitude of the change in abundance, and the lines represent the range of changes in 95% of bootstraps.

Mixed-level community composition varied with GravelProp (PERMANOVA, F = 1.79, df = 1, P = 0.036). Communities associated with low GravelProp had higher NMDS2 scores and those at sites with high GravelProp. Both groups were variable along the NMDS1 axis (Figure 5.9). Four spider taxa, two carabids, Dermaptera nymphs and *Coccinella septumpunctata* were indicative of high GravelProp, with *Pachygnatha clerki, Coccinella septumpunctata* and *Agonum viduum* occurring only at these sites (Table 5.4). Only *Porcellio scaber* was indicative of sites with low GravelProp, occurring at 60% of all sites with low GravelProp (IndVal, stat = 0.69, specificity = 0.79, fidelity = 0.60, P = 0.04).

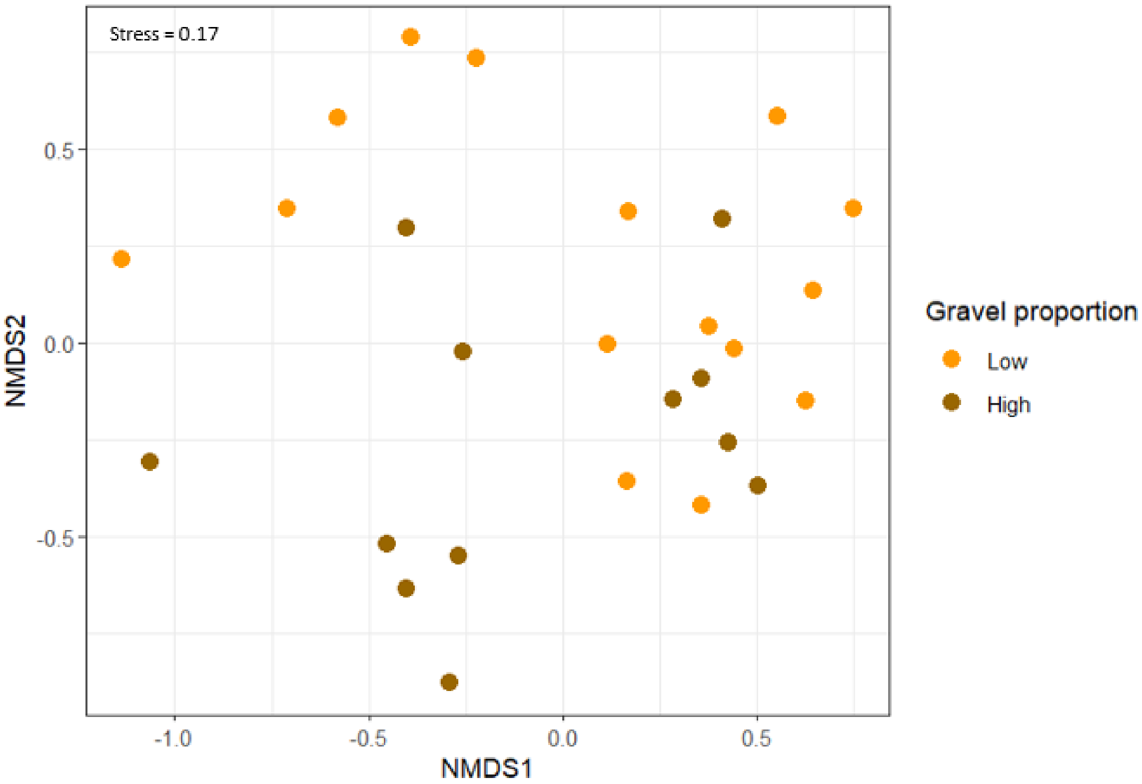

Figure 5.9. Non-metric multidimensional scaling (NMDS) ordination of mixed-level invertebrate community composition according to the Gravel proportion (low or high) at a site.

Table 5.4. Taxa indicative of sites with high GravelProp, displaying the IndVal statistic, specificity, fidelity and P value. Specificity and fidelity represent the probability (0–1) of the taxon occurring only at sites with high GravelProp and occurring at all sites with high GravelProp, respectively.

Taxa	**Specificity**	**Fidelity**	**Stat**	**P value**
Pardosa amentata	0.90	0.58	0.72	0.01
Hemiptera spp.	0.78	0.67	0.72	0.02
Pirata piracticus	0.89	0.58	0.72	0.01
Agonum viduum	1.00	0.42	0.65	0.01
Coccinella septempunctata juveniles	1.00	0.42	0.65	0.02
Dermaptera juveniles	0.95	0.42	0.63	0.03
Pterostichus rhaeticus/nigrita	0.91	0.42	0.62	0.03
Tenuiphantes tenuis	0.82	0.42	0.58	0.04
Pachygnatha clercki	1.00	0.33	0.58	0.04

Carabid communities responded to variability in site SedMoist (PERMANOVA, $R^2 = 0.07$, F = 2.49, df = 1, P = 0.006) whereas, their response to GravelProp was not significant (PERMANOVA, $R^2 = 0.04$, F = 1.91, df = 1, P = 0.09) and ordinations indicated considerable overlap between communities at sites with low and high GravelProp (Figure 5.10). A gradient of SedMoist was observed from high NMDS1 and NMDS2 values, with SedMoist increasing across the NMDS1 axis from 1 to -0.5 with the highest moistures occurring at low NMDS1 values and high NMDS2 (Figure 5.11). Taxa associated with higher SedMoist included beetles such as *A. viduum, Pt. nigrita/rhaeticus, Stenolophus mixtus* and *Elaphrus cupreus,* and taxa associated with sites with low SedMoist included *Nebria brevicollis, Pt. madidus, Harpalus rufipes* and *Amara eurynota* (Figure 5.11). Spider community composition did not vary in response to SedMoist (PERMANOVA, F = 1.99, df = 1, P = 0.134) or GravelProp (PERMANOVA, F = 1.39, df = 1, P = 0.302).

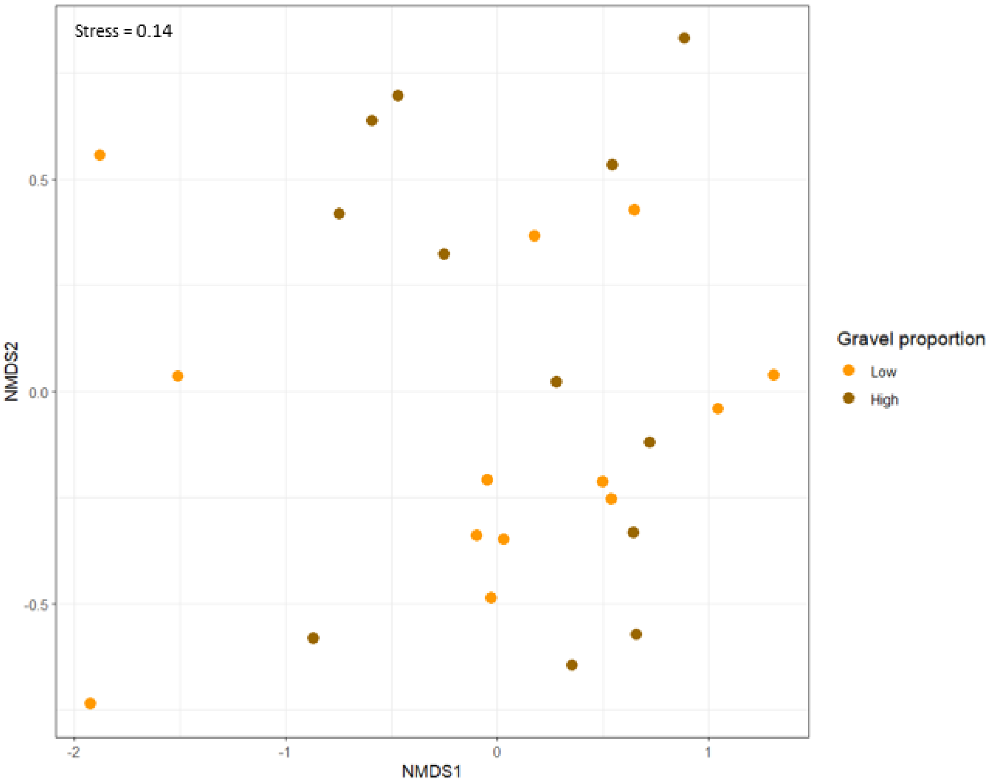

Figure 5.10. Non-metric multidimensional scaling (NMDS) ordination of carabid community composition according to the GravelProp (low or high).

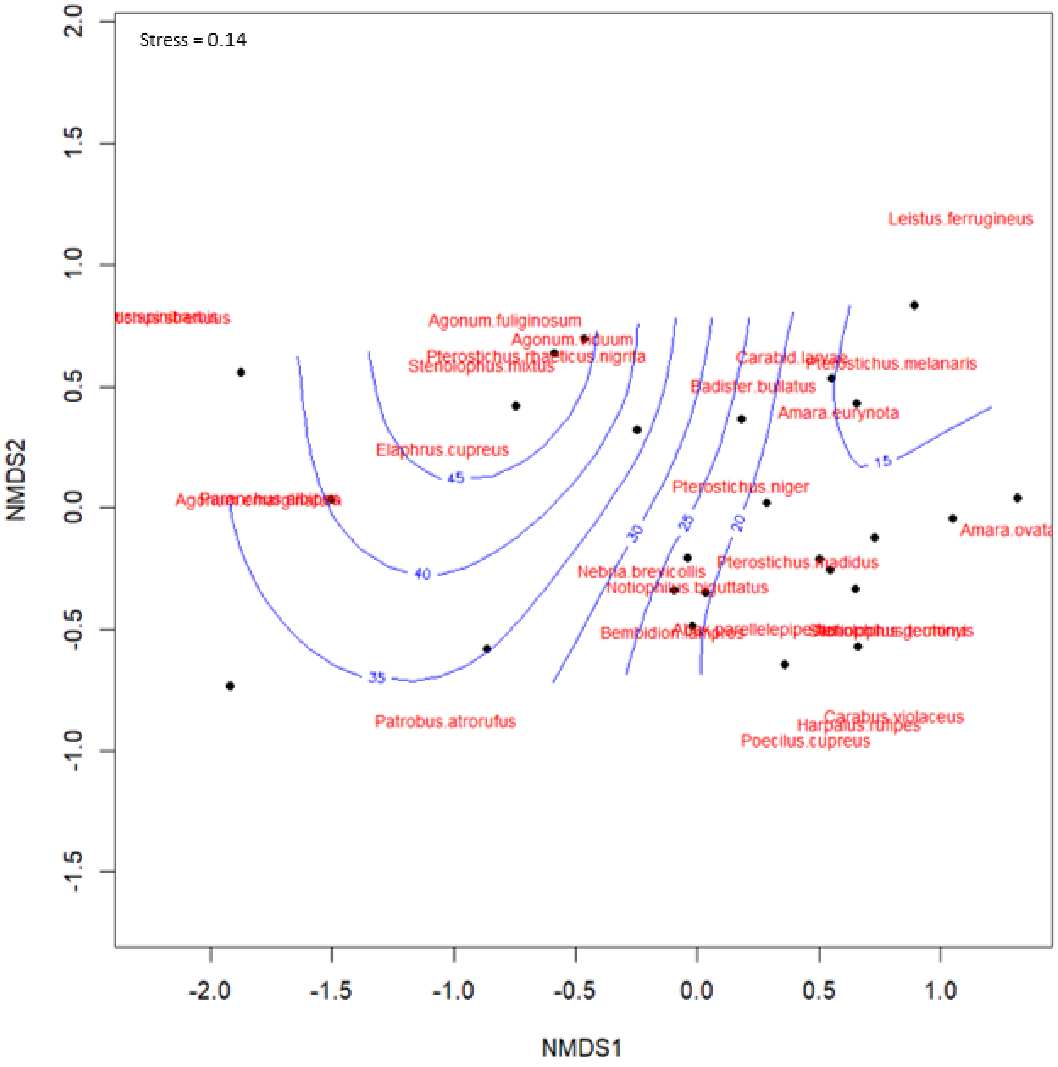

Figure 5.11. Non-metric multidimensional scaling (NMDS) ordination of carabid community composition to sediment moisture, with SedMoist represented by contours, the number of each contour denoting the value.

5.3.4.2 Metric responses

Abundance was the only metric to respond significantly to SedMoist and explained 45% of the variance in abundance, which decreased as SedMoist increased (Table 5.5). FamRich decreased with increasing SedMoist, which explained 15 % of variance of the metrics respectively, however these relationships were not significant (Table 5.5). Whilst FamRich did decrease (Figure 5.12a), SpiderRich had a u-shaped distribution and SedMoist accounted for 18 % of the variance (Figure 5.12d).

Table 5.5. The model used (Generalised Linear Mixed Model, Linear Mixed Models and Generalised Linear Model) to test the influence of sediment moisture on the taxonomic family richness, taxonomic richness and abundance, spider richness and abundance, and carabid richness and abundance of dry-phase invertebrate communities, with the associated R2 values (R2C and R2M for mixed models and R2 for generalised linear models) and results of each model. The significant results are in bold, except for the intercept which reflects a deviation of the intercept from zero.

Metric (model)	**R^2C**	**R^2M or R^2**	**Intercept**			**Sediment moisture**		
			Estimate	SE	P	Estimate	SE	P
Taxonomic family richness (GLMM)	0.45	0.15	2.69	0.10	<0.001	-0.13	0.07	0.072
Taxonomic taxa richness (GLMM)	0.71	0.05	2.92	0.15	<0.001	-0.11	0.09	0.204
Taxonomic abundance (GLMM)	0.66	0.45	5.14	0.25	<0.001	**-0.69**	**0.21**	**0.001**
Spider richness (GLMM)	0.73	0.18	1.16	0.37	0.002	-0.46	0.26	0.075
Spider abundance (LMM)	0.71	<0.001	2.83	1.06	0.038	0.04	0.70	0.952
Carabid richness (GLM)		<0.001	1.03	0.11	<0.001	0.02	0.12	0.860
Carabid abundance (GLM)		<0.001	3.17	0.36	<0.001	-0.02	0.36	0.951

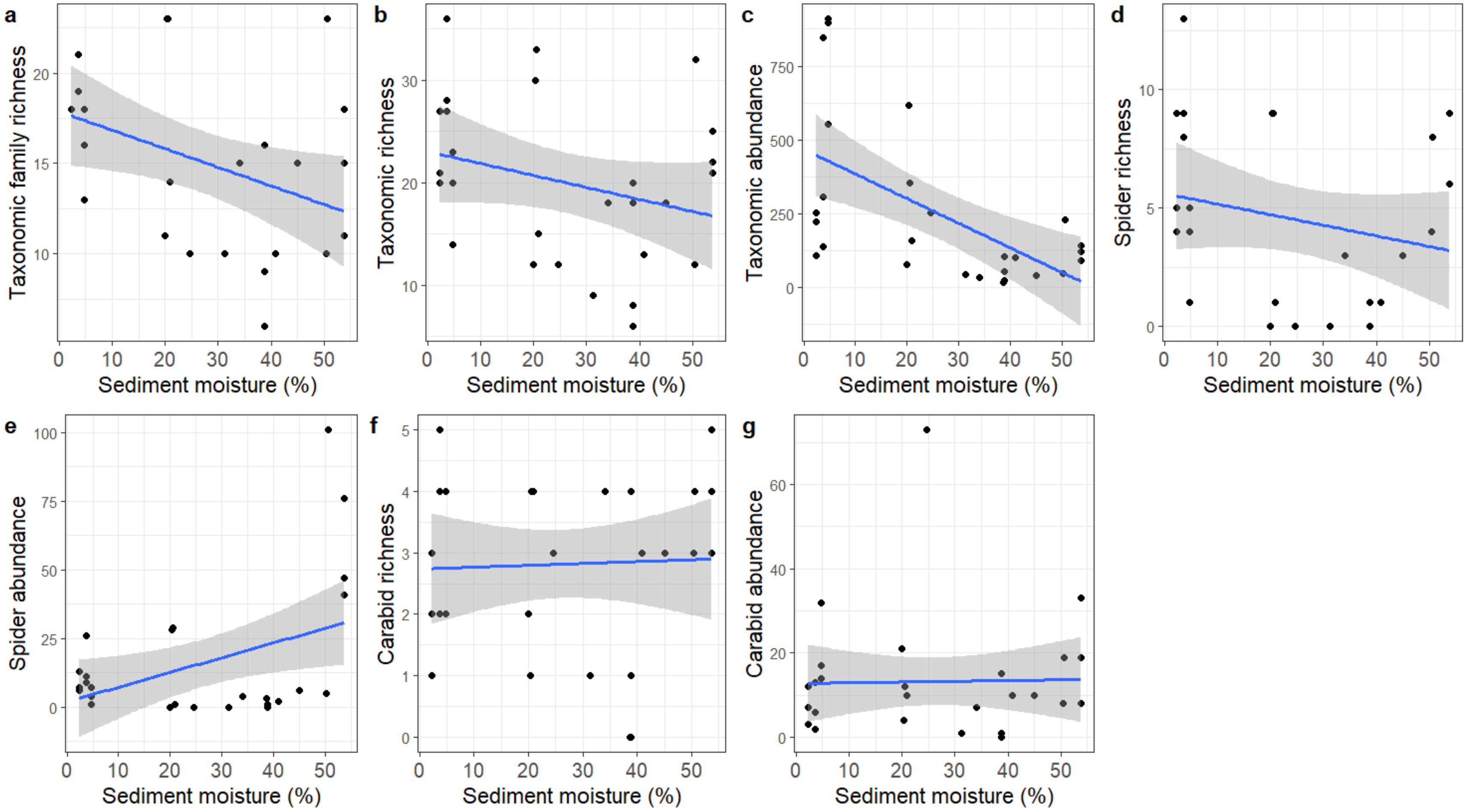

Figure 5.12. Invertebrate community metric responses to sediment moisture: a) Taxonomic family richness, b) taxonomic taxa richness, c) taxonomic abundance, d) spider richness, e) spider abundance, f) carabid richness and g) carabid abundance. The shaded area represents the 95 % confidence intervals.

SpiderAbund was higher at sites with high compared to low GravelProp (Table 5.6; Figure 5.13). CarabidRich was also higher at sites with high GravelProp but this was marginally non-significant (Table 5.6), likely due to the high variability in CarabidRich at sites with low GravelProp (Figure 5.13f). No other invertebrate metrics responded to GravelProp.

Table 5.6. The model used (Generalised Linear Mixed Model, Linear Mixed Models and Generalised Linear Model) to test the influence of Gravel proportion on the taxonomic family richness, taxonomic richness and abundance, spider richness and abundance, and carabid richness and abundance of dry-phase invertebrate communities, with the associated R^2 values (R2C and R2M for mixed models and R^2 for linear models) and results of each model. The significant results are in bold, except for the intercept which reflects a deviation of the intercept from zero.

