The specialist insects that rely on the wet-dry habitats of temporary streams

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Temporary rivers and streams are increasingly recognised as dynamic habitats in which shifts between wet and dry states support high biodiversity. Their aquatic communities are dominated by opportunists that colonise when flowing water is present. In addition, some aquatic species have adaptations that enable them to survive dry phases as desiccation-tolerant life stages. However, globally, few such species are specialists that rely on the shifts between wet and dry states that characterise temporary streams. We share evidence that our mild, wet climate has made Great Britain a global hotspot of temporary stream specialists. In particular, their seasonal predictability enables the chalk winterbournes of south England to host species that need both wet and dry habitats to complete their life cycles – including some of our rarest insects.

The scarce purple dun

Aquatic larvae of the leptophlebiid mayfly *Paraleptophlebia werneri* (Fig. 1a) live mainly in the pools and margins of calcareous streams, where they burrow into gravel, sand or muddy bed sediments, or lurk amongst aquatic plants. In England, larvae are often the sole mayfly in summer-dry streams, which are sometimes choked with vegetation. With a single generation each year, most individuals overwinter as larvae, and the rest as eggs. Adults then emerge in spring, enabling the drying-sensitive larvae to avoid dry instream conditions.

Paraleptophlebia werneri was first found in Great Britain in 1939 in the chalk Rivers Allen and Till, Hampshire (Kimmins 1939). Since

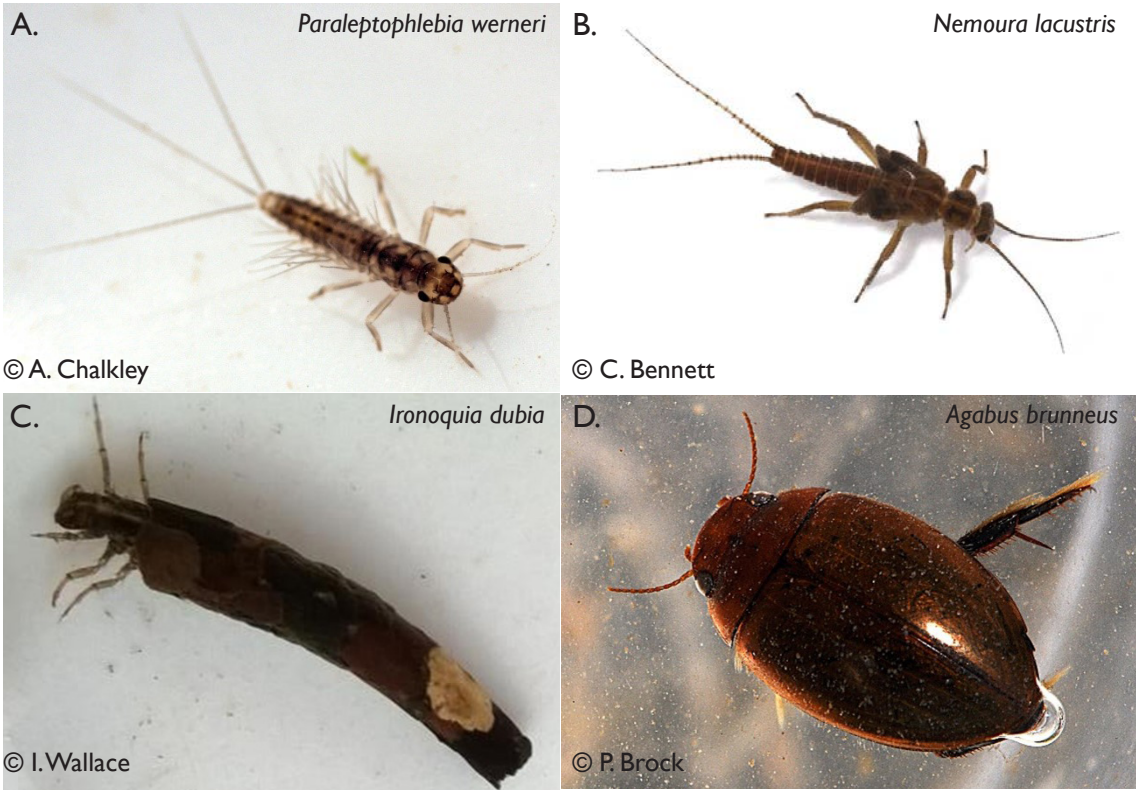

Figure 1. Four of the UK's temporary stream specialists: larvae of (a) the mayfly *Paraleptophlebia werneri*; (b) the stonefly *Nemoura lacustris*; (c) the caddisfly *Ironoquia dubia*; and (d) an adult *Agabus brunneus* beetle.

then, confirmed records have been made from temporary streams across Wiltshire, Dorset, Hampshire, Sussex and Suffolk (Fig. 2), and in particular, the species is considered characteristic of chalk winterbournes (White et al. 2018). Although populations can reach high densities, its very localised distribution has led to its designation as Nationally Scarce (Macadam 2016).

