

The terrestrial and semi-aquatic invertebrates of intermittent rivers and ephemeral streams

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ABSTRACT

Intermittent rivers and ephemeral streams (IRES), which cease flow and/or dry at some point, are the most abundant waterways on earth, and are found on every continent. They can support a diverse, and often abundant, terrestrial and semi-aquatic invertebrate (TSAI) fauna, which has been poorly explored due to its position at the fringe between aquatic and terrestrial disciplines. TSAIs can inhabit a variety of habitat types, including the shoreline, the surface of exposed gravel bars, unsaturated gravels, dry riverbeds, riparian zones, and floodplains. Much less is known about the species composition and ecological roles of TSAIs of IRES than their aquatic counterparts, with TSAIs being largely overlooked in conceptual models, legislation, policy, and ecological monitoring. Herein we review the TSAI literature that has increased substantially over the last decade and present conceptual models describing how TSAIs respond to hydrological changes in IRES. Then, we test these models with data collected during wet and dry phases in IRES from Australia and France. These generic models can be utilised by water managers and policy makers, ensuring that both wet and dry phases are considered in the management and protection of IRES. IRES should be viewed as a habitat continuum through time, with taxa from a pool of aquatic, semi-aquatic and terrestrial invertebrates inhabiting at any hydrological stage. We call for collaboration among terrestrial and aquatic ecologists to explore these invertebrates and ecosystems further.

Key words: terrestrial arthropods, Coleoptera, Carabidae, Staphylinidae, Formicidae, Lycosidae, Hebridae, taxonomic diversity, exposed riverine sediments, unsaturated sediments

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I. INTRODUCTION

Rivers and streams that cease to flow and dry up are the most abundant waterways on the planet, and are found on every continent (Larned *et al.*, 2010; Datry *et al.*, 2017). These waterways, termed ‘intermittent rivers and ephemeral streams’ (IRES) for the purposes of this review, are becoming more and more prevalent in a world undergoing climate change (Döll & Schmied, 2012; De Graaf *et al.*, 2019). The scientific literature contains numerous examples of terminology assigned to classes of streams and rivers whose flows cease for varying periods with varying predictability (e.g. Uys & O’Keeffe, 1997; Williams, 2006; Gallart *et al.*, 2012). Busch *et al.* (2020) analysed 12 widely used epithets from the literature, and concluded that many are redundant, suggesting the use of three, two of which (‘intermittent’ and ‘ephemeral’) we have adopted here.

Historically, IRES gained some attention by researchers in the 1970s (e.g. Williams & Hynes, 1976, 1977) and 1980s (e.g. Boulton, 1989; Bunn, Davies & Edward, 1989), but IRES, and in particular the dry phase, has been largely overlooked by aquatic ecologists and water managers until recently (Datry, Larned & Tockner, 2014c). In the past decade they have attracted increased attention (Leigh *et al.*, 2016; Zimmer *et al.*, 2020), and today it is acknowledged that IRES can host rich and unique biotic communities, contribute to the ecological integrity of river networks, and provide critical ecosystem services and values to society (Steward *et al.*, 2012; Datry *et al.*, 2018). However, IRES are at a high risk of degradation, as legislation worldwide fails to protect their unique values (Steward *et al.*, 2012; Acuña *et al.*, 2014) or even to recognise them as ecosystems worthy of protection (Acuña, Hunter & Ruhí, 2017).

Compared to the phases with flowing or non-flowing conditions, the dry, terrestrial phases of IRES have received less attention from scientists and water managers and have been viewed as *terra incognita* (Datry *et al.*, 2011b, 2014c; Steward *et al.*, 2012). However, the dry phases of IRES provide values to humans and ecosystems that have previously been overlooked (Steward *et al.*, 2012), including the provision of habitat for terrestrial and semi-aquatic invertebrates (TSAIs). TSAIs are poorly known, with only a handful of studies on them conducted worldwide, although momentum in this area of research has been increasing recently. A lack of data synthesis has limited the knowledge and management of TSAIs in IRES, along with the scarcity of conceptual models guiding on-going research.