Metric (model)	**R^2C**	**R^2M or R^2**	**Intercept (Low)**			**Gravel proportion (High)**		
			Estimate	SE	P	Estimate	SE	P
Taxonomic family richness (GLMM)	0.43	0.05	2.81	0.17	<0.001	0.22	0.19	0.237
Taxonomic taxa richness (GLMM)	0.69	0.07	2.62	0.13	<0.001	0.15	0.16	0.352
Taxonomic abundance (GLMM)	0.72	0.002	5.09	0.54	<0.001	-0.09	0.73	0.900
Spider richness (GLMM)	0.71	0.14	0.81	0.43	0.062	0.72	0.52	0.165
Spider abundance (LMM)	0.64	0.33	1.25	0.53	0.018	**1.59**	**0.72**	**0.028**
Carabid richness (GLM)		0.16	0.85	0.17	<0.001	0.38	0.23	0.098
Carabid abundance (GLM)		0.01	2.66	0.26	<0.001	-0.19	0.39	0.622

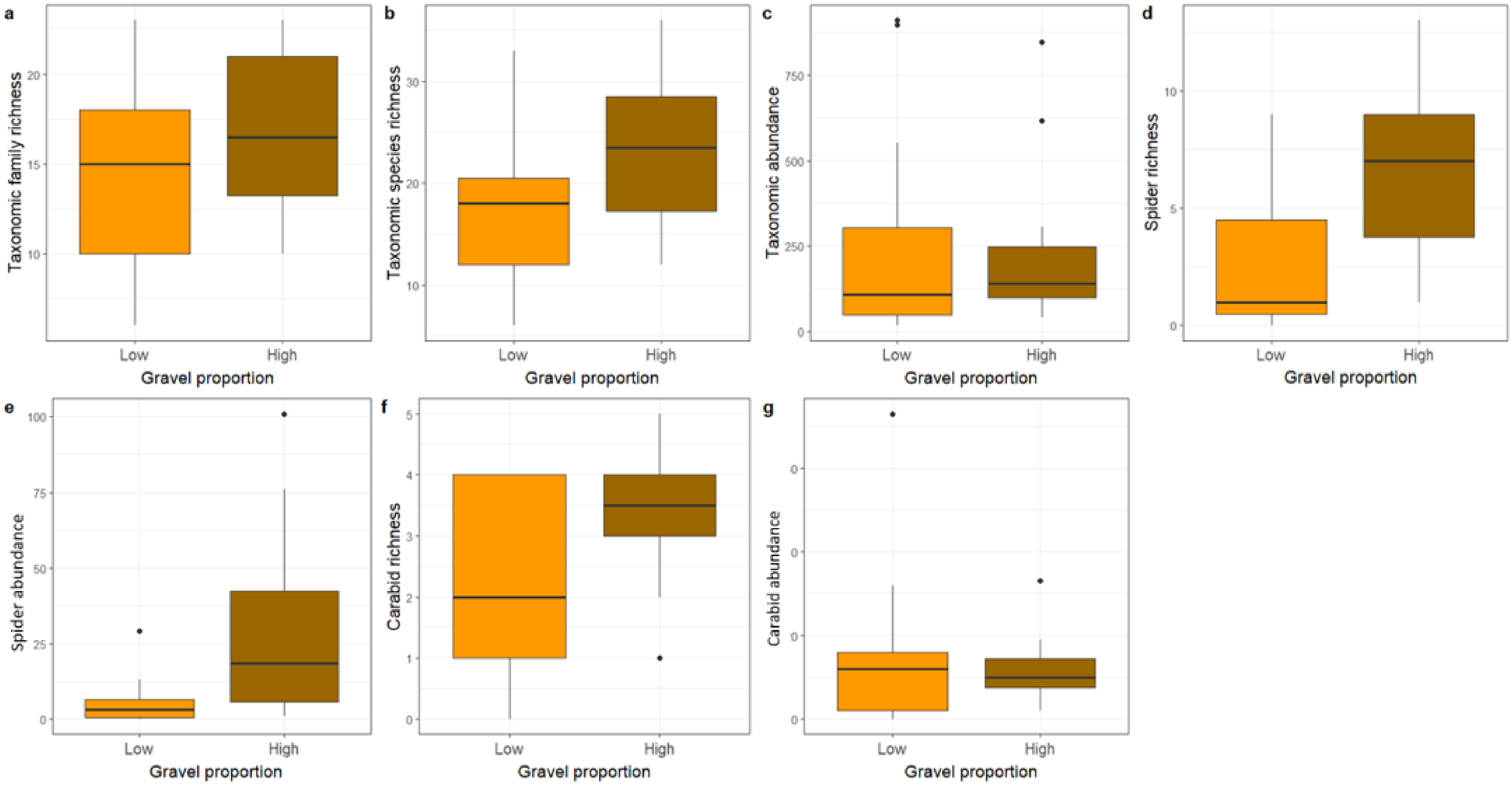

Figure 5.13. The median, interquartile range and 95% confidence intervals for a) taxonomic family richness, b) taxonomic taxa richness, c) taxonomic abundance, d) spider richness, e) spider abundance, f) carabid richness and g) carabid abundance at low and high Gravel proportion categories. Big dots represent outliers.

5.3.5 Responses to leaf litter

Due to the similar family-level and mixed-level responses of the invertebrate community composition to leaf litter cover (*LeafLitter*) only family-level responses are presented (mixed-level responses are available in Appendix 3.5). There were no significant metric responses to LeafLitter (Table A3.1). Communities differed between those at sites with absent, present and extensive LeafLitter (PERMANOVA, F = 2.83, df = 2, P = 0.001) which accounted for 13% of compositional variance.

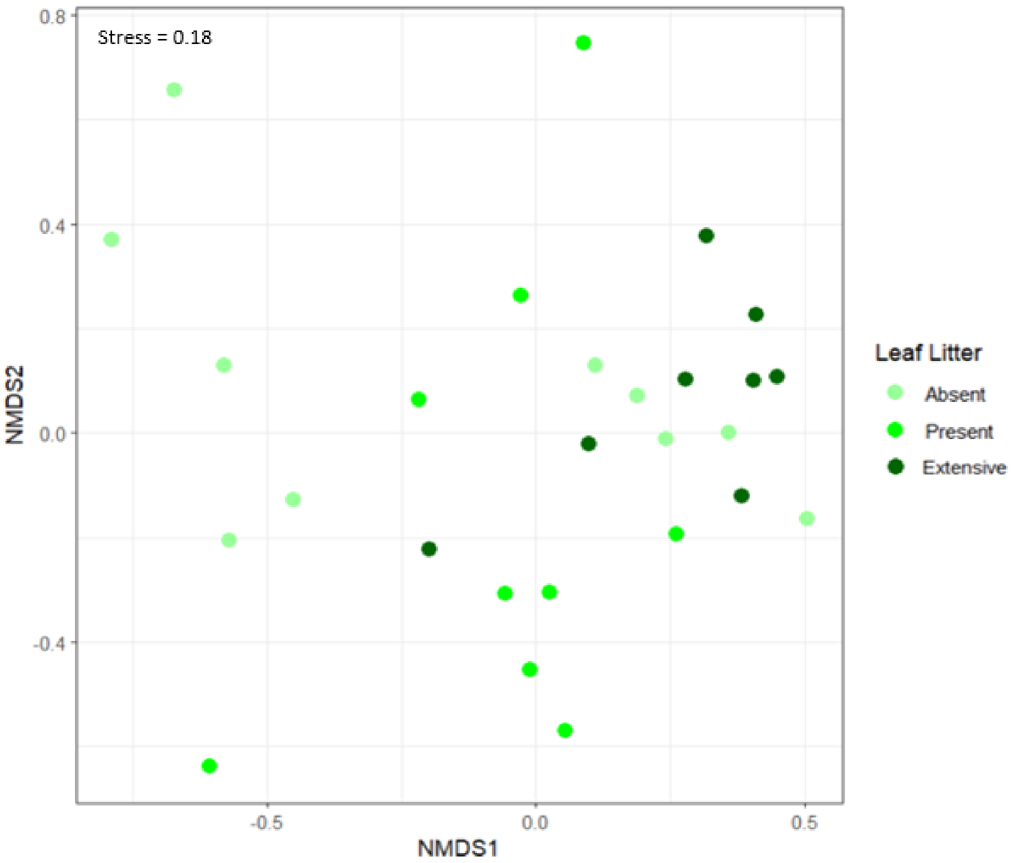

Figure 5.14. Non-metric multidimensional scaling (NMDS) ordination of invertebrate community composition according to the leaf litter cover (absent, present and extensive) categories.

Communities associated with absent LeafLitter spread across NMDS1 and had high NMDS2 scores (Figure 5.14) and included no indicator taxa (Table 5.7). Communities at sites with present LeafLitter typically had higher NMDS1 and NMDS2 scores and the family Porcellionidae was indicative of present LeafLitter (Table 5.7; Figure 5.14). Tetragnathidae and Chrysomelidae were indicative of extensive LeafLitter, but the specificity of Chrysomelidae was low (Table 5.7). Communities associated with extensive LeafLitter had low NMDS2 scores but covered a range of NMDS1 scores (Figure 5.14). Formacine was found almost entirely at sites with present or extensive LeafLitter (Table 5.7).

Table 5.7. Families indicative of sites with present, extensive and the combination of absent and present, and present and extensive leaf litter cover, displaying the IndVal statistic, specificity, fidelity and P value. Specificity and fidelity represent the probability (0–1) of the family occurring only at sites with a LeafLitter category and taxa occurs at all sites with a LeafLitter category, respectively

Leaf litter cover	Family	Stat	Specificity	Fidelity	P value
Present	Porcellionidae	0.78	0.69	0.88	0.035
Extensive	Tetragnathidae	0.67	1.00	0.44	0.020
	Chrysomelidae	0.60	0.30	0.44	0.035
Absent and present	Armadillidae	0.80	0.87	0.72	0.050
	Forficulidae	0.71	1.00	0.50	0.040
Present and extensive	Formacinae	0.80	0.98	0.65	0.005

LeafLitter explained the most variance (out of all the environmental variables) in carabid community composition, (PERMANOVA, $R^2 = 0.17$, F = 3.48, df = 2, P = 0.001). Spider community composition showed no response to vegetation (PERMANOVA, Leaf litter, F = 0.89, df = 2, P = 0.602). Carabid communities at sites with absent LeafLitter were dispersed along both axes, and had no indicative taxa (Figure 5.15). Communities associated with present LeafLitter mostly had high NMDS1 scores and low NMDS2 scores, and there were no indicative taxa. *Agonum viduum* was indicative of extensive LeafLitter (IndVal, stat = 0.63, specificity = 0.90, fidelity = 0.44, P = 0.02) and communities were split into two site-specific groups along the NMDS2 axis (Figure 5.15).

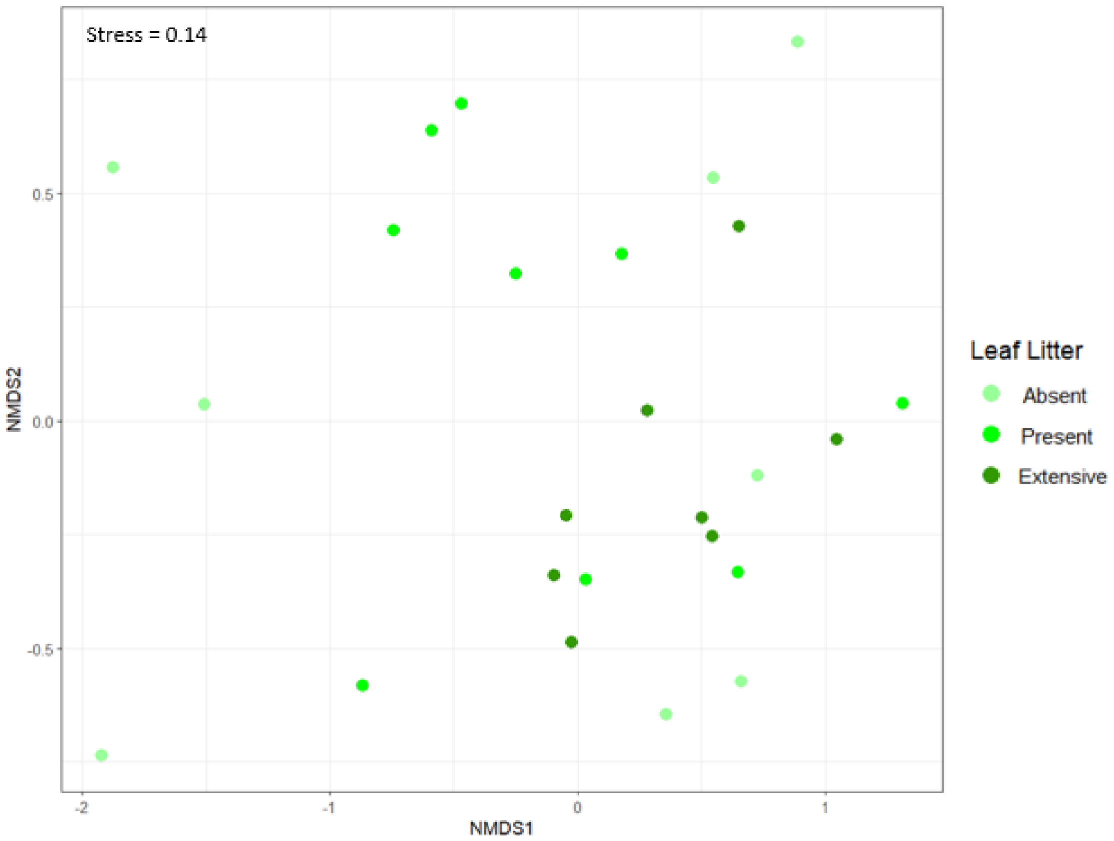

Figure 5.15. Non-metric multidimensional scaling (NMDS) ordination of carabid community composition according to the leaf litter cover (absent, present and extensive).

5.4 Discussion

Our knowledge of dry-phase communities is limited and currently we lack biomonitors to assess temporary stream ecological health. However, dry-phase invertebrates have demonstrated potential as biomonitors for ecological health (Steward et al., 2018; Sánchez-Montoya et al., 2020; Steward et al., 2022). In this research, I investigated the responses of dry-phase community composition (H1) and biological metrics (H2) reflective of communities to various environmental parameters indicative of human impact. Vegetation was the primary influence on both community composition and metrics, and sediment also affected communities. Family-level and mixed-level responses to all environmental parameters were similar. Both carabid community composition and metrics responded to vegetation morphology, leaf litter and sediment (moisture and diversity). Whereas only spider metrics responded to vegetation richness and sediment (moisture and diversity).

5.4.1 Vegetation

I hypothesised that vegetation morphology would affect invertebrate community composition due to the effect of vegetation structures on microclimates and habitat

(Bhriain, 2001; Cole et al., 2008), which ground-dwelling invertebrates respond to (Siemann et al., 1998; Boscaini et al., 2000; Perner & Malt, 2003). Vegetation morphology (*VegMorph*) accounted for 15% of the variation in invertebrate community composition. Invertebrate communities with lower beta diversity, composed mostly of generalist taxa, were recorded across sites with simple VegMorph than at sites with complex VegMorph which varied among sites. Differences in environmental resistance to invertebrate movement could limit the influence of VegMorph on the invertebrate activity densities (Thiele, 1977), however, field observations indicated that vegetation was never sufficiently dense to hinder invertebrate movement and thus capture in pitfall traps. At simple VegMorph sites, plant communities were largely comprising grass species, which provide limited cover in terms of shade and are less dense, making it easier to manoeuvre through. In contrast, complex VegMorph sites, at which plant communities comprised larger branching broad-leaf species such as stinging nettles (*Urtica dioica*), watercress (*Nasturtium officinale*) and broadleaf dock (*Rumex obtusifolius*). Simple VegMorph sites thus likely had higher levels of solar radiation and temperature and lower humidity (Cole et al., 2008). Therefore, invertebrate taxa that can tolerate harsher, more variable conditions, such as *Nebria brevicollis, Armadillidum vulgare, Porcello scaber* and *Pterostichus madidus* (see Appendix 3) were indicative of simple VegMorph sites, whereas taxa which prefer more stable conditions occurred at complex VegMorph sites (Lambeets et al., 2005). However, no taxa were indicative of complex VegMorph sites, likely due to the higher turnover of taxa between complex VegMorph sites.

The lower turnover of taxa between simple VegMorph communities explains the community compositional similarities seen. Communities at nearly all simple VegMorph sites were composed of the same generalist predators: *A. vulgare, N. brevicollis* and *Pt. madidus*, and in high activity densities. Complex VegMorph invertebrate communities had different taxa in lower abundance at each site and a higher spatial beta diversity, with no indicative taxa. Complex VegMorph sites also comprised a mixture of grasses and herbs, even if dominated by branching plant species, creating heterogeneity in microhabitat conditions, and thus likely to supports a more variable invertebrate community (Sadler et al., 2004; Datry et al., 2014b).

It was hypothesised (H2) that richness of all taxa, carabids and spiders would be higher at complex VegMorph sites due to the increased microclimate and habitat heterogeneity (Brose, 2003; Datry et al., 2014b). However, richness metrics were comparable at simple and complex VegMorph sites. This could be because the invertebrate taxa that colonise dry channels are likely mobile generalists adapted to tolerate the harsher conditions associated with simple VegMorph sites or because these sites have similar resources available to each other (Steward et al., 2017). Therefore, abiotic conditions did not restrict taxa richness at simple VegMorph sites. In addition, taxonomically different invertebrate communities with comparable richness can occur in complex, heterogeneous riparian habitats and relatively homogeneous adjacent terrestrial habitats (Sabo et al., 2005a).

Community composition differed and spider richness increased with increasing VegRich. VegRich may have influenced invertebrate communities through their preferences for plants as a food source. Although most species were predatory, herbivorous or omnivorous taxa from the order/families Hemiptera, Elateridae and Coccinellidae were associated with higher VegRich which provided a greater diversity of food resources. The increase in spider richness (all of which were predatory) could also be influenced by the availability of food, reflecting their prey abundances (Crist et al., 2006; Zieche & Roth, 2008).

5.4.2 Sediment

Sediment characteristics, although not as influential on dry-phase community composition as vegetation, influenced more invertebrate metrics (abundance, family richness and spider richness and abundance) than vegetation. Sediment moisture (*SedMoist*) influenced community composition, as hypothesised (Epstein & Kulman, 1990). Aquatic species such as the water scorpion (*Nepa cinerea*) and water measurer (*Hydrometra stagnorum*) were found at sites with high sediment moisture, likely promoted by denser vegetation, and in some cases in-channel ponding. Terrestrial taxa such as Armadillidae, Formicinae and Myrmicinae were found at drier sites due to their ability to tolerate harsher conditions. Many terrestrial groups were found at sites with moderate SedMoist such as Carabidae and Gastropoda, as they likely prefer sites which have some water availability, to support potential prey, for drinking and to aid in cooling (Wenninger & Fagan, 2000; Ramey & Richardson, 2017). Within the Carabidae, contrasting species-specific responses reflected habitat preferences, with species such as *Agonum viduum, Stenolophus mixtus* and *Elapharus cupreus* preferring wetter, river margin conditions (Grandchamp et al., 2005; Gerisch et al., 2006; Eyre et al., 1996) whilst *N. brevicollis, Pt. madidus* and *Harpalus rufipes* prefer drier conditions (Greenslade, 1964; Small et al., 2002).