The scarce summer mayfly

Like *P. werneri*, larvae of the mayfly *Siphlonurus armatus* typically live in pools and marginal waters, preferring slow-flowing streams with mud and sand sediments and aquatic plant growth. In particular, they are associated with temporary streams. Here, their eggs lay dormant in dry sediments until water returns and triggers egg hatching. Larvae then develop over the winter before adults emerge in spring, enabling aquatic life stages to avoid the next dry phase.

The distribution of *S. armatus* suggests a strong southern bias, with just one unconfirmed report of a population in the River Winster, Cumbria. In any case, *S. armatus* is feared lost from much of its historical range, with only one population (Spital Brook, Herefordshire) now confirmed in Great Britain (Fig. 2; Macadam & Farr 2021). The species is thus currently listed as both Endangered and Nationally Rare (Macadam 2016), and if the Spital Brook population is confirmed as supporting our only remaining *S. armatus* population, it will qualify as Critically Endangered (Macadam & Farr 2021).

The winterbourne stonefly

First discovered in Great Britain in 2009 (Hammett 2012), larvae of the winterbourne stonefly *Nemoura lacustris* (Fig. 1b) have – to date – been found only in summer-dry temporary streams in the UK (Hammett 2012, Tapia et al. 2018). As for both mayflies, the species survives the dry phase as dormant eggs, requiring cool, damp conditions to remain viable. Exposure to cold conditions is also needed to trigger development, with eggs kept at ambient temperatures failing to hatch (Tapia et al. 2018). After egg hatching in flowing water as late as December, the larvae develop quickly and reach maturity in time to emerge in spring, with the adult flight period extending from April to June (Hammett 2012, Jon Bass pers. comm.).

Nemoura lacustris has a localised distribution in south England, with records from Dorset, Wiltshire, Hampshire and West Sussex (Fig. 2; Tapia et al. 2018, Jon Bass pers. comm.) and is listed as Nationally Rare (Macadam 2015).

The scarce brown sedge

Caddisflies of the family Limnephilidae are among the most common insects of summer-dry freshwaters, typically emerging as adults before waters recede and returning in autumn to lay eggs in damp, soon-to-be inundated habitats. Most prefer still water, but one is a true temporary stream specialist: *Ironoquia dubia* (Fig. 1c), which is mainly found in summer-dry reaches, but also those in which flows recede to a trickle. In recent years, I. dubia has been found in only two British stream systems, one in Norfolk, and another in Hampshire (Fig. 2). As such, this unusual species is among our rarest caddisflies, and is listed as Critically Endangered (Wallace 2016).

Uniquely among European caddisflies, final instar *I. dubia* larvae actively leave the water in late spring and hide amongst riparian leaf litter and plant roots (Fig. 3a). Here, their survival relies on sediments remaining damp. If so – and in contrast to both mayflies and stoneflies – they pupate and emerge as adults in the autumn. Females then lay eggs in plant litter, and the species awaits the return of water as dormant eggs or first instar larvae. Whilst over-summering in these resting states, larvae are particularly vulnerable to physical disturbance such as trampling by