The distributions of TSAI communities in space and time are even less understood in river networks. The response of aquatic macroinvertebrates to drying, by contrast, is well

understood. Pivotal work by Boulton (2003) described the effects of drying on stream macroinvertebrate assemblages, and a conceptual model was presented. As flow discharge or water level decreases, habitats such as littoral vegetation or riffles disappear, and aquatic taxa richness declines sharply. Taxa richness continues to decline when surface water is lost, and refuges become dry. Many aquatic taxa can take refuge in the hyporheic zone; however, once that dries then taxa richness reduces again. When a stream has dried and the hyporheic zone is no longer saturated, taxa richness is low but may not reach zero, as taxa may persist in desiccation-resistant forms of their life history, such as eggs, cysts, larvae, pupae, or even adults. This model was well supported in the past decade (Datry *et al.*, 2017) and recent research has expanded the effects of drying on aquatic biodiversity at larger scales (i.e. regional, national) where drying acts as an agent of fragmentation (e.g. Jaeger, Olden & Pelland, 2014; Crabot *et al.*, 2020; Gauthier *et al.*, 2020).

We argue that TSAIs can be found in IRES habitats during all stages of riverbed wetting and drying, and we propose the IRES habitat continuum model to describe the dynamics involved (Fig. 1). In contrast to aquatic invertebrates, we propose that terrestrial and semi-aquatic invertebrates initially increase in taxonomic richness and abundance as surface water disappears. Drying of IRES removes habitat for aquatic invertebrates (Stanley, Fisher & Grimm, 1997) but represents an expansion of habitat for terrestrial invertebrates to colonise as more and more riverbed area is exposed (Steward *et al.*, 2017). Over time, the ‘terrestrialisation’ of the riverbed may reduce richness and abundance as the channel becomes favourable only for tolerant and specialist terrestrial taxa, and unsuitable for semi-aquatic taxa that require water for some part of their life history. Rewetting of the riverbed by flooding or flow from upstream resets the TSAI assemblage composition and abundance as (i) water physically removes terrestrial and semi-aquatic invertebrates by drift in the water column or *via* rafting on top of floating material; (ii) individuals retreat into the riparian zone or into upland habitats through flight or crawling; or (iii) individuals take refuge in riverbed sediments to either perish or survive submersion and then recolonise the newly exposed sediment. Terrestrial and semi-aquatic individuals may also recolonise by flying or crawling from upstream, downstream, or adjacent (i.e. riparian or upland) habitats.

The aim of this review is to: (i) compile the fragmented knowledge available on the TSAIs of IRES; (ii) present a conceptual model of how TSAIs are organised; (iii) test our model through case studies in Australia and France; and (iv) highlight research needs based on knowledge gaps that we have identified.