Contrary to my hypothesis (H2), all responsive (significant and nearly significant) metrics (abundance, family richness and spider richness) decreased with increasing sediment moisture. These responses were largely driven by drier sites, which often had the high abundances of the generalist species, which potentially outcompeted other species through having greater tolerances for low sediment moisture (e.g. *N. brevicollis*), whereas wetter sites had lower abundances of species with higher sediment moisture tolerances (e.g. *E. cupreus*). Therefore, the low moisture at sites may not be as harsh for taxa in comparison to those found in dry channels in desert or Mediterranean climates (Steward et al., 2018; Sánchez-Montoya et al., 2020). Additionally, drier sites typically had not rewetted the previous year or had a more regular flowing and dry regime. Carabid richness and abundance did not respond to SedMoist, which could reflect turnover of taxa with contrasting moisture preferences along the SedMoist gradient.

The proportion of gravel (*GravelProp*; also indicative of the proportion of fine sediment inputs) in the sediment, which correlated with shading, influenced community composition, spider abundance and carabid richness. GravelProp was likely the greater influence on invertebrate responses in this research (Eyre & Luff, 2002; Lambeets et al., 2009), particularly because most taxa sampled were ground-dwelling (Thiele, 1977). Gravels in the sediment can provide habitable interstitial space for protection from predation or harsh surface conditions and create a higher heterogeneity in microhabitat conditions, increasing biodiversity (Lambeets et al., 2005; Steward et al., 2017). This could explain the observed higher spider abundance and carabid richness, with gravels providing shelter from predation, and as predators themselves, potential food sources. Whilst some species prefer the higher gravel proportions, other species prefer finer sediments to burrow into (Steward et al., 2017), which may explain the differences seen in composition between the communities at sites with low and high gravel proportions. However, the only species indicative of lower gravel proportions, and therefore higher fine sediments, was *Porcellio scaber*. This species is not known for burrowing, but is detritivorous (Riggio, 2013) and finer sediments can be linked to higher sediment organic matter (Burone et al., 2003), which may explain its preference.

5.4.3 Leaf litter

Carabid, family-level and mixed-level community composition responded to leaf litter, whilst metrics did not. Leaf litter can provide food for detritivores, prey for predators, and shelter (Uetz, 1991; Adis & Junk, 2002; Sabo et al., 2005b). The lack of metric response could be due to the turnover of taxa with different preferences. Contrary to H1, spider communities did not respond to leaf litter, whereas previous research highlights its importance for spiders to as structures for web building (Bultman & Uetz, 1984; Topping, 1993; Wagner et al., 2003). Leaf litter provides habitat for Collembola, an important food source for spiders (Lawrence & Wise, 2000), and Lycosidae, the most common spider family found in this research, use leaf litter for mating (Uetz, 1976). However, one spider family (Tetragnathidae) was indicative of extensive leaf litter, an orb weaver family which use the leaf litter as attachment points in web building (Topping, 1993; Wagner et al., 2003). The lack of response in spider communities could be due the greater influence of other variables such as vegetation richness, sediment moisture and gravel proportions on spider communities, overriding any influence of leaf litter.

5.4.4 Shade

Shading (reflective of riparian vegetation removal), like complex VegMorph, provides cooling effects and stabilises temperatures (Feld et al., 2018). Shading also can be associated with increased leaf litter from riparian vegetation, although these variables were not correlated in this study, which could be due to the proximity of the trees or channel orientation. Community composition responded significantly to shade (as indicated by the analysed variable GravelProp), which again could be influenced by the stability in temperature conditions provided by shading (Feld et al., 2018). The indicative taxa found in response to low and high GravelProp, and therefore high and low shading respectively, were more associated with the sediment as described above. However, *Pardosa amentata* was associated with low shading and prefers open habitats (Naturespot, 2021).

5.4.5 Biomonitoring implications

Invertebrates have been widely used in biomonitoring of riparian and other ecosystems (Perner & Malt, 2003; Lambeets et al., 2008; Seeney et al., 2016), with many studies focusing on carabids (Bhirain, 2001; Eyre & Luff, 2002; Cole et al., 2008) and spiders (Eyre & Luff, 2002; Lambeets et al., 2005; Zieche & Roth, 2008). This research has shown that these biotic groups are informative of ecosystem health and human impact in the dry phases of temporary streams. Family-level and mixed-level community composition responded similarly to vegetation, sediment and leaf litter, abundance was fairly responsive, and family richness was more responsive than taxa richness. These results indicated that family-level identification may enable terrestrial invertebrates to act as biomonitors in dry-phase ecological health assessments, facilitating easy implementation by regulatory bodies.

Most taxa found in this research are classified as generalist predators, making them typically common and abundant in the dry phase: a requirement for a good biomonitor (Borchard et al., 2014). Additionally, invertebrate and carabid but not spider community composition, and invertebrate and spider but not carabid-based metrics, responded to environmental variables, highlighting both community composition and biotic metrics should both be considered (McGeoch, 1998; Lambeets et al., 2005). Spiders were also more useful for indicating sediment complexity, carabids for sediment moisture and whole community metrics for vegetation morphology.

The responses to VegMorph are particularly useful as the different plant structures reflected the surrounding land use at sites. Sites with arable land use had simple VegMorph and those with complex VegMorph had either residential or more natural land use. Agricultural intensification has caused a decline in biodiversity, and fragments potentially suitable habitats (Bakker and Berendse, 1999; Borchard et al., 2014; Schirmel et al., 2016). Furthermore, complex VegMorph sites differed in composition and had a higher beta diversity, potentially reflective of the different sediment and shading conditions, creating a variety of microhabitat conditions (Cole et al., 2008; Ramey & Richardson, 2017). At simple VegMorph types, communities were similar despite having different sediment and shading conditions, indicating that VegMorph may be the overriding influence on invertebrate communities at these sites and that the microhabitat conditions created by grasses and other simple structured vegetation may only support generalist species. This highlights the potential to focus on invertebrates at sites with complex vegetation structure, where taxa may respond to other environmental variables indicative of human impact such as fine sediment. Metrics that reliably indicate impact levels despite high spatial variability among communities at complex VegMorph sites will require development.

Dry-phase invertebrates responded to different environmental variables, reflective of human impact, and thus have potential as biomonitors of ecological health – and specifically indicators of agricultural impact. This research has additionally highlighted the use of different invertebrate groups (whole communities, carabids and spiders) for monitoring different environmental conditions relating to vegetation and sediment, and in turn land use impacts. With sufficient dry-phase biomonitors, temporary stream health can be assessed accurately to inform effective management actions.

Chapter Six: General discussion

6.1 Introduction

Temporary streams account for > 50% of watercourses globally (Messager et al., 2021) and are subjected to multiple stressors resultant of anthropogenic pressures including climate change and agricultural and urban land use (Larned et al., 2010; Stubbington et al., 2017). It is important that all our watercourses, including temporary streams, are in good health and meet national statutory requirements under the EU Water Framework Directive 2000/60/EC (WFD), with similar requirements required by the US Clean Water Act and the Australian National Water Initiative. To accurately assess the health of temporary streams and target management actions, biomonitoring must shift away from perennial-focused means and incorporate temporary streams and the dry phase (Corti & Datry, 2016; Steward et al., 2018; Stubbington et al., 2018). The responses of macroinvertebrate communities to flow, sediment and vegetation complexity are well studied in perennial systems (William & Mundie, 1987; Extence et al., 1999; Schröder et al., 2013; Beermann et al., 2018), but this knowledge does not necessarily translate over to temporary streams. Whilst biomonitoring is beginning to include dry-phase communities (Robinson, 2019; Steward et al., 2018; Sánchez-Montoya et al., 2020), focus is still upon aquatic species responses to drying (Prat et al., 2014), or at a coarse taxonomic resolution for studies on dry-phase taxa (Holmes et al., 1999; Westwood et al., 2021). To address these research gaps, the overall aim of this thesis was to investigate temporary stream community responses to a range of stressors to inform both biomonitoring and restoration. The overall aim was split into three areas:

1) To investigate aquatic macroinvertebrate community responses to flow, sediment and vegetation, and identify any differences in community response between perennial and intermittent sites (Chapter 3).
2) To characterise dry-phase plant communities and investigate plant responses to human impacts and thus establish their potential as biomonitors to specific impacts and overall degradation (Chapter 4).
3) To characterise dry-phase invertebrate communities and investigate invertebrate responses to human impacts and thus establish their potential as biomonitors to specific impacts and overall degradation (Chapter 5).

6.2 Summary of research/fulfilment of thesis aims

6.2.1 Aim 1: to characterise the independent and interactive aquatic macroinvertebrate community responses to variability in flow, sediment and vegetation conditions

Through the analysis of a long-term 23-year Environment Agency dataset (Chapter 3), this study assesses the macroinvertebrate responses, both community composition and as summarised by metrics, to flow, sediment and vegetation, and the interacting effects of these influences. The results of Chapter 3, which supported my hypotheses, indicated that the highest energy flow type found at a site was the main influence on all communities (perennial, near perennial, partially intermittent and intermittent), and the number of vegetation morphotypes significantly influenced communities at perennial and intermittent sites (hereafter, perennial and intermittent communities; Rempel et al., 2000; Blöcher et al., 2020). Differences in flow energy and vegetation structure create a mosaic of differing microhabitat conditions, thus supporting more diverse macroinvertebrate communities (Stanley et al., 1997; Rosenfeld, 2017; Beerman et al., 2018). Macroinvertebrate responses to sediment complexity partially supported my hypothesis, but only had a small (but significant) influence on communities across all flow regimes. Nonetheless, this study showed that silt influenced intermittent communities, perhaps due to effects such as gill abrasion, accumulation in macroinvertebrate organs, and the loss of access to interstitial spaces (Armitage et al., 1999; Wood et al., 2005; McKenzie et al., 2020). As such, models with all three variables, with or without interactions, accounted for the highest variance in metric responses, indicating that whilst flow is the master variable, sediment and vegetation should also be considered to inform health assessments and effective restoration. Chapter 3 also highlighted that perennial and intermittent community metrics responded similarly to environmental variables, contrary to my hypothesis, perhaps reflecting the generalist intermittent communities or adaptations to intermittence itself, particularly since flow was the master variable for each community.

Building on the responses to the individual environmental variables, and previous work (Clarke, 2002; Gurnell & Grabowski, 2016), Chapter 3 highlighted that interactions between environmental variables influenced macroinvertebrate communities across all flow regimes. Thus, reflecting both natural interactions between variables (e.g. vegetation trapping sediments and slowing flows; Clarke, 2002; Gurnell, 2014), and long-term human impacts (e.g. low energy flows enabling the accumulation of fine sediment inputs from agricultural land; Acornley & Sear, 1999; Grabowski & Gurnell, 2016).

Finally, the results of Chapter 3 also identified temporal changes in community composition, with perennial sites community composition more influenced by drought in comparison to intermittent sites, likely due to a higher prevalence of drying-adapted taxa in intermittent communities. However, some post-drought community recovery occurred at perennial and near perennial sites, where flow, sediment and vegetation conditions were diverse. Therefore, restoring streams by increasing habitat complexity and promoting flowing water refuges could improve community resilience to drought (Chester & Robson, 2011).

Overall, Chapter 3's results provide valuable information for communities at sites with a range of flow regimes, particularly comparing those in perennial and intermittent reaches, and their responses to hydrogeomorphology. The results indicated that restoration focusing on improving both habitat complexity, primarily by increasing flow and vegetation complexity, would benefit communities from different flow regimes. Additionally, I found some evidence that greater site-specific vegetation, flow and sediment complexity enhanced the resilience of a perennial community after drought. However, this was based on one site, and a larger sample size is needed to determine if this response is typical.

6.2.2 Aim 2: to characterise dry-phase plant communities and their responses to variability in habitat conditions and investigate plant responses to human impacts thus establish their potential as biomonitors.

The aims of Chapter 4 were addressed as two objectives: firstly, by characterising the plant communities found in the dry phase, including terrestrial species, and their compositional responses to environmental variables, and secondly, by quantifying plant community metric responses to human impact, to identify potential biomonitors. Dry-phase plant communities have been largely uncharacterised, and studies often refer to terrestrial grasses and herbs as such (e.g. Holmes et al., 1999; Westwood et al., 2021). Therefore, characterising the aquatic and terrestrial species present in dry-phase communities and their responses to both natural and anthropogenic variables, demonstrates that these communities can be diverse and abundant in channel, and respond to environmental variables, thus warranting future research. Community variability among sites emphasised the diversity in dry-phase plant communities and their abundance in-channel highlighted their importance (as primary producers) in temporary stream ecosystems. The dry-phase communities incorporated a range of species from fully aquatic to fully terrestrial, with particular taxa often dominating sites including both aquatic species (*Apium nodiflorum, Mentha aquatica* and *Nasturtium officinale*) and terrestrial taxa (Poaceae and *Urtica* *dioica*) often dominating sites. Compositional changes were primarily driven by sediment moisture and sediment organic matter (SOM), and land use, which reflected multiple measured environmental variables. Changes reflected individual species preferences or tolerances and the central influence of sediment moisture and SOM on plant growth and soil health, including affecting nutrient availability, respectively (Veihmeyer & Hendrickson, 1927; Halvin et al., 2005; Milić et al., 2019).

No metrics representing the plant communities responded to the total human impact score. This is likely to be because all sites were at least moderately impacted and the range of impact scores was insufficient to detect a response (Feld et al., 2016). Nonetheless, I detected responses to nutrient concentrations in dry-phase communities. These results align with those reported in other ecosystems and perennial rivers, nutrients (particularly phosphorus and nitrogen) and thus eutrophication, are a major influence on plant communities, and the latter a major cause of biodiversity loss (Schindler, 2006; Conley et al., 2009). Chapter 4 gave evidence to support responses to nutrients in the dry phase. Phosphorus and nitrate-nitrogen influenced plant community metrics, with grass richness and Berger-Parker dominance increasing with increasing phosphorus, showing the strongest increases with increasing phosphorus and thus having the highest potential as biomonitors for eutrophication. Herb richness and Ellenberg N decreased and increased, respectively, with increasing nitrate-nitrogen and had the highest potential as a biomonitor for nitrate-nitrogen. High nutrient concentrations are commonly associated with an increase in the dominance of competitive species, particularly grasses, allowing them to increase in both richness and dominance (Grime, 1979; Critchley et al., 2002). Additionally, whilst the multimetric index (comprised of herb richness, Ellenberg N and Berger-Parker dominance) responded to phosphorus, it did not respond to nitrate-nitrogen and the individual metrics responded comparably to phosphorus. The lack of multimetric response to nitrate-nitrogen could also indicate that phosphorus is the limiting variable in plant communities. Despite, the different metrics that did respond, the metrics for phosphorus are more suitable given that they follow hypothesised responses, based on previous research. In particular I recommend Berger-Parker dominance as the most informative and reliable biomonitoring metric, followed closely by grass richness, because both metrics followed a linear response that followed the hypothesised response (unlike herb richness and Ellenberg N for nitrate-nitrogen which had a u-shaped response) and, particularly for dominance, have an easy sample protocol. Additionally, the increase in dominance with higher phosphorus concentrations reflects the typical responses of aquatic macrophytes to eutrophication (Hilton et al., 2016; Wurtsbaugh et al., 2019).

The results of Chapter 4 characterised dry-phase plant communities and has shown their potential as biomonitors for nutrient concentrations (further information on plant and invertebrate advantages and disadvantages as biomonitors is discussed in section 6.4). As such dry-phase plant communities can provide a complementary biomonitor to aquatic communities for eutrophication, using a slight adaptation of the LEAFPACS2 method currently used in the UK (WFD-UK TAG, 2014).

6.2.3 Aim 3: to characterise dry-phase invertebrate communities and their responses to variability in habitat conditions, and investigate plant responses to human impacts thus establish their potential as biomonitors

Dry-phase invertebrate communities are better characterised than dry-phase plant communities, and their potential as biomonitors of environmental variables, including those indicative of human impact, has been characterised in hotter, drier climates (e.g. semi-arid and hot Mediterranean climates; Steward et al., 2018; Robinson, 2019; Sánchez-Montoya et al., 2020). However, little research has characterised communities in cooler, wetter climates such as those in the UK, (see Corti & Datry, 2016; Bunting et al., 2021). Chapter 5 identified the dry-phase invertebrate community metric and compositional responses (including family-level, mixed-level, spider and carabid datasets) to vegetation, sediment (moisture and diversity and here, gravel proportions were used to represent diversity), leaf litter and shading: known influences on invertebrates (Eyre et al., 1996).

Vegetation, which differed in structure and richness according to site-specific land use, was the predominant variable influencing dry-phase invertebrates. Sites with simple vegetation morphotypes comprised grasses or bare ground; associated with agricultural land use, and complex vegetated sites had large branching species or multiple morphotypes and were associated with more natural land uses. Invertebrate communities at simple vegetation morphotype sites had lower beta diversity than those with complex vegetation, despite having comparable alpha diversity (i.e. taxonomic richness). Complex vegetation provides greater habitat heterogeneity and more diverse food sources, and also protection from solar radiation, higher temperatures and predation (Cole et al., 2008). Species indicative of simple sites included more generalist species which were able to tolerate the harsher conditions (i.e. higher solar radiation, temperatures and predation risk).

Although not as influential as vegetation, sediment moisture and gravel proportions influenced invertebrate communities. In particular, carabid composition responded to moisture and spider abundance increased in response to increasing gravels. The influence of moisture was hypothesised due to the importance of water as a source of hydration and prey, and also cooling (Wenninger & Fagan, 2000; Ramey & Richardson, 2017). However, the decrease in taxonomic richness in response to increasing moisture was not hypothesised, and reflected the high abundances of generalist species with higher tolerances of drying. The increase in gravels co-occurred with a decrease in shading, meaning that the responses seen could not be distinguished as caused by shading or gravels. Gravels in the sediments provide interstitial spaces for refuge from both predation and harsh conditions (i.e. higher temperatures and solar radiation), and can increase habitat heterogeneity (Lambeets et al., 2005; Steward et al., 2017). The refuge from inhospitable conditions could be particularly crucial when shading was low at sites with high gravel proportions, as shade typically stabilises temperatures.

The results from Chapter 5 demonstrate that invertebrates have potential as biomonitors in cooler, wetter climates, similarly to those in hotter, drier climates. Community composition and metrics were informative of vegetation and sediment conditions (moisture and gravel proportions), vegetation structure and gravel proportions in particular were indicative of general degradation. Although family-level composition and metrics were more informative of human impact, spiders and carabids were still provided insight into the influences of environmental variables. In this study, spider abundance and richness responded to sediment variables and carabids composition responded to leaf litter and sediment moisture.

6.3 Contributions to temporary river ecology

This thesis has built upon previous work researching macroinvertebrate responses to hydrogeomorphology (e.g. Rempel et al., 2000; Beermann et al., 2018), providing insights into how intermittent and perennial responses to flow, sediment and vegetation differ. The research has also moved beyond previous understanding of dry-phase community responses to flow cessation and drying (e.g. Holmes et al., 1999; Sanchez-Montoya et al., 2020; Westwood et al., 2021; Bunting et al., 2021), to investigate responses to environmental variables in spite of drying, including evaluating plants and invertebrates as potential biomonitors of human impact.