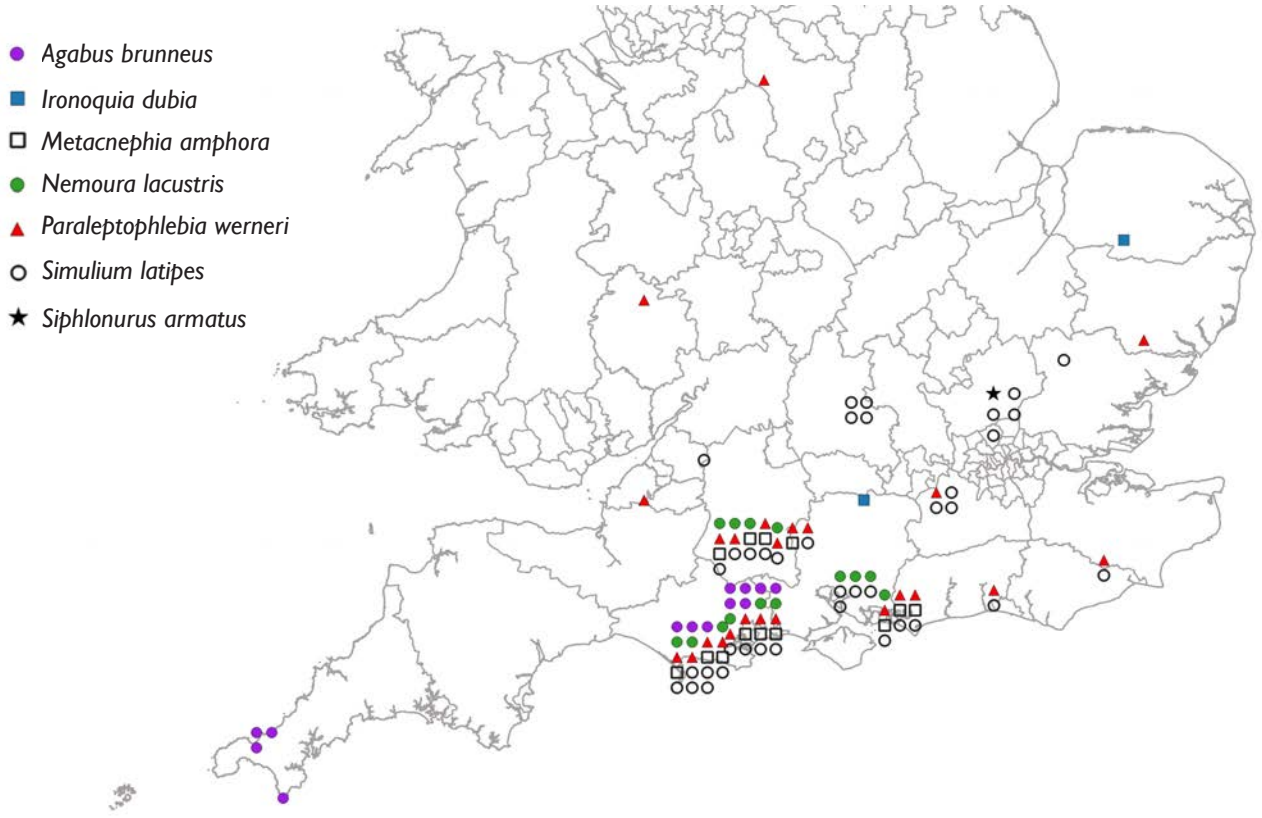

Figure 2: The UK distribution of temporary stream specialist species. Vertically stacked points represent observations from the same hectad. No confirmed observations from other UK areas have been excluded.

livestock, which can release moisture and push larvae past their limited capacity to tolerate desiccation. Then, when flow resumes, surviving larvae continue their development.

Water beetles including the brown diving beetle Many water beetles have adaptations that allow them to inhabit temporary streams, notably the dytiscids. One, the brown diving beetle *Agabus brunneus* (Fig. 1d) is among nine listed as priority species in the UK Biodiversity Action Plan (Foster 2010). Classified as Vulnerable, its worsening conservation status is expected to result in reclassification as Endangered (G. Foster, pers. comm.). A second dytiscid associated with temporary waters, *Hydroporus marginatus*, is also Nationally Scarce (Foster 2010).

South England is a northern limit for *A. brunneus*, with populations in two areas, west Cornwall and the New Forest (Fig. 2). Here, it inhabits lowland temporary streams in which porous gravels allow migration into deeper, wetter sediments as the water table falls, hence its sensitivity to fine sediment pollution. Limited evidence suggests a lifecycle comparable to our specialist mayflies and stoneflies, with eggs laid in autumn, larvae that overwinter in flowing water, and adults that breed in early spring (Foster 2010).

Winterbourne blackflies

First described from a temporary reach of the South Winterbourne, Dorset (Ladle & Bass 1975), larvae of the simuliid *Metacnephia amphora* may be restricted to streams with predictable, seasonal dry phases, limiting their British distribution to southern England, where they can be very abundant (Fig. 2; Armitage & Bass 2013). Armitage & Bass (2013) also recorded larvae of the blackfly *Simulium latipes* exclusively – and

again at high densities – from temporary sites on the South Winterbourne, with recent records from other European sites also describing its association with summer-dry reaches.