The results presented in Chapters 4 and 5 have characterised dry-phase communities, demonstrating the biodiversity of both plant and invertebrate communities and improving our knowledge of dry-phase ecology for two common, biodiverse and functionally important groups. The communities found were dominated by generalist taxa, supporting the concept proposed in Stubbington et al. (2017; Figure 6.1) that similarly to flowing phases, dry phases are dominated by generalists. Additionally, no temporary stream dry-phase specialists were recorded, supporting Stubbington et al. (2017), which noted that no specialists have been found in temperate climates. The lack of dry-phase specialists may reflect the long-term human impacts at sites, which may have caused uninhabitable conditions for specialist species which can be more sensitive to environmental conditions (Tscharntke et al., 2002; Rainio & Neimelä, 2003). However, this could also be due to unpredictable or long (in some cases multi-year) flowing phases that occur in temporary streams in cooler, wetter climates, which could be difficult to adapt to. The research presented in Chapter 4 is the first to characterise true aquatic-terrestrial communities, demonstrating that plant communities occur on a range from fully aquatic to fully terrestrial, with communities of varying proportions of each. Whilst the invertebrate communities were predominantly composed of terrestrial species in the results of Chapter 5, the alpha and beta diversity of the dry phase was highlighted.

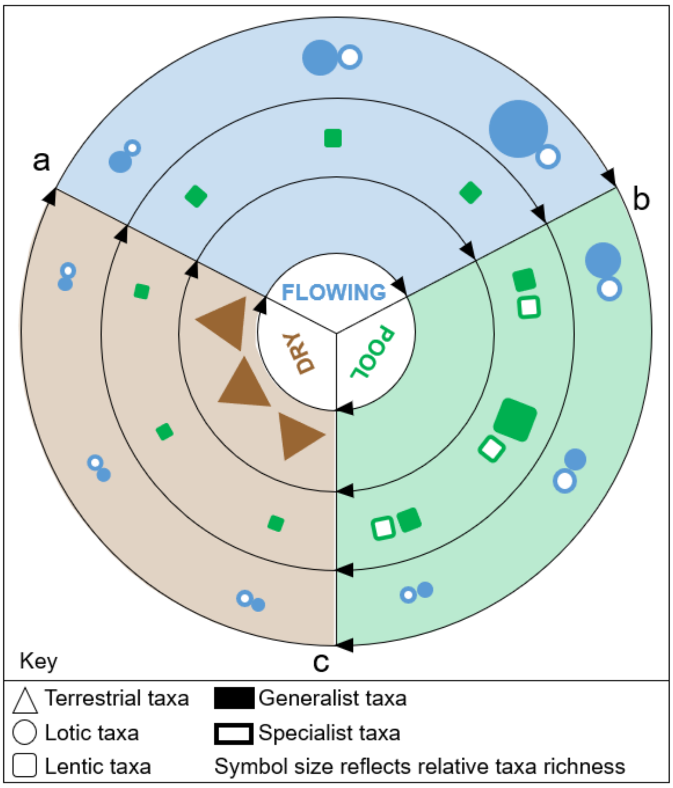

Figure 6.1. The lotic, lentic and terrestrial generalist and specialist taxa found in a temporary stream during the flowing, pooled and dry phases (adapted from Stubbington et al., 2017, CC BY-NC 4.0: https://creativecommons.org/licenses/by-nc/4.0/).

Additionally, although not the aim of Chapter 5, the data collected captured temporal changes from May-July (spring-summer) at two-week intervals and in September (autumn). Steward et al. (2022) proposed that terrestrial and semi-aquatic invertebrate taxa richness increased sharply following drying before decreasing slowly over the dry-phase duration (Figure 6.2a). The temporal changes in invertebrate communities reported in Chapter 5 were variable, although they did not include shoreline taxa. Invertebrate richness at the site with the shortest dry phase (ponded until early June; summer, and then dry June–mid September; autumn) remained fairly stable throughout the survey period (Figure 6.2b), contrary to Steward et al., 2022). Other communities at sites with shorter dry phases (i.e. April; spring–October; autumn) reached peak richness in May (spring), before declining slowly until July (summer), with the lowest richness found in September, potentially supporting Steward et al. (2022; Figure 6.2c). However, in the UK, May to June (summer) is considered the peak for carabid activity (Webb et al., 2017) and June to September (autumn) the peak for spider activity, thus, these peaks in richness may reflect drying and/or season. Additionally, invertebrate communities at sites that had been dry since the previous summer differed, reaching peak richness in June or July (summer), which could suggest a seasonal influence (Figure 6.2d). These insights gained in this study and highlighted in Steward et al. (2022), indicate that further study is needed to try and disentangle the influence of season and drying on how invertebrates colonise dry channels.

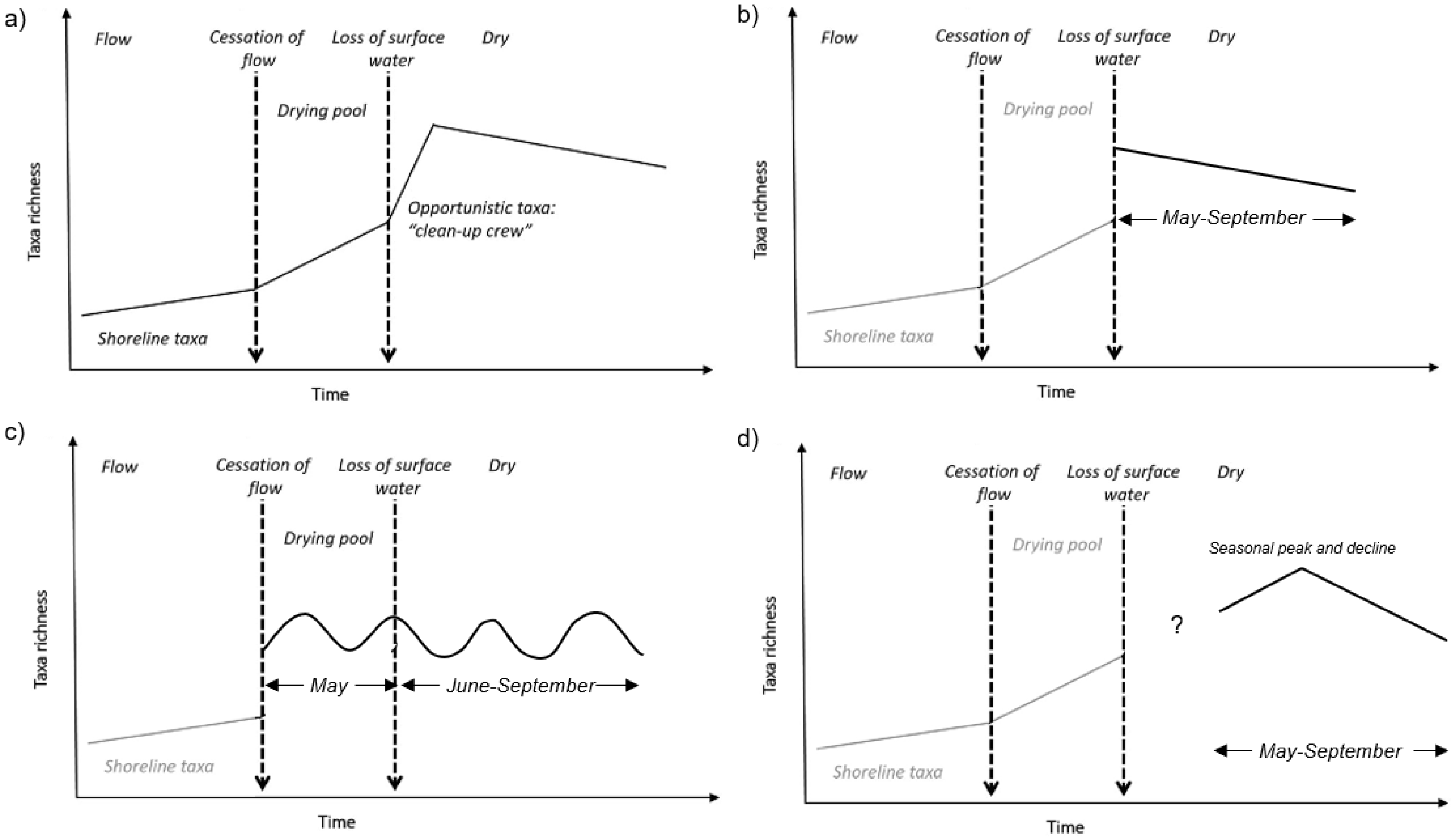

Figure 6.2. The responses of the terrestrial and semi-aquatic invertebrate richness over time from flowing to dry conditions (Steward et al., 2022). Greyed out areas and ? represent unknown taxa richness (not sampled). See text for more information regarding a) – d).

Aquatic macroinvertebrate community responses to environmental variables have been well-studied in perennial streams and temporary streams (Rempel et al., 2000; Dunbar et al., 2010; Blöcher et al., 2020). The research in Chapter 3 covered a range of flow regimes and expanding on characterising macroinvertebrate responses to intermittency (Sarremejane et al. (2019, 2020, 2021), to include macroinvertebrate responses to environmental variables, including comparisons between perennial and intermittent communities. I found a comparable response across these communities to a master variable (flow), whilst sediment and vegetation, and their interactions with flow, still had some influence. I have also characterised temporal changes across communities at perennial, near perennial, partially intermittent and intermittent, reflecting the differences in community resilience to drought. Results indicated that habitat complexity at a site could aid in community resilience, however, analyses were limited to one site, and therefore further study is needed to determine if this result is accurate across different sites and catchments.

6.4 Implications for biomonitoring

The results of this thesis have characterised the potential of aquatic-terrestrial plant and terrestrial invertebrate assemblages as dry-phase biomonitors that could compliment those used in the flowing phase, aiming to enable biomonitoring during any phase. Therefore, allowing managers to conduct ecological health assessments regardless of the in-channel conditions encountered at a site. The documented responses of the dry-phase plants and invertebrates to habitat conditions meet most the criteria for an ‘ideal’ biomonitoring tool (Bonada et al., 2006; the criteria and the response of plant and invertebrate communities are summarised in Table 6.1). The hypothesised responses of dry-phase plant community responses to nutrients were based on those of aquatic macrophyte species (Holmes et al., 1999) and the dry-phase invertebrate community responses to vegetation and sediment variables based on those in other ecosystems (Siemann et al., 1998; Eyre & Luff, 2002; Crist et al., 2005). Plant communities showed limited responses to overall human impact, whereas invertebrates did respond to vegetation structure which reflected land use and general degradation. Despite the influence of other environmental conditions, including those not necessarily indicative of human impact (e.g. sediment moisture), the responses of plants to nutrients and invertebrates to vegetation structure were still detectable.

Both plants and invertebrates are easily sampled/surveyed by cost-effective means, which is beneficial for biomonitoring as programmes typically have limited funding. Additionally, plants have the benefit of being sedentary, meaning communities are unlikely to be able to escape any impact (Doust et al., 1994). Additionally, plant communities are unlikely change between different months of the same survey season, thus only one annual survey is likely needed to assess ecological health. Although species-level identification for invertebrates typically requires experience, family-level and mixed-level (mostly to species or genus, but some higher taxonomic resolutions) responses were comparable in this research, suggesting that family-level would be a sufficient taxonomic resolution for biomonitoring purposes, reducing the experience and time needed for identification and thus the costs (Beketov et al., 2009). Additionally, many aquatic invertebrate biomonitoring tools use family-level identification (Hawkes, 1997; Marshall et al., 2006; Turley et al., 2016), so having comparable taxonomic resolutions across the flowing and dry phases would be beneficial. However, as for aquatic invertebrate communities (Chadd et al., 2017), species-level identification is required to identify species of conservation concern, and although not found in this research, could include nationally rare terrestrial species, and potentially, temporary stream specialists (Bunting et al., 2021). For plant communities, using dominance as a biomonitoring metric for monitoring phosphorus concentrations only requires the identification of the one dominating species, which is an advantage over the calculation of grass richness, which requires identification of multiple, often taxonomically challenging species (Holmes et al., 1999).

Table 6.1. A summary of each criterion suggested in Bonada et al. (2006) for an 'ideal' biomonitor and how dry-phase plants and invertebrates meet each criterion.

Criteria	Description	Plants	Invertebrates
I	Derived from sound theoretical concepts in ecology	Hypothesised responses based on previous research	
II	A priori predictive		
III	Potential to assess ecological functions	Important for multiple ecosystem processes	Important for processing organic matter, food source
IV	Potential to discriminate overall human impact	Limited response	Responded to general degradation, relating to land use
V	Potential to discriminate different types of human impact	Responded to nutrients	Limited response

VI	Low costs for sampling and sorting	On site surveying	Pitfall traps are cost-effective and simple
VII	Simple sampling protocol	Using dominance as a biomonitoring metric only requires identifying one species	and family-level identification is easier than species-level, reducing costs.
VIII	Low cost for taxa identifications	Taxa can mostly be identified in the field	Lab-based identification, but family-level would reduce costs
IX	Large-scale applicability	Only tested on one catchment	
X	Reliable indication of changes in overall human impact	Limited response	Responded to general degradation, relating to land use
XI	Reliable indications of changes in different types of human impact	Responded to nutrients	Limited response
XII	Human impact indication on a linear scale	Responses of dominance and grass richness linear to phosphorus concentrations	More complex multivariate responses

This research was conducted in one catchment for Chapters 4 and 5 and two neighbouring for Chapter 3, covered only groundwater-fed temporary chalk stream. Therefore, further research is needed to determine if the biomonitors identified in this research translate to other temporary streams in chalk catchments, and potentially other types of temporary stream. Comparable responses of plant biomonitors may be limited to temporary streams cooler, wetter climates, since plant cover can be limited in arid temporary streams (Davis et al., 1993). However, the potential use of these dry-phase plant and invertebrate biomonitors in other chalk streams is promising, given their similar hydrogeomorphological characteristics and biodiversity. Additionally, because chalk streams are of high conservation value (Mainstone, 1999), they are a priority for biomonitoring, protection and restoration (Rangley-Wilson, 2021).

Another benefit of dry-phase plants and invertebrates as biomonitors is their mostly linear responses to environmental variables. Two metrics representing plant communities (dominance and grass richness) responded linearly to phosphorus and are therefore more suitable for detecting eutrophication than the plant metric responses to nitrate-nitrogen, which were unimodal. Additionally, some invertebrate metrics, such as taxonomic and spider richness, did respond linearly to environmental variables such as vegetation richness and sediment moisture. Also, although the complex, multivariate invertebrate compositional responses, which were more informative of general degradation, are not typically linear, they could be summarised as a metric of NMDS1 axis scores (Stubbington et al., 2019).

The observed strengths and weaknesses of plants and invertebrates as biomonitors suggests that both biological groups could enable monitoring of different aspects of ecological health. Plant communities could enable dry-phase biomonitoring of the effects of nutrient concentrations whilst invertebrate communities can indicate the ecological effects of general degradation, through responses to vegetation structure and sediment composition. Additionally, invertebrates are often used in biomonitoring because of their average growth rates and turnover times, and their effective dispersal allowing recolonisation after a disturbance. In comparison, plants are slow dispersers and have longer turnover times (Perner & Malt, 2003; Hodkingson & Jackson, 2005). Therefore, dry-phase invertebrates respond more quickly to impacts, such as influxes of fine sediment, and could also be used to determine how restoration has influenced ecological health, whilst plant communities could be used for biomonitoring impacts, such as nutrient inputs, over longer time periods (Hodkingson & Jackson, 2005).

One recurrent finding throughout the thesis is that both community composition and metrics contributed to characterisation of responses to environmental variables, and different aspects of ecological health. For dry-phase plant communities, there was a clear distinction between whether composition or metrics were more informative. Plant metrics (dominance and grass richness) are recommended for detecting the influence of elevated nutrients, whereas compositional responses were masked by responses to environmental conditions potentially unrelated to human impacts (e.g. sediment moisture and SOM). However, for invertebrate communities the responses were more varied. Community composition and beta diversity were most informative, and therefore recommended, for monitoring vegetation structure (relating to general degradation), however, metrics such as taxonomic family richness and activity densities could still be suitable. Spider metrics are recommended for monitoring sediment composition (and potential fine sediment inputs).

6.5 Implications for restoration

Restoring habitat heterogeneity should increase biodiversity by providing a greater variety of microhabitat conditions than homogenous habitats (Levin, 1992; Pianka, 2000). The results presented in Chapters 3 and 5 support this theory and suggest that restoration which improves habitat heterogeneity, by increasing flow velocity, sediment and vegetation complexity, will improve biodiversity across a gradient of flow regimes from intermittent to perennial. Additionally, vegetation was a significant influence at temporary stream communities during the flowing phase (Chapter 3) and dry phase (Chapter 5), indicating that restoration that increases vegetation complexity or broadleaf cover has the potential to improve both flowing and dry phase invertebrate biodiversity, in particular beta diversity. However, restoring the diversity of aquatic macrophyte communities can be complex (Ecke et al., 2016) and further research is needed to devise methods to restore plant diversity. Additionally, the highest energy flows (i.e. free fall) and extensive emergent broadleaf vegetation created unfavourable conditions for some macroinvertebrate species (Baker et al., 2011; Gurnell, 2014; Wolters et al., 2017), suggesting there could be a ‘goldilocks’ zone, characterised by moderate flow and vegetation conditions.

6.6 Limitations of research and future studies

A notable limitation of this study – including results presented in Chapters 3 and, in particular, 4 and 5 – was that whilst study sites incorporated a range of human impacts and on differing scales of severity, all sites were relatively anthropogenically impacted by agricultural and urban influences. The study did not represent sites with low human impact nor did it represent other human influences such as sewage effluent. Therefore, future studies should characterise other chalk stream catchments to include sites least and most impacted by humans to test, and potentially adapt, the proposed biomonitors from this study across a larger gradient of human impact.

A second limitation is that not all dry-phase invertebrates were identified to species level (Chapter 5) due to the prioritisation of carabids and spiders: two biological groups with the highest potential indicators based on previous research (Rainio & Niemelä, 2003; Lambeets et al., 2008; Borchard et al., 2014). Further research could investigate Collembola morphotypes or species responses to environmental variability, with their diversity and potential to monitor for pesticides and general soil health identified in other work (Sahana, 2018).

A third limitation was that whilst the 23-year dataset analysed in Chapter 3 enabled the identification of temporal change, the survey/sampling period for Chapters 4 and 5 only spanned one season/several months in one year (2019). This was a particularly dry year, therefore, to improve the dataset and biomonitoring recommendations made, further research shoulder cover sufficient survey seasons to encompass a gradient from high flow years to drought years.

6.7 Concluding remarks

Temporary streams are subjected to numerous stressors due to anthropogenic pressures, and most UK perennial streams do not meet the WFD requirement of good ecological status, with few temporary streams assessed (Environmental Audit Committee, 2022). There is still a lack of biomonitoring methods required to assess ecological health during the dry-phase, and thus lack the data required to inform identification of temporary streams in need for restoration to improve ecological resilience (Stubbington et al., 2018). The results in Chapter 3 indicated that whilst temporary stream macroinvertebrate communities – like their perennial stream counterparts – benefit from higher habitat heterogeneity, mostly relating to flow complexity, they also benefitted from higher emergent broadleaf cover. I also characterised dry-phase plant (Chapter 4) and invertebrate (Chapter 5) communities and evaluated their potential as biomonitors of human impact. This research is the first to characterise dry-phase plant communities including terrestrial species as well as persisting aquatic species and identify their potential as biomonitors for nutrient concentrations, aligning with aquatic methods already in practice (WFD-UK TAG, 2014). Additionally, it supports the use of dry-phase invertebrates as biomonitors, providing novel information on the responses of communities to vegetation and sediment, indicative of land use. In the ongoing context of climate change and increasing land-use change, this research contributes towards our understanding of dry-phase communities and their responses to human impact. It also identifies potential dry-phase biomonitoring tools, enabling managers to conduct ecological health assessments regardless of in-channel flow conditions.