The filter-feeding larvae of these species are particularly numerous at sites with dense vegetation. In common with other specialists, the survival of blackflies in temporary streams is enabled by a sequence of life stages adapted to exploit contrasting abiotic conditions, in this case, eggs that lay dormant in dry sediments, aquatic larvae and pupae that develop rapidly after flow resumes, and adults that emerge in early spring (Armitage & Bass 2013).

winterbournes, because tolerance of desiccation is less physiologically demanding in sediments in which mild temperatures and year-round rainfall maintain interstitial humidity. Accordingly, our temporary freshwaters also support many other species that that are adapted to, but not reliant, on shifts between wet and dry instream states, including limnephilid caddisflies, dytiscids and other beetles (e.g. Wood et al. 2005) – species which may be outcompeted in perennial waters.

Specialists can be rarer in drier climates. For example, despite being a hotspot of biodiversity and endemicity for freshwater invertebrates, we know of few temporary stream specialists in

Figure 3: Habitats in Thompson Common, Norfolk, in which the caddisfly *Ironoquia dubia* lives: (a) damp streambed sediments suitable for dormant eggs and first instar larvae; (b) Stowbedon Stream, where later instar larvae were found at sites with sandy sediments and moderate flow in 2018 (Wallace, unpublished); (c) a grass clump suitable as a pupation site.

Is south England a global hotspot of temporary stream specialists?

Temporary streams have only recently been recognised as natural, valuable and biodiverse ecosystems in temperate regions such as the UK (Stubbington et al. 2017) – and now, we are celebrating the notable diversity of their specialist species. Drying acts as a strong selective pressure with the potential to drive evolution of specialisation in systems in which dry phases are sufficiently frequent and predictable – but not too severe. Our climate could thus favour the evolution of adapted specialists in seasonal temporary streams such as chalk

the Mediterranean Basin, such as the limnephilid *Mesophylax aspersus* and the very rare leptophlebiid mayfly *Choroterpes prati*. In addition, in the truly arid southwest USA, hydrological isolation can prevent generalists from colonising from perennial streams, driving the evolution of specialists including many true flies, the winter stonefly *Mesocapnia arizonesis* and the dobsonfly *Neohermes filicornis*, all of which can spend years as dormant larvae in dry sediments, then develop rapidly when water returns.

Protecting specialists in temporary streams

Our exploration of UK temporary streams has shown that, without exception, their specialist invertebrate species have life cycles adapted to seasonal shifts between wet and dry states, with individual life stages reliant on contrasting habitat types. Collectively, these species can enhance the conservation value of temporary stream communities compared to those at nearby perennial sites (White et al. 2018).

Changing flow regimes driven by river regulation – including both abstraction that extends dry phase durations and effluent release that causes artificial perennialisation – are among the multiple threats faced by biota within temporary streams. In addition, increasing climatic severity presents risks at both extremes of the hydrological continuum, with wet years preventing seasonal drying whilst droughts extend dry phases in both space and time. In addition, heatwaves promote evaporation of crucial moisture, turning damp into truly dry habitats in which species' capacity to tolerate desiccation is surpassed. Physical disturbance of dry habitats can have comparably damaging effects, be it livestock trampling that leaves dormant eggs and larvae exposed to desiccation, or activities that add, excavate or rework bed sediments, thus burying, removing or disturbing these vulnerable life stages (Armitage & Bass 2013).

We now recognise the need for environmental flows that support aquatic biodiversity in temporary streams, but dry channels are still viewed as symbolic of drought and over-abstraction – and devoid of life. We call for recognition that dry channels can instead be natural and full of life – both the terrestrial communities that colonise as waters recede, and the desiccation-tolerant 'aquatic' biota that persist unseen beneath the bed. Management plans may thus require adaptation to support biodiversity in dry habitats, for example by developing strategies that keep 'dry' sediments not truly dry, but damp, cool and undisturbed.

The aquatic–terrestrial biodiversity of winterbourne chalk streams – where most of our specialists have been recorded – is becoming better documented than perhaps any other temporary river type globally (e.g. Bunting et al. 2021, but see Corti & Datry 2016). We now call for greater exploration of the full range of diverse temporary stream types that occur in the UK (Stubbington et al. 2017), to ensure that we identify and act to protect their specialist species within functional ecosystems as they adapt to global change.

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Do you like freshwater invertebrates?

If you are interested in freshwater invertebrates, be sure to check out these organisations if you would like to be involved in their conservation!

Buglife: https://www.buglife.org.uk/

The Riverfly Partnership: https://www.riverflies.org/

The Riverfly Recording Schemes: https://www.brc.ac.uk/schemes/RRS/homepage.htm