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Appendix 1 (Chapter Three)

Appendix 1.1 SIMPER results for community responses to flow, sediment and vegetation variables

Table A1.1. Taxa, and their mean ± SD abundances, contributing to >1% of dissimilarity between perennial and intermittent communities of most influential taxa.

	Order/Class	Contribution	SD	Perennial	Intermittent	P
Gammarus pulex/fossarum	Amphipoda	0.04	0.03	4.61	2.25	0.001
Baetis rhodani/atlanticus	Ephemeroptera	0.03	0.02	2.65	1.38	0.001
Elmis aenea	Coleoptera	0.02	0.02	2.67	0.65	0.001
Agapetus spp.	Trichoptera	0.02	0.02	2.1	0.56	0.001
Potamopyrgus antipodarum	Gastropoda	0.02	0.02	1.97	0.12	0.001
Caenis luctuosa/macrura	Ephemeroptera	0.02	0.02	1.6	0.38	0.001
Hydropsyche angustipennis	Trichoptera	0.02	0.02	1.63	0.55	0.001
Simulium spp.	Diptera	0.02	0.02	1.52	0.61	0.002
Ephemera danica	Ephemeroptera	0.01	0.02	1.27	0.23	0.001
Limnephilus lunatus	Trichoptera	0.01	0.01	1.03	0.4	0.001
Sericostoma personatum	Trichoptera	0.01	0.01	1.22	0	0.001
Athripsodes cinereus	Trichoptera	0.01	0.01	1.02	0.18	0.001
Mystacides azurea	Trichoptera	0.01	0.02	0.97	0.25	0.001
Limoniidae	Diptera	0.01	0.01	0.62	0.13	0.001
Sphaerium	Bivalvia	0.01	0.01	0.83	0	0.001

Silo nigricornis/pallipes	Trichoptera	0.01	0.01	0.67	0.01	0.001
Rhyacophila dorsalis/fasciata	Trichoptera	0.01	0.01	0.68	0.08	0.001
Ancylus fluviatilis	Gastropoda	0.01	0.01	0.68	0	0.001
Limnius volckmari	Coleoptera	0.01	0.01	0.63	0.03	0.001
Paraleptophlebia submarginata	Ephemeroptera	0.01	0.01	0.53	0.04	0.001
Bathyomphalus contortus	Gastropoda	0.01	0.01	0.54	0.1	0.001
Hydroptila spp.	Trichoptera	0.01	0.01	0.46	0.12	0.001
Serratella ignita	Ephemeroptera	0.01	0.01	0.47	0.09	0.001
Valvata piscinalis	Gastropoda	0.01	0.01	0.55	0	0.001
Dixa spp.	Diptera	0.01	0.01	0.37	0.14	0.003
Dicranota spp.	Diptera	0.01	0.01	0.75	0.39	0.005
Glossiphonia complanata	Hirundinea	0.01	0.01	0.99	0.57	0.013
Empididae	Diptera	0.01	0.01	0.46	0.22	0.023
Baetis vernus	Ephemeroptera	0.01	0.01	0.52	0.24	0.024

Table A1.2. Taxa, and their mean ± SD abundances, contributing to >1% of dissimilarity between perennial sites where the highest flow type was smooth and unbroken waves.

	Order/Class	**Contribution**	**SD**	**Smooth**	**UBW**	**p**
Gammarus pulex/fossarum	Amphipoda	0.03	0.03	3.11	5.39	0.043
Simulium spp.	Diptera	0.02	0.01	1.16	2.94	0.001
Ephemera danica	Ephemeroptera	0.02	0.01	2.07	2.63	0.049
Athripsodes cinereus	Trichoptera	0.02	0.01	2.1	0.34	0.002
Hydropsyche angustipennis	Trichoptera	0.02	0.01	1.71	2.23	0.033
Limnius volckmari	Coleoptera	0.01	0.01	1.47	0.35	0.01
Odontocerum albicorne	Trichoptera	0.01	0.01	0	1.21	0.001
Serratella ignita	Ephemeroptera	0.01	0.01	0.63	0.84	0.017
Physa heterostropha	Gastropoda	0.01	0.01	0.12	0.97	0.012
Goera pilosa	Trichoptera	0.01	0.01	0.98	0.29	0.006
Oulimnius tuberculatus	Coleoptera	0.01	0.01	0.81	0.15	0.003
Calopteryx splendens	Odonata	0.01	0.01	0.27	0.65	0.009
Polycentropus flavomaculatus	Trichoptera	0.01	0.01	0.11	0.6	0.002
Platambus maculatus	Coleoptera	0.01	0.01	0.52	0.38	0.002
Micronecta poweri/scholtzi	Hemiptera	0	0.01	0.35	0.03	0.013
Glyphotaelius pellucidus	Trichoptera	0	0.01	0.37	0	0.026
Orectochilus villosus	Coleoptera	0	0.01	0.24	0.35	0.001
Muscidae	Diptera	0	0	0.39	0.07	0.003

Lepidostoma hirtum	Trichoptera	0	0	0.22	0	0.01
Leuctra fusca	Plectoptera	0	0	0.11	0	0.037

Table A1.3. Taxa, and their mean ± SD abundances, contributing to >1% of dissimilarity between perennial sites where emergent broadleaf vegetation was absent and extensive.

	Order/Class	**Contribution**	**SD**	**Absent**	**Extensive**	**p**
Agapetus spp.	Trichoptera	0.03	0.01	0.09	3.17	0.006
Chironomidae	Diptera	0.02	0.02	3.50	3.00	0.035
Sericostoma personatum	Trichoptera	0.02	0.01	0.06	2.48	0.001
Simulium spp.	Diptera	0.02	0.02	2.10	2.46	0.02
Limnephilus lunatus	Trichoptera	0.01	0.01	0.84	1.91	0.008
Odontocerum albicorne	Trichoptera	0.01	0.01	0.00	1.51	0.001
Silo nigricornis/pallipes	Trichoptera	0.01	0.01	0.06	1.37	0.001
Paraleptophlebia submarginata	Ephemeroptera	0.01	0.01	0.00	1.38	0.02
Physa heterostropha	Gastropoda	0.01	0.01	0.37	1.07	0.004
Hydroptila spp.	Trichoptera	0.01	0.01	1.24	0.00	0.022
Calopteryx splendens	Odonata	0.01	0.01	0.31	0.63	0.013
Acroloxus lacustris	Gastropoda	0.01	0.01	0.81	0.24	0.003
Polycentropus flavomaculatus	Trichoptera	0.01	0.01	0.61	0.46	0.001
Micronecta poweri/scholtzi	Hemiptera	0.01	0.01	0.55	0.00	0.031

Table A1.4. Taxa, and their average abundances, contributing to >1% of dissimilarity between perennial sites with 1 and 3 sediment types.

	Order/Class	**Contribution**	**SD**	**1**	**3**	**p**
Gammarus pulex/fossarum	Amphipoda	0.05	0.03	5.44	0.00	0.003
Chironomidae	Diptera	0.03	0.02	3.90	0.77	0.002
Oligochaeta		0.03	0.02	3.58	0.00	0.012
Pisidium spp.	Bivalvia	0.03	0.02	1.71	3.71	0.008
Baetis rhodani/atlanticus	Ephemeroptera	0.02	0.02	2.96	0.56	0.028
Ephemera danica	Ephemeroptera	0.02	0.02	1.39	2.39	0.024
Polycelis spp.	Tricladida	0.02	0.01	0.26	2.56	0.003
Anisus vortex	Gastropoda	0.02	0.01	0.87	2.44	0.016
Ceratopogonidae	Diptera	0.02	0.01	0.90	2.31	0.014
Limnius volckmari	Coleoptera	0.02	0.01	0.18	2.29	0.005
Sericostoma personatum	Trichoptera	0.02	0.01	0.62	2.32	0.013
Limnephilus lunatus	Trichoptera	0.02	0.01	1.13	2.30	0.021
Valvata piscinalis	Gastropoda	0.01	0.01	0.73	1.61	0.038
Micronecta poweri/scholtzi	Hemiptera	0.01	0.02	0.02	0.98	0.002
Silo nigricornis/pallipes	Trichoptera	0.01	0.01	0.56	1.62	0.009
Bathyomphalus contortus	Gastropoda	0.01	0.01	0.25	1.46	0.049
Glyphotaelius pellucidus	Trichoptera	0.01	0.01	0.00	0.70	0.004
Hydropsyche siltalai	Trichoptera	0.01	0.01	0.00	1.19	0.006
Psychodidae	Diptera	0.01	0.01	0.20	1.06	0.004

Drusus annulatus	Trichoptera	0.01	0.01	0.00	0.95	0.005
Acroloxus lacustris	Gastrapoda	0.01	0.01	0.41	0.85	0.023
Physa fontinalis	Gastropoda	0.01	0.01	0.06	1.04	0.039
Piscicola geometra	Hirudinea	0.01	0.01	0.08	0.96	0.001
Scirtidae	Coleoptera	0.01	0.01	0.12	0.87	0.002
Stagnicola palustris/fuscus/corvus	Gastrapoda	0.01	0.01	0.02	0.94	0.005
Polycentropus irroratus	Trichoptera	0.01	0.01	0.09	0.45	0.01

Table A1.5. Taxa, and their average abundances, contributing to >1% of dissimilarity between intermittent sites where the highest flow type was smooth and unbroken waves.

	Order/Class	Contribution	SD	NPF	Rippled	p
Chironomidae	Diptera	0.05	0.05	4.52	2.30	0.001
Oligochaeta		0.05	0.04	4.36	2.24	0.001
Gammarus pulex/fossarum	Amphipoda	0.05	0.04	2.91	1.58	0.012
Asellus aquaticus	Isopoda	0.04	0.03	3.09	0.64	0.001
Radix balthica	Gastropoda	0.03	0.02	1.44	0.98	0.038
Helobdella stagnalis	Hirudinea	0.02	0.02	1.29	0.43	0.001
Hydropsyche angustipennis	Trichoptera	0.02	0.02	0.08	1.13	0.002
Simulium spp.	Diptera	0.02	0.02	0.19	1.10	0.018
Erpobdella octoculata	Hirudinea	0.02	0.02	1.07	0.00	0.001
Glossiphonia complanata	Hirudinea	0.01	0.02	0.96	0.03	0.02
Polycelis spp.	Tricladida	0.01	0.02	0.86	0.19	0.02
Caenis luctuosa/macrura	Ephemeroptera	0.01	0.02	0.01	0.88	0.001
Crangonyx pseudogracilis /floridanus	Amphipoda	0.01	0.02	0.09	0.67	0.003

Table A1.6. Taxa, and their average abundances, contributing to >1% of dissimilarity between intermittent sites where emergent broadleaf vegetation was absent and extensive.

	Order/Class	Contribution	SD	Absent	Extensive	p
Gammarus pulex/fossarum	Amphipoda	0.05	0.03	4.42	0.76	0.001
Pisidium spp.	Bivalvia	0.05	0.03	1.75	4.48	0.012
Anisus vortex	Gastropoda	0.03	0.02	2.09	0.00	0.001
Helobdella stagnalis	Hirudinea	0.02	0.02	0.70	1.92	0.009
Glossiphonia complanata	Hirudinea	0.02	0.02	1.62	0.07	0.001
Erpobdella octoculata	Hirudinea	0.02	0.02	1.48	0.46	0.001
Stagnicola palustris/fuscus/corvus	Gastropoda	0.02	0.02	0.26	1.33	0.021
Agapetus spp.	Trichoptera	0.02	0.02	1.29	0.00	0.005
Hydracarina		0.02	0.02	1.17	0.00	0.003
Polycelis spp.	Tricladida	0.02	0.02	0.93	0.67	0.018
Dugesia lugubris/polychroa	Tricladida	0.01	0.01	0.07	0.61	0.026
Muscidae	Diptera	0.01	0.01	0.60	0.00	0.003
Haliplus spp.	Coleoptera	0.01	0.01	0.45	0.11	0.013
Tetanocera spp.	Diptera	0.01	0.01	0.02	0.51	0.017

Table A1.7. Taxa, and their average abundances, contributing to >1% of dissimilarity between intermittent sites with 3 and 5 sediment types.

	Order/Class	**Contribution**	**SD**	**3**	**5**	**p**
Gammarus pulex/fossarum	Amphipoda	0.09	0.04	0.00	4.90	0.001
Oligochaeta		0.08	0.03	0.00	4.56	0.001
Chironomidae	Diptera	0.08	0.04	0.67	4.55	0.001
Asellus aquaticus	Ispoda	0.04	0.02	0.00	2.42	0.003
Anisus vortex	Gastropoda	0.04	0.02	0.43	2.32	0.001
Glossiphonia complanata	Hirudinea	0.03	0.02	0.07	1.79	0.001
Erpobdella octoculata	Hirudinea	0.03	0.02	0.00	1.64	0.001
Baetis rhodani/atlanticus	Ephemeroptera	0.03	0.02	0.29	1.50	0.596
Agapetus spp.	Trichoptera	0.02	0.03	0.00	1.43	0.001
Hydracarina		0.02	0.02	0.00	1.30	0.001
Elmis aenea	Coleoptera	0.02	0.02	1.06	0.77	0.007
Polycelis spp.	Tricladida	0.02	0.02	0.21	1.03	0.007
Limnephilus lunatus	Trichoptera	0.02	0.02	0.84	0.50	0.016
Stratiomyidae	Diptera	0.02	0.02	0.63	0.49	0.036
Dicranota spp.	Diptera	0.02	0.02	0.33	0.82	0.004
Muscidae	Diptera	0.01	0.02	0.07	0.63	0.001
Musculium lacustre	Bivalvia	0.01	0.02	0.55	0.00	0.009
Haliplus spp.	Coleoptera	0.01	0.01	0.00	0.50	0.008

Galba truncatula	Gastropoda	0.01	0.02	0.40	0.00	0.022
Dixa spp.	Diptera	0.01	0.01	0.41	0.05	0.012

Appendix 1.2 GLMM and LMM model results

Table A1.8. The estimates, standard errors, and P values for all top models for all biological metrics in all regimes with significant results in bold. Models were numbered if there was more than one top model. The flow types are defined as NP (no perceptible flow), SM (smooth), RP (rippled), UBW (unbroken waves), BW (broken waves) and FF (free fall), and emergent broad leaf vegetation cover categories as EBA (absent), EBMin (minimal), EBMod (moderate) and EBE (extensive).

Biological metric		**Intercept**	**Flow**					**Sediment**		**In-channel vegetation**				**Flow × sediment**	**Flow × sediment**	**Flow × vegetation**	**Sediment × vegetation**
			Highest flow type					**Silt bed cover**	**Number of sediment types**	**Number of morphotypes**	**Emergent broadleaf**						
			SM	**RP**	**UBW**	**BW**	**FF**				**Minimal**	**Moderate**	**Extensive**				
Richness		**NP**							Not in model		Not in model			**SM × silt**	**UW × silt**	NS	NS
	Estimate	**3.032**	0.135	0.13	-0.192	0.494	**0.531**	-0.003		0.162				**0.36**	**-0.861**		
	SE	**0.122**	0.151	0.142	0.205	0.276	**0.261**	0.09		0.139				**0.154**	**0.321**		
	P	**<0.001**	0..371	0.359	0.35	0.074	**0.043**	0.965		0.243				**0.019**	**<0.001**		
Diversity 1	**Estimate**	**1.831**	Not in model						0.035	Not in model							
	SE	**0.065**							0.053								
	P	**<0.001**							0.513								
Diversity 2	**Estimate**	**0.1831**	Not in model							0.082	Not in model						
	SE	**0.0638**								0.054							
	P	**<0.001**								0.136							
WHPT ASPT		**NP**						Not in model									
	Estimate	**4.223**	0.391	0.507	**0.926**	0.984	0.853										
	SE	**0.249**	0.281	0.278	**0.288**	0.501	0.503										
	P	**<0.001**	0.169	0.074	**0.002**	0.055	0.096										
WHPT ASPT 2	**Estimate**	**4.756**	Not in model					-0.169	Not in model								
	SE	**0.112**						0.083									
	P	**<0.001**						0.047									
DEHLI 1	**Estimate**	**4.598**	Not in model					-0.098	Not in model								
	SE	**0.079**						0.058									
	P	**<0.001**						0.092									
DEHLI 2		**NP**						Not in model									
	Estimate	**4.275**	0.243	0.276	**0.553**	**0.841**	0.516										
	SE	**0.172**	0.193	0.191	**0.199**	**0.342**	0.345										
	P	**<0.001**	0.214	0.154	**0.007**	**0.017**	0.141										

EPSI family		NP + EBA						Not in model		Not in model				**RP*sediment type**	NS	NS	NS
	Estimate	18.366	36.106	23.319	45.658	53.021	-23.56		12.526		63.555	54.54	44.287	**-19.032**			
	SE	38.94	39.181	35.13	38.218	35.273	32.47		19.153		66.178	60.059	40.342	**6.81**			
	P	0.64	0.363	0.511	0.241	0.142	0.473		0.518		0.344	0.37	0.28	**0.008**			
EPT richness 1	**Estimate**	**1.851**	Not in model					**-0.203**	Not in model								
	SE	**0.083**						**0.08**									
	P	**<0.001**						**0.011**									
EPT richness 2	**Estimate**	**1.857**	Not in model					**-0.197**	Not in model	0.079	Not in model			NS	NS	NS	-0.064
	SE	**0.082**						**0.079**		0.0768							0.068
	P	**<0.001**						**0.013**		0.306							0.348
Functional richness	**Estimate**	**0.147**	Not in model						-0.005	Not in model							
	SE	**0.005**							0.004								
	P	**<0.001**							0.182								
Functional diversity	**Estimate**	**0.707**	Not in model						-0.002	Not in model							
	SE	**0.004**							0.003								
	P	**<0.001**							0.586								
Functional redundancy	**Estimate**	**0.162**	Not in model					-0.001	Not in model								
	SE	**0.005**						0.005									
	P	**<0.001**						0.822									

Table A1.9. The estimates, standard errors, and P values for all top models for all biological metrics that were significant in perennial regimes, with significant results in bold. Models were numbered if there was more than one top model. The flow types are defined as SM (smooth), RP (rippled), UBW (unbroken waves), and emergent broad leaf vegetation cover categories as EBA (absent), EBMin (minimal), EBMod (moderate) and EBE (extensive).

Biological metric		Intercept	Flow		Sediment		In-channel vegetation				Flow × sediment	Flow × vegetation	Flow × vegetation	Sediment × vegetation	Sediment × vegetation
			Highest flow type		Silt bed cover	Number of sediment types	Number of morphotypes	Emergent broadleaf							
			RP	UBW				Minimal	Moderate	Extensive					
Richness		**EBA**	Not in model		Not in model		Not in model				Not in model			**Sed × EBMi**	**Sed × EBE**
	Estimate	**3.346**				**0.437**		-0.004	-0.152	-0.068				**-0.386**	**-0.722**
	SE	**0.113**				**0.152**		0.131	0.119	0.162				**0.163**	**0.198**
	P	**< 0.001**				**0.004**		0.974	0.202	0.676				**0.018**	**< 0.001**
Diversity		**SM**				Not in model		Not in model			NS	NS	NS	**Silt × Morphotypes**	
	Estimate	**2.228**	-0.519	8.954	0.363		0.283							**0.584**	
	SE	**0.241**	0.29	7.094	0.212		0.443							**0.258**	
	P	**< 0.001**	0.127	0.23	0.151		0.539							**0.047**	
DEHLI		**SM + EBA**			Not in model						Not in mode	**RP × EBMin**	**BW × EBMi**	Not in model	
	Estimate	**4.218**	**0.649**	**1.023**				**0.889**	**0.669**	-0.067		**-1.125**	**-1.359**		
	SE	**0.193**	**0.319**	**0.219**				**0.303**	**0.212**	0.183		**0.424**	**0.398**		
	P	**< 0.001**	**0.046**	**< 0.001**				**0.006**	**0.002**	0.718		**0.011**	**0.006**		
EPSI		**SM**			Not in model			Not in model			NS	**UBW × Morphotypes**		**Sediment × Morphotypes**	
	Estimate	**43.796**	**16.457**	7.811		-1.775	2.933					**-22.112**		**-37.029**	
	SE	**7.457**	**7.661**	10.398		3.93	10.488					**8.434**		**8.663**	
	P	**< 0.001**	**0.045**	0.458		0.657	0.781					**0.016**		**< 0.001**	
Functional Richness	**Estimate**	**0.147**	Not in model				**-0.014**	Not in model							
	SE	**0.008**					**0.004**								
	P	**0.034**					**0.002**								
Functional redundancy 1	**Estimate**	**0.161**	Not in model			**0.025**	Not in model								
	SE	**0.008**				**0.008**									
	P	**< 0.001**				**0.013**									
Functional redundancy 2		**EBA**	Not in model								Not in model				
	Estimate	**0.098**						**0.092**	**0.08**	**0.055**					
	SE	**0.017**						**0.024**	**0.019**	**0.022**					
	P	**< 0.001**						**< 0.001**	**< 0.001**	**0.016**					

Table A1.10. The estimates, standard errors, and P values for all top models for all biological metrics that were significant in intermittent regimes, with significant results in bold. Models were numbered if there was more than one top model. The flow types are defined as NP (no perceptible flow), RP (rippled), and emergent broad leaf vegetation cover categories as EBA (absent), EBMin (minimal), EBMod (moderate) and EBE (extensive).

Biological metric		Intercept	Flow	Sediment		In-channel vegetation			Flow × sediment	Flow × vegetation	Flow × vegetation	Sediment × vegetation	Sediment × vegetation
			Highest flow type	Silt bed cover	Number of sediment types	Number of morpho types	Emergent broadleaf						
			RP				Moderate	Extensive					
Richness 1	**NP**			Not in model			Not in model		**RP × Sed**	NS	NS	NS	NS
	Estimate	**3.325**	**0.689**		**0.542**	**0.999**			**-1.859**				
	SE	**0.132**	**0.259**		**0.092**	**0.201**			**0.481**				
	P	**< 0.001**	**0.008**		**< 0.001**	**< 0.001**			**< 0.001**				
Richness 2	**EBA**		Not in model			Not in model			Not in model			**Sed × EBMo**	
	Estimate	**3.088**			-0.104		**-1.232**	**-0.816**				**1.03**	
	SE	**0.181**			0.097		**0.233**	**0.396**				**0.179**	
	P	**< 0.001**			0.286		**< 0.001**	**0.039**				**< 0.001**	
WHPT ASPT	**NPF + EBA**			Not in model					Not in model	NS	NS	Not in model	
	Estimate	**3.498**	**0.997**				0.067	**-0.795**					
	SE	**0.132**	**0.317**				0.34	**0.132**					
	P	**< 0.001**	**0.002**				0.829	**< 0.001**					
WHPT ASPT 2	**NP**				Not in model				NS	Not in model			
	Estimate	**3.62**	**0.746**	**-0.332**									
	SE	**0.143**	**0.153**	**0.055**									
	P	**< 0.001**	**< 0.001**	**< 0.001**									
DEHLI 1	**Estimate**	**3.942**	Not in model	**-0.351**	Not in model								
	SE	**0.115**		**0.058**									
	P	**< 0.001**		**0.029**									

DEHLI 2	**NP + EBA**											
	Estimate	**3.979**	0.047	Not in model			0.075	**-1.049**	Not in model	NS	NS	Not in model
	SE	**0.124**	0.32				0.313	**0.135**				
	P	**< 0.001**	0.883				0.812	**< 0.001**				
EPSI	**Estimate**	**47.052**	Not in model	**-11.774**	Not in model							
	SE	**2.708**		**1.839**								
	P	**0.005**		**0.042**								
EPT Richness 1	**NP**									**RP × Morphotypes**		
	Estimate	-0.117	**1.541**	Not in model		**-0.781**	Not in model			**1.457**		Not in model
	SE	0.451	**0.455**			**0.307**				**0.333**		
	P	0.793	**< 0.001**			**0.011**				**< 0.001**		
EPT Richness 2	**Estimate**	**1.285**	Not in model	**-0.412**	Not in model	**0.297**	Not in model			**-0.657**		Not in model
	SE	**0.12**		**0.145**		**0.091**				**0.171**		
	P	**< 0.001**		**0.004**		**< 0.001**				**<0.001**		

Table A1.11. The interaction terms between flow, sediment and vegetation at all flow regimes, perennial, and intermittent communities.

All	**Flow**	**Sediment**	**Vegetation**	**Flow × Sediment**	**Flow × Vegetation**	**Sediment × Vegetation**
Taxonomic Richness	Additive	NS	Additive	Positive opposing (SM) and negative synergistic (UBW)	NS	NS
WHPT ASPT	Singular	Not in model				
DEHLI	Singular	Not in model				
EPSI	NS	NS	Not in model	Negative antagonistic	NS	NS
EPT Richness 1	Singular	Not in model				
EPT Richness 2	Singular	Not in model				
Perennial	**Flow**	**Sediment**	**Vegetation**	**Flow × Sediment**	**Flow × Vegetation**	**Sediment × Vegetation**
Taxonomic Richness	Not in model	Singular	NS	Not in model		Negative opposing
Diversity	NS	NS	NS	NS	NS	Positive synergistic
DEHLI	Singular	Not in model	Singular	Not in model	Negative antagonistic	Not in model

EPSI	Singular	Not in model			Negative antagonistic	Negative opposing
Functional richness	Not in model		Singular	Not in model		
Functional redundancy 1	Not in model	Singular	Not in model			
Functional redundancy 2	Not in model		Singular	Not in model		

Intermittent	**Flow**	**Sediment**	**Vegetation**	**Flow × Sediment**	**Flow × Vegetation**	**Sediment × Vegetation**
Taxonomic Richness 1	Singular	Singular	Additive	Negative antagonistic	NS	NS
Taxonomic Richness 2	Not in model	NS	Singular	Not in model		Positive antagonistic
WHPT ASPT 1	Additive	NS	Additive	NS	NS	NS
WHPT ASPT 2	Additive	Additive	Not in model	NS	Not in model	
DEHLI 1	Not in model	Singular	Not in model			
DEHLI 2	NS	Not in model	Singular	Not in model	NS	Not in model

EPSI	Not in model	Singular	Not in model			
EPT Richness 1	Singular	Not in model	Singular	Not in model	Positive opposing	Not in model
EPT Richness 2	Not in model	Singular	Singular	Not in model		Negative opposing

Appendix 1.3 SIMPER results for community responses to drought

Table A1.12. Taxa, and their average abundances, contributing to >1% of dissimilarity at the perennial site on the Gade between pre and drought, drought and post, and pre and post-drought communities.

Pre vs drought	**Order/Class**	**Average**	**SD**	**Pre**	**Drought**	**P**
Physella acuta	Gastropoda	0.03	0.01	0.00	3.28	0.004
Sphaerium	Bivalvia	0.02	0.01	2.43	0.00	0.007
Valvata piscinalis	Gastropoda	0.02	0.01	2.46	0.00	0.023
Hydracarina		0.02	0.01	2.37	0.00	0.01
Limnephilus lunatus	Trichoptera	0.02	0.01	2.39	0.88	0.048
Ancylus fluviatilis	Gastropoda	0.01	0.01	1.73	0.23	0.021
Hydropsyche angustipennis	Trichoptera	0.01	0.01	1.70	0.23	0.036
Empididae	Diptera	0.01	0.01	0.10	1.43	0.051
Drought vs Post				**Drought**	**Post**	
Potamopyrgus antipodarum	Gastropoda	0.04	0.02	4.96	2.01	0.002
Baetis rhodani/atlanticus	Ephemeroptera	0.03	0.02	1.39	4.48	0.001
Physella acuta	Gastropoda	0.03	0.01	3.28	0.41	0.001
Limoniidae	Diptera	0.03	0.02	0.00	2.81	0.005
Gammarus pulex/fossarum	Amphipoda	0.03	0.01	4.46	6.78	0.001
Agapetus spp.	Trichoptera	0.03	0.02	0.00	2.35	0.054
Asellus aquaticus		0.02	0.01	1.95	0.09	0.009
Mystacides azurea	Trichoptera	0.02	0.01	1.57	0.00	0.023
Oligochaeta		0.02	0.01	3.85	4.43	0.03
Acroloxus lacustris	Gastropoda	0.01	0.01	0.54	0.66	0.024
Pacifastacus leniusculus	Decapoda	0.01	0.01	0.83	0.31	0.026
Sialis lutaria	Megaloptera	0.01	0.00	0.60	0.09	0.034
Pre vs Post				**Pre**	**Post**	
Caenis luctuosa/macrura	Ephemeroptera	0.04	0.01	4.68	0.48	0.001

Sphaerium	Bivalvia	0.02	0.01	2.43	0.00	0.001
Valvata piscinalis	Gastropoda	0.02	0.01	2.46	0.00	0.001
Anisus vortex	Gastropoda	0.02	0.01	2.05	0.00	0.001
Asellus aquaticus	Isopoda	0.02	0.01	2.07	0.09	0.005
Radix balthica	Gastropoda	0.01	0.01	1.79	0.00	0.003
Ancylus fluviatilis	Gastropoda	0.01	0.01	1.73	0.17	0.002
Bathyomphalus contortus	Gastropoda	0.01	0.01	1.36	0.00	0.004
Glossiphonia complanata	Hirudinea	0.01	0.01	1.29	0.00	0.002
Bithynia tentaculata	Gastropoda	0.01	0.01	1.21	0.00	0.002
Erpobdella octoculata	Hirudinea	0.01	0.01	1.18	0.00	0.002

Table A1.13. Taxa, and their average abundances, contributing to >1% of dissimilarity at the near perennial site on the Mimram between pre and drought, drought and post, and pre and post-drought communities.

Pre vs Drought	**Order/Class**	**Average**	**SD**	**Pre**	**Post**	**p**
Tipulidae	Diptera	0.03	0.00	5.63	1.32	0.002
Agapetus spp.	Trichoptera	0.02	0.01	2.93	2.54	0.048
Planorbis carinatus/planorbis	Gastropoda	0.02	0.01	5.82	3.13	0.033
Ephydridae	Diptera	0.02	0.01	4.78	2.09	0.024
Isoperla grammatica	Plectoptera	0.01	0.00	3.62	1.10	0.014
Haliplus spp.	Coleoptera	0.01	0.00	3.65	2.08	0.037
Theromyzon tessulatum	Hirudinea	0.01	0.01	1.52	0.00	0.003
Culicidae	Diptera	0.01	0.01	1.39	0.00	0.052
Psychodidae	Diptera	0.01	0.00	1.32	0.00	0.007
Hydracarina		0.01	0.01	4.90	4.10	0.028
Elmis aenea	Coleoptera	0.01	0.00	1.15	0.00	0.001
Baetis rhodani/atlanticus	Ephemeroptera	0.01	0.00	0.00	1.10	0.047
Stagnicola palustris/fuscus/corvus	Gastropoda	0.01	0.01	0.90	0.00	0.003
Drought vs Post				Drought	Post	
Agapetus spp.	Trichoptera	0.01	0.01	1.32	3.84	0.022

Elmis aenea	Coleoptera	0.01	0.00	2.09	4.54	0.006
Paraleptophlebia submarginata	Ephemeroptera	0.01	0.01	0.00	2.30	0.016
Ancylus fluviatilis	Gastropoda	0.01	0.01	2.17	2.91	0.016
Hydroptila spp.	Trichoptera	0.01	0.01	0.55	2.67	0.012
Ephemera danica	Ephemeroptera	0.01	0.01	1.04	3.07	0.027
Hydracarina		0.01	0.01	1.10	3.06	0.007
Polycelis spp.	Tricladida	0.01	0.01	0.00	1.84	0.002
Rhyacophila dorsalis/fasciata	Trichoptera	0.01	0.00	0.00	1.77	0.003
Hydropsyche angustipennis	Trichoptera	0.01	0.00	2.08	3.53	0.004
Erpobdella octoculata	Hirudinea	0.01	0.00	1.39	0.25	0.008
Helobdella stagnalis	Hirudinea	0.01	0.00	1.10	0.29	0.051
Pre vs Post				Pre	Post	
Ephemera danica	Ephemeroptera	0.01	0.01	0.55	3.07	0.014
Tipulidae	Diptera	0.01	0.00	1.15	0.07	0.017
Gyraulus albus	Gastropoda	0.01	0.00	2.59	0.28	0.025
Limnius volckmari	Coleoptera	0.01	0.00	2.63	4.53	0.033
Glossiphonia complanata	Hirudinea	0.01	0.00	1.59	0.43	0.038
Baetis rhodani/atlanticus	Ephemeroptera	0.01	0.00	4.90	4.55	0.044

Table A1.14. Taxa, and their average abundances, contributing to >1% of dissimilarity at the partially intermittent site on the Beane between pre and drought, drought and post, and pre and post-drought communities.

Pre vs drought	**Order/Class**	**Average**	**SD**	**Pre**	**Drought**	**P**
Gammarus pulex/fossarum	Isopoda	0.02	0.01	2.84	5.11	0.013
Erpobdella octoculata	Hirudinea	0.02	0.01	2.69	0.83	0.025
Crangonyx pseudogracilis/floridanus	Amphipoda	0.01	0.02	0	1.54	0.096
Gyraulus albus	Gastropoda	0.01	0	0	1.13	0.003
Dugesia lugubris/polychroa	Tricladida	0.01	0.01	0.4	1.01	0.082
Trocheta pseudodina	Annelida	0.01	0.01	0	0.83	0.075
Anisus vortex	Gastropoda	0.01	0.01	0.9	0	0.02

Caenis luctuosa/macrura	Ephemeroptera	0.01	0.01	0.17	0.96	0.024
Dendrocoelum lacteum	Tricladida	0.01	0.01	0	0.96	0.021
Drought vs post				**Drought**	**Post**	
Agapetus spp.	Trichoptera	0.02	0.01	0.73	2.58	0.002
Hydropsyche angustipennis	Trichoptera	0.02	0.01	1.54	1.04	0.018
Psychodidae	Diptera	0.01	0.01	1.34	0.38	0.029
Gyraulus albus	Gastropoda	0.01	0	1.13	0.08	0.032
Caenis luctuosa/macrura	Ephemeroptera	0.01	0.01	0.96	0.15	0.043
Pre vs post				**Pre**	**Post**	
Baetis rhodani/atlanticus	Ephemeroptera	0.03	0.02	1.56	3.71	0.001
Agapetus spp.	Trichoptera	0.03	0.01	0	2.58	0.001
Sphaerium	Bivalvia	0.03	0.03	2.61	0.48	0.001
Gammarus pulex/fossarum	Amphipoda	0.03	0.01	2.84	5.28	0.001
Erpobdella octoculata	Hirudinea	0.02	0.01	2.69	0.69	0.011
Pisidium spp.	Bivalvia	0.02	0.02	3.99	2.34	0.016
Asellus aquaticus	Isopoda	0.02	0.02	2.92	1.19	0.016
Radix balthica	Gastropoda	0.02	0.01	1.49	0	0.017
Glossiphonia complanata	Hirudinea	0.01	0.01	1.49	0.35	0.019
Anisus vortex	Gastropoda	0.01	0.01	0.9	0.08	0.023
Polycelis spp.	Tricladida	0.01	0.01	0.72	0.08	0.026
Goera pilosa	Trichoptera	0.01	0	0	0.71	0.027
Culicidae	Diptera	0.01	0.01	0.45	0	0.034
Tipulidae	Diptera	0.01	0.01	0.45	0	0.036

Table A1.15. Taxa, and their average abundances, contributing to >1% of dissimilarity at the near intermittent site on the Beane between pre and drought, drought and post, and pre and post-drought communities.

Pre vs Drought	**Order/Class**	**Average**	**SD**	**Pre**	**Drought**	**P**
Anisus vortex	Gastropoda	0.06	0.01	5.81	1.65	0.047
Hesperocorixa sahlbergi	Hemiptera	0.04	0.00	2.77	0.00	0.025
Anacaena lutescens	Coleoptera	0.02	0.00	1.61	0.00	0.025
Aeshna cyanea	Odonata	0.02	0.00	1.39	0.00	0.025
Gyrinus spp.	Coleoptera	0.02	0.00	1.39	0.00	0.025
Agabus spp.	Coleoptera	0.01	0.00	1.10	0.00	0.016
Cloeon dipterum	Ephemeroptera	0.01	0.00	1.10	0.00	0.025
Colymbetes fuscus	Coleoptera	0.01	0.00	1.10	0.00	0.025
Notonecta	Hemiptera	0.01	0.00	1.10	0.00	0.025
Corixa iberica punctata	Coleoptera	0.01	0.00	0.69	0.00	0.025
Lymnaea stagnalis	Gastropoda	0.01	0.00	0.69	0.00	0.025
Planorbis carinatus planorbis	Gastropoda	0.01	0.00	0.69	0.00	0.025
Sigara spp.	Hemiptera	0.01	0.00	0.69	0.00	0.025
Drought vs Post				**Drought**	**Post**	
Stagnicola palustris/fuscus/corvus	Gastropoda	0.02	0.02	1.45	0.00	0.024
Pre vs Post				**Pre**	**Post**	
Ilybius fuliginosus		0.01	0.00	1.10	0.00	0.016
Gammarus pulex/fossarum	Amphipoda	0.06	0.02	0.00	4.90	0.018
Haliplus spp.	Coleoptera	0.02	0.01	2.08	0.23	0.018
Anisus vortex	Gastropoda	0.06	0.02	5.81	1.56	0.046

Appendix 2 (Chapter Four)

Appendix 2.1 Descriptive summary of study sites.

Table A.2.1. Descriptive summary of the plant study sites. For channel shape, wide and narrow channels are >3 m and <3 m, respectively; a gentle slope and steep slope are <40^{o} and > 55^{o} respectively, any slope between those gradients is moderate. Shading, nutrient levels and fine sediment (<63 μm) categories are described below in Tables A..2 and A.4.3.

River	Site	Channel shape	Land use	Sediment composition	Fine sediment	Shade	Trampling	Nutrients	Road proximity
Ver	Chequers Pub	Steep slope, wide	Wooded	Soil	Moderate	Heavy	No	Low P and N	Medium
	Luton Lane	Steep slope, narrow	Agriculture (arable)	Some cobbles, mostly soil	Low	None	No	Medium P, very low N	Close
	Friars Wash	Steep slope, narrow	Urban	Soil	Low	None	No	Medium P, low N	Very close
	Long Meadows	Gentle slope, narrow	Urban	Soil	Low	Moderate	No	Low P, medium N	Close
Gade	Four Ways Farm	Moderate slope, moderate width	Agriculture (arable)	Some gravels, some soil	High	None	No	High P, medium N	Far
	Gade Cottages	Gentle slope, wide	Fen	Gravels, cobbles	Low	Moderate	Yes	Low P, high N	Very far
	D/S Garden Centre	Gentle slope, shallow, wide	Fen	Gravels, cobbles, some silt	Very low	Low	Yes	Low P, medium N	Far

Bulbourne	Northchurch	Gentle slope, narrow	Recreation	Soil, some gravels	High	Heavy	No	Low P, low N	Ver far
	Mandelyns	Steep slope, wide	Urban	Soil, some gravels	Low	Heavy	No	High P, very high N	Close
	Stags Lane	Steep slope, narrow	Urban	Soil	Very low	Low	No	Low P, very low N	Medium
Misbourne	Missenden Abbey	Steep slope, wide	Agriculture (pasture)	Soil, some gravels	Low	Low	Yes	High P, low N	Very far
	Chalfont Church	Gentle slope, narrow	Wooded	Soil	High	Heavy	No	Medium P, very low N	Very far
	Chalfont Playground	Reinforced slope, wide	Recreation	Soil	Low	Moderate	No	Medium P, high P	Medium
	Community Centre	Steep slope, narrow, deep	Recreation	Soil, some gravels	Very high	Moderate	No	Very low P, very low N	Very close

Appendix 2.2 Category assignments for environmental variables

Table A.2.2. The Department for Environmental and Rural Affairs (DEFRA) soil index for phosphorus and the mg/kg range for each category, with the phosphorus concentration category used for analysis.

DEFRA index	Mg/kg	Phosphorus concentration categories
0	0-9	0 – Very Low
1	10-15	1 – Low
2	16-25	2 – Medium
3	26-45	3 – High
4	46-70	4 – Very high
5	71-100	

Table A.2.3. Data ranges for each impact category (0-4, reflective of least to most impacted) for nitrate-nitrogen, fines and shading.

Environmental variables	Impact category	Range
Nitrate-nitrogen (mg/kg)	0 – Very low	0 – 20
	1 – Low	21 – 35
	2 – Medium	36 – 50
	3 – High	51 – 70
	4 – Very high	71+
Fines (%)	0 – Very low	< 1
	1 – Low	1 – 3
	2 – Medium	4 – 6
	3 – High	7 – 10
	4 – Very high	> 10
Shading (%)	0 – Heavy	81 – 100
	1 – High	61 – 80
	2 – Medium	31 – 60
	3 – Low	5 – 30
	4 – None	<5
Trampling	0 – None	No trampling
	1 – Low	Very limited tramping
	2 – Medium	Trampling occasionally

	3 – High	Trampling often in sections of the channel
	4 – Most impact	Trampling often and across the entire channel
Road proximity	0 – Very far	> 50 m
	1 – Far	31 – 50 m
	2 – Medium	11 – 30 m
	3 – Close	1 – 10 m
	4 – Very close	On edge of the bank

Appendix 2.3 Summary of the influence of month on plant communities

Table A.2.4. Mixed-model results for testing the influence of month on each biological metric for dry-phase plant communities

Metric	**Month**	**Estimate**	**SE**	**P**
Richness	(Intercept)	2.470	0.116	< 0.001
	April			
	May	0.290	0.100	0.003
	June	0.419	0.097	< 0.001
	July	0.452	0.097	< 0.001
	August	0.445	0.097	< 0.001
	September	0.345	0.100	< 0.001
Diversity	(Intercept)	2.345	0.143	<0.001
	April			
	May	0.281	0.124	0.027
	June	0.431	0.124	0.001
	July	0.457	0.124	0.000
	August	0.439	0.124	0.001
	September	0.349	0.124	0.007
PoaRich	(Intercept)	0.726	0.324	0.025
	April			
	May	0.288	0.230	0.210
	June	0.547	0.218	0.012
	July	0.614	0.216	0.004
	August	0.564	0.217	0.009
	September	0.493	0.220	0.025

Poa%	(Intercept)	3.667	0.851	0.007
	April			
	May	0.294	0.652	0.653
	June	0.913	0.652	0.165
	July	1.262	0.652	0.057
	August	0.955	0.652	0.147
	September	0.697	0.652	0.288
HerbRich	(Intercept)	2.082	0.134	< 0.001
	April			
	May	0.364	0.121	0.003
	June	0.456	0.119	< 0.001
	July	0.450	0.119	< 0.001
	August	0.483	0.118	< 0.001
	September	0.388	0.120	0.001
Dominance	(Intercept)	0.656	0.045	< 0.001
	April			
	May	-0.034	0.042	0.414
	June	-0.029	0.042	0.494
	July	-0.014	0.042	0.749
	August	-0.032	0.042	0.449
	September	-0.028	0.042	0.510
Ellenberg N	(Intercept)	6.206	0.195	< 0.001
	April			
	May	0.013	0.149	0.932
	June	-0.112	0.149	0.454
	July	-0.061	0.149	0.682
	August	-0.038	0.149	0.800
	September	-0.008	0.149	0.958
NumMorph	(Intercept)	1.982	0.445	0.004
	April			
	May	0.286	0.384	0.459
	June	0.286	0.384	0.459
	July	0.357	0.384	0.356
	August	0.500	0.384	0.197
	September	0.500	0.384	0.197

Table A.2.5. Site-specific flowing and drying conditions both before surveying began and in a monthly breakdown for each survey.

River	Site	Pre-survey conditions (months since water)	Survey conditions					
			April	May	June	July	Aug	Sept
Ver	Chequers Pub	Flowing	Pools	Damp streambed	Pools	Damp streambed	Dry	Flowing
	Luton Lane	Dry (46)	Dry	Dry	Dry	Dry	Dry	Dry
	Friars Wash	Flowing	Standing water	Damp streambed	Standing water	Standing water	Dry	Dry
	Long Meadows	Dry (57)	Dry	Dry	Dry	Dry	Dry	Flowing
Gade	Four Ways Farm	Dry (55)	Dry	Dry	Dry	Dry	Dry	Dry
	Gade Cottages	Dry (3)	Dry	Dry	Damp streambed	Dry	Dry	Dry
	D/S Garden centre	Flowing	Flowing	Trickling	Flowing	Damp streambed	Pools	Pools
Bulbourne	North Church playing fields	Dry (7)	Dry	Dry	Dry	Dry	Dry	Dry
	Mandelyns	Dry (7)	Damp streambed	Damp streambed	Damp streambed	Dry	Dry	Damp streambed

	Stag Lane	Flowing	Standing water	Flowing	Flowing	Flowing	Damp streambed	Damp streambed
Misbourne	D/S Missenden Abbey	Dry (55)	Dry	Dry	Dry	Dry	Dry	Dry
	Chalfont Church	Dry (21)	Dry	Dry	Dry	Dry	Dry	Dry
	Chalfont playground	Dry (21)	Dry	Dry	Damp streambed	Dry	Dry	Trickling
	Community centre	Dry (21)	Dry	Dry	Dry	Dry	Dry	Dry

Table A.2.6. Taxa indicative of sites with agricultural, fen, recreational, urban and wooded land use, specificity (the probability of the taxa occurring only at sites with agricultural land use), displaying the fidelity (the probability that the taxa occur at all surveys with agricultural land use), IndVal statistic and P value. Taxa are ranked by Indval statistic and P value. P values are stated according to standard precision thresholds (De Cáceres et al., 2010).

Taxa (Agricultural)	**Order**	**IndVal stat**	**Specificity**	**Fidelity**	**P value**
Lamium album	Lamiales	0.82	1	0.67	0.005
Poa pratensis	Poales	0.75	1	0.56	0.005
Bromus hordeaceus	Poales	0.75	0.71	0.78	0.005
Elymus repens	Poales	0.71	1	0.50	0.005
Achillea millefolium	Asterales	0.67	1	0.44	0.005
Cynosurus cristatus	Poales	0.67	1	0.44	0.005
Helminthotheca echioides	Asterales	0.58	1	0.33	0.005
Taraxacum officinale	Asterales	0.58	1	0.33	0.005
Agrostis capillaris	Poales	0.58	1	0.33	0.005
Symphytum officinale agg.	Boraginales	0.53	1	0.28	0.005
Dipsacus fullonum	Dipsacales	0.53	1	0.28	0.005
Lotus corniculatus	Fabales	0.53	1	0.28	0.005
Trifolium repens	Fabales	0.53	1	0.28	0.005
Alopecurus pratensis	Poales	0.52	0.82	0.33	0.005
Arctium minus	Asterales	0.47	1	0.22	0.005
Reseda luteola	Brassicales	0.47	1	0.22	0.005
Malva moschata	Mavales	0.47	1	0.22	0.005
Artemisia vulgaris	Asterales	0.41	1	0.17	0.020
Lactuca serriola	Asterales	0.41	1	0.17	0.020
Scorzoneroides autumnalis	Asterales	0.41	1	0.17	0.030
Fen					
Veronica anagallis-aquatica	Lamiales	0.707	1	0.5	0.005
Lemnoideae spp.	Alismatales	0.645	1	0.42	0.005
Impatiens capensis	Ericales	0.577	1	0.33	0.005
Rumex conglomeratus	Caryophyllales	0.500	1	0.25	0.005

Mimulus luteus	Lamiales	0.500	0.75	0.33	0.005
Juncus inflexus	Poales	0.500	1	0.25	0.005
Lysimachia nummularia	Ericales	0.447	0.8	0.25	0.020
Recreational					
Myosoton aquaticum	Caryophyllales	0.624	1	0.40	0.005
Calystegia sepium	Solanales	0.615	0.76	0.50	0.005
Glechoma hederacea	Lamiales	0.594	0.63	0.56	0.005
Senecio vulgaris	Asterales	0.577	1	0.33	0.005
Pentaglottis sempervirens	Boraginales	0.577	1	0.33	0.005
Stachys sylvatica	Lamiales	0.527	1	0.28	0.005
Plantago major	Lamiales	0.471	1	0.22	0.005
Deschampsia cespitosa	Poales	0.471	1	0.22	0.01
Lapsana communis	Asterales	0.433	0.84	0.22	0.03
Barbarea vulgaris	Asterales	0.408	1	0.17	0.02
Arrhenatherum elatius	Poales	0.408	1	0.17	0.025
Crataegus monogyna	Rosales	0.408	1	0.17	0.045
Urban					
Glyceria fluitans	Poales	0.645	1	0.42	0.005
Iris pseudacorus	Asparagales	0.5	1	0.25	0.015
Wooded					
Caltha palustris	Ranunculales	0.83	0.42	0.589	0.005

Appendix 2.4 Sediment analysis methods

Sediment moisture

In the field, the soil moisture was measured by inserting a probe into the sediments and taking the reading. In the lab, approximately 100 g of soil/sediment was weighed and placed into trays to air dry over at least 24 h or until dry. Moisture content (%) was then calculated by the following equation:

$$Moisture\ content\ (\%) = \frac{Weight\ of\ wet\ soil - Weight\ of\ dry\ soil}{Weight\ of\ wet\ soil} \times 100$$

Sediment diversity

Air-dried sediments were passed through a series of sieves to determine the % of each grain size fraction: 64 mm, 4 mm, 2 mm, 1 mm, 500 μm, 250 μm, 150 μm and 63 μm. The sediment present in each sieve was weighed and from this the percentage of total weight calculated.

Sediment organic matter

A crucible was weighed and approximately 2 g of dry soil (passed through a 0.5 mm sieve) was added to the crucible, which was then weighed again. The crucible was placed into the furnaced at 550℃ for 3 h as per Hoogsteen et al. (2015). After 3 hours the crucibles were removed, cooled and then weighed immediately. The organic matter content (%) was calculated using this equation:

$$Organic\ matter\ content\ (\%) = \frac{Weight\ of\ dry\ soil - Weight\ of\ soil\ after\ furnace}{Weight\ of\ dry\ soil} \times 100$$

Phosphorus analysis

The ‘Olsen’s method was used to determine phosphorus (P) availability within the soil. NaHCO^3 (42 g) was dissolved in 1 dm^{-3} distilled water (pH adjusted to 8.5) to create the Olsen’s solution (0.5 mol dm^{-3} sodium hydrocarbonate). Ten grams of air-dried (<2 mm sieved) soil was added to a flask and 100 cm^3 Olsen’s solution added. The flask was shaken and then filtered through filter paper. Twenty cm^3 of the filtrate was added to a 100 m^3 flask and the solution neutralised by adding dropwise 5 mol dm^{-3} HCl and the pH checked. To release any carbonate present, 1 cm^3 of 1.5 mol dm^{-3} sulphuric acid was added. The solution was diluted to 80 cm^3 with distilled water, and then 8 cm^3 of ammonium molybdate solution and ascorbic acid added. Distilled water was added to make up to the flask mark and the left for 30 minutes for the colour to develop. The concentration of P in the solution was then read from the calibration curve (see below).

Calibration curve

A 1 μg cm^{-3} P solution was prepared for the calibration curve by pipetting 10 cm^3 of the standard P solution (1 mg P cm^{-3}) into a 100 cm^3 flask and made up to the mark with distilled water. From this solution a further 10 cm^3 is pipetted into a 1 dm^3 flask and made up to the mark again to create the 1 μg cm^{-3} solution. Six phosphorus solutions were then prepared by adding 0, 5, 10, 15, 20 and 30 cm3 of the 1 μg cm^{-3} solution to a 100 cm^3 volumetric flask. 20 cm3 of the Olsen’s solution was then added, the pH checked and then neutralised dropwise (if needed) with 5 mol dm^{-3} HCl. Each flask was then diluted with distilled water to 80 cm^3 and 8 cm^3 of the ammonium molybdate solution added followed by 8 cm^3 of ascorbic acid. Distilled water was then added up to the 100 cm^3 mark, a stopped added and the solution mixed thoroughly through inverting the flask several times. The colour was allowed to develop over 30 minutes and the absorbance of each solution was measured using a spectrometer at 800 nm wavelength. From the absorbance results for the 0, 5, 10, 20 and 30 μg P solutions a calibration curve was drawn which was then used to read the concentration of the P in the soil sample solutions.

Phosphorus calculation

Once the P concentration (Ψ) has been read from the calibration curve the following equation was applied to work out the concentration in the 10 g soil extract:

$$\Psi\ \mu\text{g P kg} - 1 \ = \ \Psi \ \times \ \frac{100}{20} \times \frac{1000}{10}$$

Nitrate analysis

Firstly, a 250 ml 2M KCl was prepared by dissolving 37.25 KCl in 200 ml of water (which was then topped up to 250ml). Air-dried soil (8 g at <2 mm) was added to 20 ml 2M l^{-1} KCl solution and mixed for 1 hour before being filtered. A Nitracheck colourimeter was used to measure the nitrate within the soil sample, using nitrate sticks. The stick was immersed into the filtered solution for 2 secs, held in the air for 2 further seconds before being inserted into the colourimeter when indicated to do so. The nitrate value (Ψ) was read from the meter and the nitrate in the soil sample calculated as follows:

$$Nitrate\ in\ soil\ (ug/g) = \Psi \text{ x } \frac{20}{8}$$

pH analysis

Soil (20 ml) and 50 ml of distilled water was added to a flask and stirred frequently for 30 mins. The pH meter (soil FieldScout meter) was calibrated with buffers (before the first reading) and then lowered into the soil solution, the pH was then noted after 30 secs.

Appendix 3 (Chapter Five)

Appendix 3.1 The influence of Collembola on taxonomic abundance responses

With Collembola included in taxonomic abundance metrics, the amount of variance accounted for by models is reduced and any differences seen in abundance in relation to the environmental variables are masked (Table A.3.1 and Table A.3.2), in comparison to the models run without Collembola included.

Table A.3.1. The R^2M and R^2C values for models run to test the influence of the environmental variables on abundance including Collembola.

	R^2M	R^2C
VegMorph	0.822	0.133
VegRich	0.867	0.039
GravelProp	0.818	0.098
SedMoist	0.847	0.070
LeafLitter	0.828	0.024

Table A.3.2. The model estimate, SE and P value from the models used to test the influence of all environmental variables on the taxonomic abundance including Collembola.

	Estimate	SE	P
VegMorphSimple	6.79	0.79	
VegMorphComplex	-0.96	0.97	0.32
VegRich	0.28	0.20	0.16
SedMoist	-0.36	0.27	0.19
GravelPropLow	5.76	0.65	
GravelPropHigh	0.80	0.93	0.39
LeafLitterAbsent	5.33	0.73	
LeafLitterPresent	1.48	0.92	0.11
LeafLitterExtensive	1.05	0.91	0.25

Appendix 3.2 Mixed-level responses to vegetation, sediment moisture and leaf litter, and family-level responses to sediment composition

Vegetation (VegMorph and VegRich) accounted for 23% of the variation at mixed-level (PERMANOVA, VegMorph; $R^2 = 0.15$, VegRich: $R^2 = 0.08$). Communities differed between VegMorph categories (PERMANOVA, F = 8.95, df = 1, P = 0.001) with communities at sites with simple VegMorph having high NMDS1 values and between -0.5 and 0.5 NMDS2 values, whilst communities at complex VegMorph sites were variable, distributed across both the NMDS1 and NMDS2 axes (Figure A.3.1). Taxa associated with simple VegMorph included Armadillidum vulgare, Philoscia muscarum and Pterostichus maddidus (Table A.3.3), there were no taxa associated with complex VegMorph.

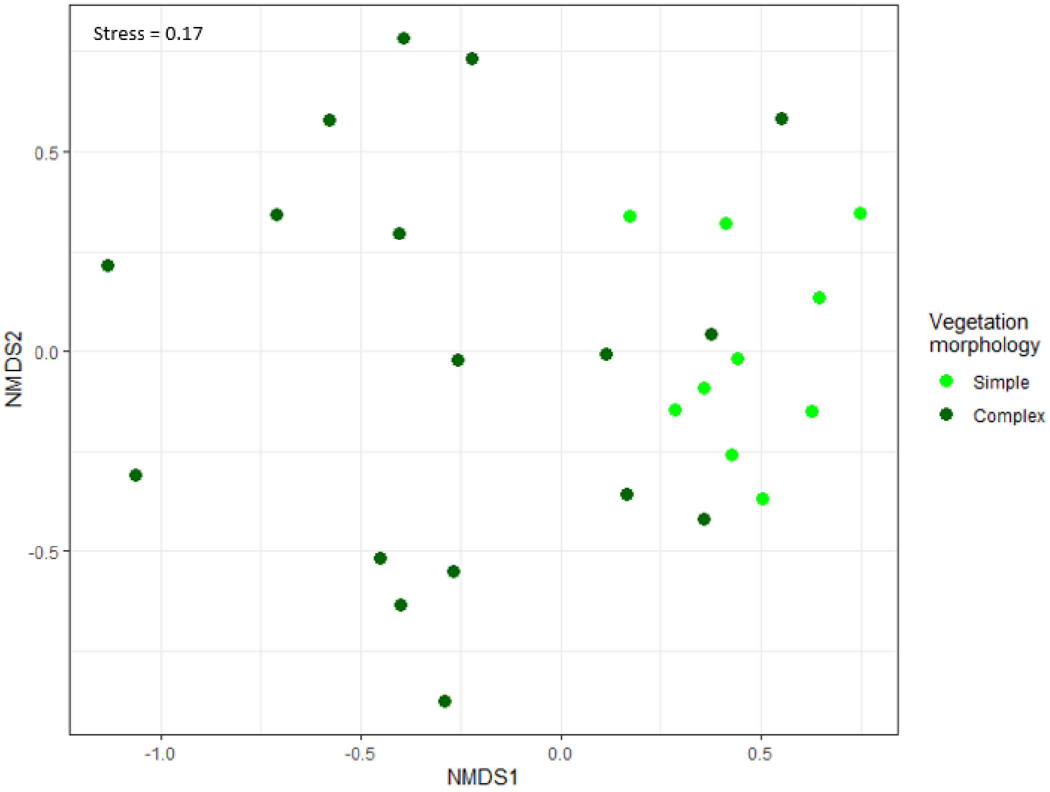

Figure A.3.1. NMDS ordination of invertebrate community composition at mixed-level according to vegetation morphology (simple or complex).

Table A.3.3. Taxa indicative of sites with simple vegetation morphotypes, displaying the IndVal statistic, specificity, fidelity and P value. Specificity and fidelity represent the probability (0–1) of the family occurring only at sites with simple VegMorph and taxa occurs at all sites with simple VegMorph, respectively. P values are stated according to standard precision thresholds (De Cáceres et al., 2010).

Taxa	**Order**	**IndVal**	**Specificity**	**Fidelity**	**P**
Myrmicinae spp.	Hymenoptera	0.95	0.90	1.00	0.005
Armadillidium vulgare	Isopoda	0.88	0.78	1.00	0.005
Philoscia muscorum	Isopoda	0.88	0.77	1.00	0.005
Pterostichus madidus	Coleoptera	0.84	0.71	1.00	0.01
Dermaptera juvenile	Dermaptera	0.70	0.96	0.50	0.005

Polydesmida spp.	Polydesmida	0.60	0.90	0.40	0.045

Community composition also differed according to VegRich (PERMANOVA, F = 4.72, df = 1, P = 0.001). Invertebrate communities with higher VegRich (22-24 plant taxa) occurred mostly centrally on the ordination (Figure A.3.2) though slightly skewed towards the high NMDS1 values. From this cluster, VegRich at sites decreased towards the invertebratecommunities at the outer edges of the ordination.

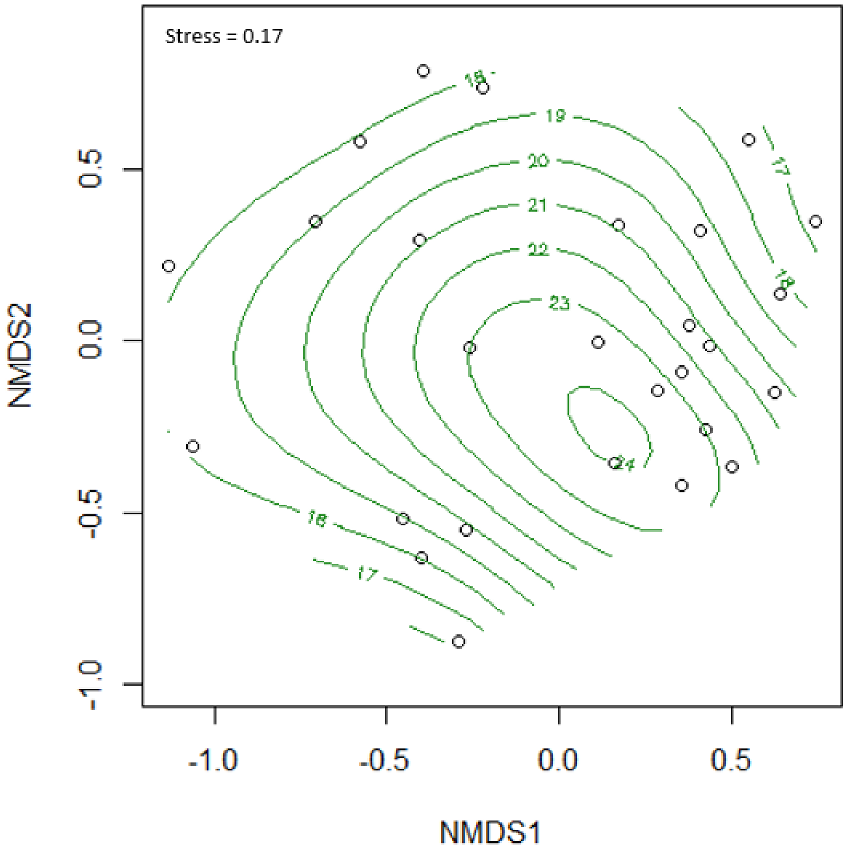

Figure A.3.2. NMDS ordination of mixed-level community composition according to vegetation richness, which is represented by contours, the number of each contour denoting the value. Species labels were not included due to overlap.

Sediment moisture accounted for 6% of variance in community composition, with communities differing according to sediment moisture values (PERMANOVA, F = 3.56, df = 1, P = 0.002). Sediment moisture was highest at low NMDS1 and NMDS2 values, which then decreased towards higher NMDS2 values and was lowest at high NMDS1 values (Figure A.3.3).

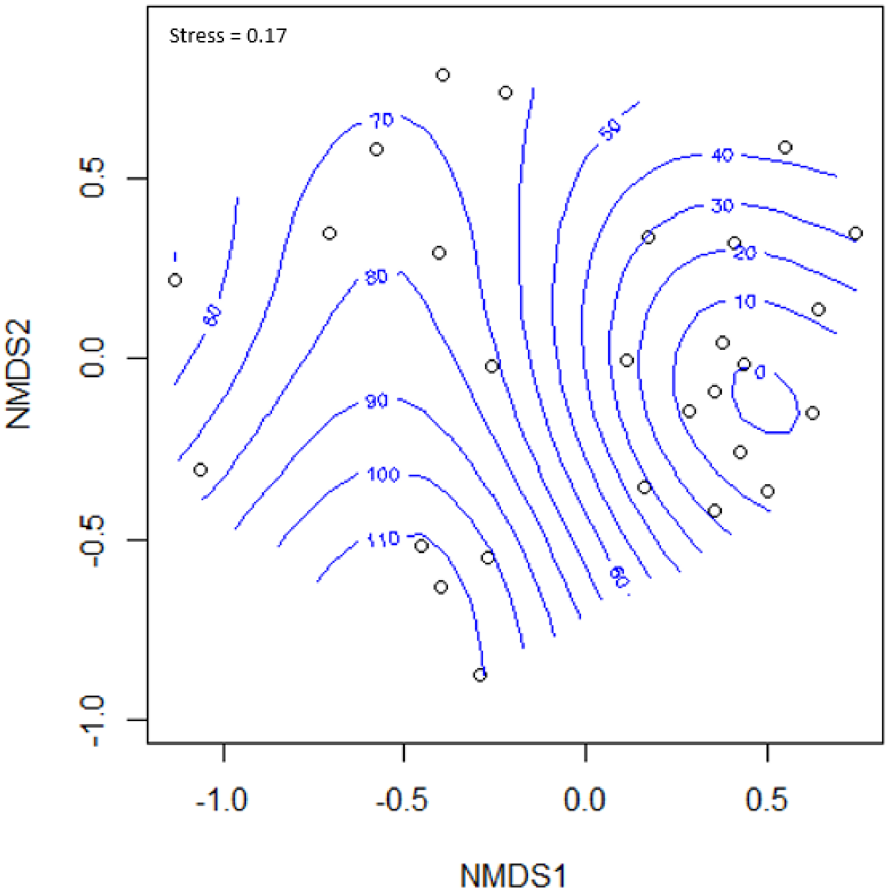

Figure A.3.3 NMDS ordination of mixed-level community composition according to sediment moisture, which is represented by contours, the number of each contour denoting the value.

GravelProp accounted for 7% of family-level composition and communities differed significantly between GravelProp categories (PERMANOVA, F = 4.05, df = 1, P = 0.001). Sites with low GravelProp had high NMDS2 values and sites with high GravelProp had low NMDS2 values, and both were evenly distributed along NMDS1 (Figure A.3.4). Taxa associated with high GravelProp included Coccinellidae, Hemiptera spp. and Tetragnathidae (Table A.3.4) and no taxa were associated with low GravelProp.

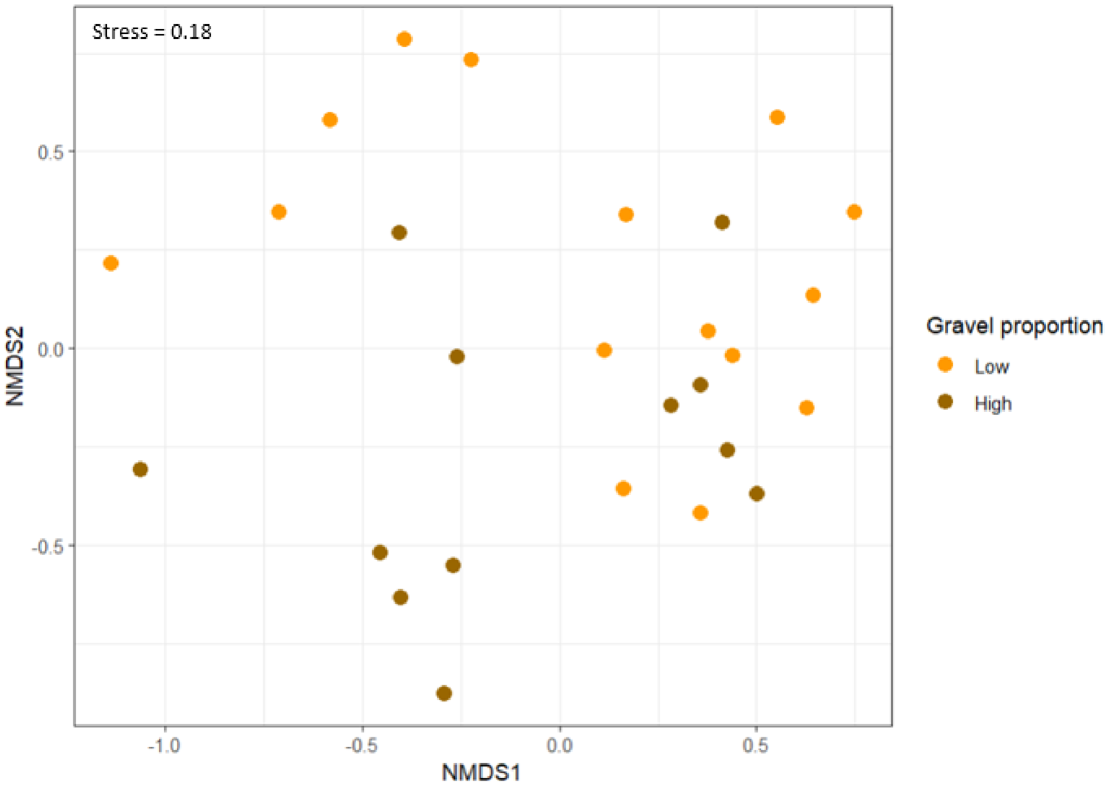

Figure A.3.4. NMDS ordination of family-level community composition according to low and high gravel proportions.

Table A.3.4 Taxa indicative of sites with high gravel proportions, displaying the IndVal statistic, specificity, fidelity and P value. Specificity and fidelity represent the probability (0–1) of the family occurring only at sites with high VegMorph and taxa occurs at all sites with high VegMorph, respectively. P values are stated according to standard precision thresholds (De Cáceres et al., 2010).

Family	Order	IndVal	Specificity	Fidelity	P
Coccinellidae	Coleoptera	0.77	0.89	0.67	0.005
Hemiptera spp.	Hemiptera	0.72	0.78	0.67	0.015
Tetragnathidae	Araneae	0.58	1.00	0.33	0.05

LeafLitter accounted for 11% of mixed-level community composition with communities differing between differing LeafLitter categories (PERMANOVA, F = 3.47, df = 2, P = 0.001). Sites with absent LeafLitter are split into site-specific groups along the NMDS1 axis, whilst all but one of the sites with present LeafLitter had high NMDS1 values. Those with extensive LeafLitter typically had lower NMDS1 and NMDS2 scores, with the exception of two samples at higher NMDS1 and NMDS2 values (Figure A.3.5). There were no taxa associated with present LeafLitter. Three taxa were associated with extensive LeafLitter and Dermaptera juveniles were indicative of absent LeafLitter (Table A.3.5). Formacine spp. and *Nebria brevicollis* were indicative of sites with present and extensive LeafLitter and *A. vulgare* and *Forficula auricularia* were indicative of absent and present LeafLitter sites.

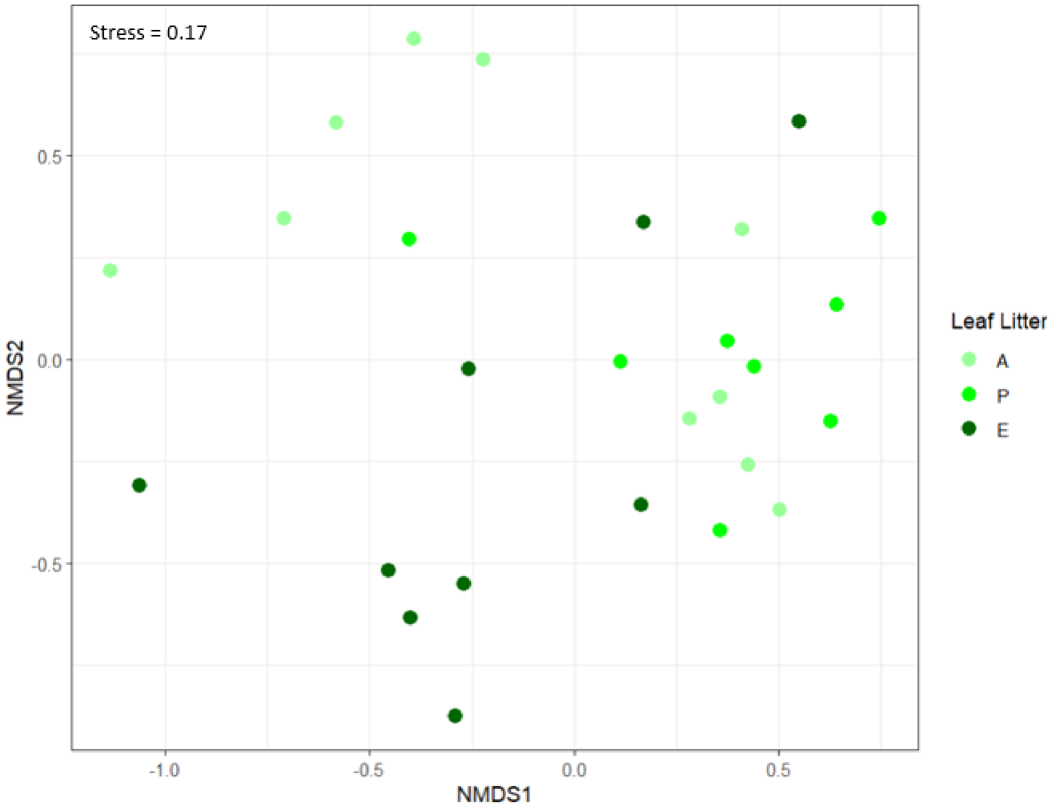

Figure A.3.5. NMDS ordination of mixed-level community composition according to absent, present and extensive leaf litter cover.

Table A.3.5. Taxa indicative of sites with absent, extensive and the combination of absent and present, and present and extensive leaf litter cover, displaying the IndVal statistic, specificity, fidelity and P value. Specificity and fidelity represent the probability (0–1) of the taxa occurring only at sites with a LeafLitter category and taxa occurs at all sites with a LeafLitter category, respectively. P values are stated according to standard precision thresholds (De Cáceres et al., 2010).

Leaf litter cover	**Taxa**	**Order**	**IndVal**	**Specificity**	**Fidelity**	**P value**
Absent	Dermaptera juvenile	Dermaptera	0.68	0.93	0.50	0.020
Extensive	*Pachygnatha clercki*	Araneae	0.67	1.00	0.44	0.005
	Agonum viduum	Coleoptera	0.63	0.90	0.44	0.005
	Pterostichus rhaeticus/nigrita	Coleoptera	0.61	0.83	0.44	0.035
Absent and present	*Armadillidium vulgare*	Isopoda	0.79	0.87	0.72	0.050
	Forficula auricularia	Dermaptera	0.67	1	0.44	0.045
Present and extensive	Formacinae spp.	Hymenoptera	0.79	0.98	0.65	0.005
	Nebria brevicollis	Coleoptera	0.72	0.99	0.53	0.030

Appendix 3.3 Model results for dry-phase invertebrate metric responses to leaf litter cover

Table A.3.6. The model used (Generalised Linear Mixed Model, Linear Mixed Models and Generalised Linear Model) to test the influence of in-channel leaf litter on the taxonomic family richness, taxonomic richness and abundance, spider richness and abundance, and carabid richness and abundance of dry-phase invertebrate communities, with the associated R^2 values (R^2C and R^2M for mixed models and R^2 for linear models) and results of each model.

Metric (model)	**R^2C**	**R^2M or R^2**	**Intercept (Absent)**			**Leaf litter (Present)**			**Leaf litter (Extensive)**		
			Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Taxonomic family richness (GLMM)	0.46	0.009	2.69	0.16	<0.001	0.03	0.20	0.886	-0.05	0.19	0.785
Taxonomic taxa richness (GLMM)	0.71	0.01	2.95	0.22	<0.001	-0.03	0.24	0.904	-0.08	0.23	0.727
Taxonomic abundance (GLMM)	0.71	0.07	4.87	0.58	<0.001	0.60	0.73	0.413	-0.02	0.71	0.978
Spider richness (GLMM)	0.75	0.02	1.10	0.60	0.066	0.24	0.70	0.735	-0.11	0.69	0.871
Spider abundance (LMM)	0.58	0.12	1.69	0.72	0.020	0.03	0.98	0.976	0.95	0.96	0.321
Carabid richness (GLM)		0.05	0.92	0.20	<0.001	0.10	0.29	0.744	0.25	0.27	0.352

Carabid abundance (GLM)	0.46	0.21	2.02	0.81	0.072	1.90	1.10	0.143	1.68	1.06	0.176