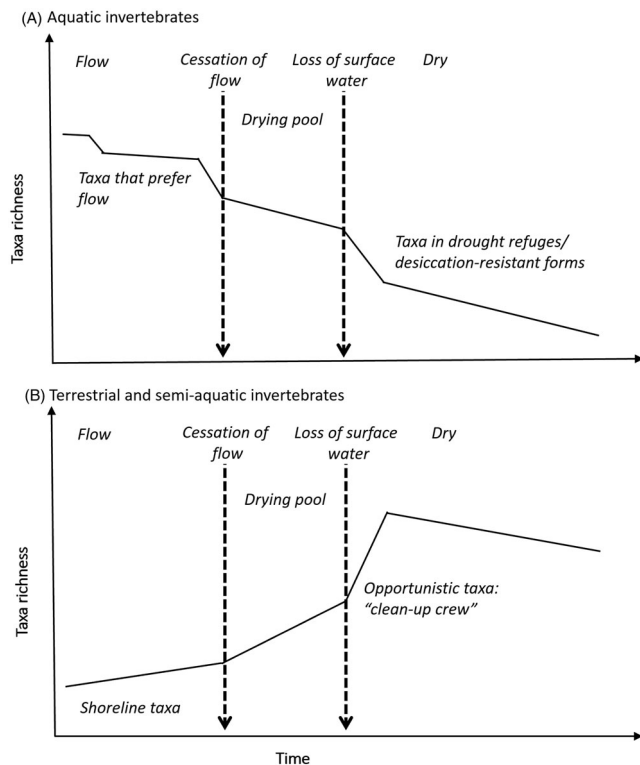


Fig. 1. The intermittent rivers and ephemeral streams (IRES) habitat continuum model. The aquatic invertebrates plot (A) represents taxa that inhabit flowing, cessation of flow, and drying pool habitats (modified from Boulton, 2003), as well as taxa that persist by utilising drought refuges in the riverbed and hyporheic zone and/or as desiccation-resistant forms (eggs, cysts, larvae, pupae, adults). The terrestrial and semi-aquatic invertebrates plot (B) includes terrestrial shoreline invertebrate taxa, with an increase in terrestrial and semi-aquatic invertebrate taxa once surface water disappears, due to the addition of opportunistic predatory and scavenging taxa (the 'clean-up crew'). Once the aquatic resources of dead and dying fish, insects, algae, etc., have been consumed, the assemblage is dominated by dry riverbed specialists. Dashed lines indicate when cessation of flow and the loss of surface water occurs.

II. CURRENT ECOLOGICAL UNDERSTANDING OF TSAIS

(1) Diversity of TSAI communities

(a) Taxonomic diversity

A wide range of terrestrial and semi-aquatic taxa from several phyla (Annelida, Arthropoda, Mollusca, Nematoda) have been documented to inhabit IRES (Wishart, 2000; Lalley *et al.*, 2006; Steward *et al.*, 2011, 2012, 2017; Corti & Datry, 2016). Steward *et al.* (2017) present a list of TSAI taxa recorded from IRES in Australia, Canada, France, Greece, Italy, New Zealand, Portugal, Spain, and South Africa. The list is dominated by insects (class Insecta) and includes taxa from the orders Archaeognatha (bristletails), Blattodea

(cockroaches), Coleoptera (beetles), Diptera (true flies), Hemiptera (true bugs), Hymenoptera (wasps and ants), Mantodea (mantids), Neuroptera (lacewings), Orthoptera (grasshoppers, crickets), Psocoptera (book lice), Thysanoptera (thrips), and Zygentoma (silverfish). Other arthropods listed include Arachnida (spiders, mites, harvestmen, pseudoscorpions), Chilopoda (centipedes), Collembola (springtails), Diplopoda (millipedes), Diplura, and Protura. Coleoptera has the most recorded families to date (51), followed by Hemiptera (15), Diptera (14), Araneae (11), and Orthoptera (7), with eight subfamilies recorded from the family Formicidae (Steward *et al.*, 2017). Additional taxa not in this list include Megaloptera (fishflies), of which active larvae have been found to persist in dry riverbeds (Cover, Seo & Resh, 2015). This list will most certainly increase as TSAIs are collected and identified from IRES yet to be sampled around the world.

The taxonomic composition of TSAI communities depends on the flow regime and hydrological connectivity of IRES, with a different suite of fauna being present during wet, drying, and dry phases. TSAIs have been recorded from a variety of IRES habitats, even including an advancing wetting front as it flowed down a dry channel (Corti & Datry, 2012). In the first bore sampled during a rewetting event following a 4-month dry spell in the Albarine River (France), 74 TSAI taxa including 24 living taxa were collected, which is approximately three times higher than the total number of aquatic invertebrate taxa collected (28). Steward *et al.* (2011) found that the taxonomic richness of TSAIs sampled from dry riverbeds was significantly different from the terrestrial invertebrates collected within the riparian zone, indicating that the assemblages of TSAIs of dry riverbeds can be distinct. However, half of the taxa were shared between dry riverbeds and riparian zones. Three hundred and twenty invertebrate morphospecies from 24 orders were identified from 22 sites, of which 66 taxa were unique to dry riverbeds. Steward *et al.* (2011) suggested that some taxonomic groups, such as beetles from the genus *Mecynotarsus* (Fig. 2B), may indeed be specialists of dry riverbed habitats, as they were encountered in high numbers from sandy riverbeds, and rarely encountered from riparian zones. Beetles from this genus typically occur in sandy habitats such as dunes, and sandy riverbeds may be a new and undocumented habitat for them.

The taxonomic diversity and abundance of invertebrates in dry riverbeds of IRES can be high, and communities are typically dominated by ants, beetles, and spiders (Wishart, 2000; Steward *et al.*, 2011; Fig. 2). Similar patterns in invertebrate composition have been found in dry riverbeds around the world. High abundances of ants, beetles, and spiders were recorded in Australia (Steward, 2012), Italy (Steward, 2012), Namibia (Lalley *et al.*, 2006), USA (Moody & Sabo, 2017) and South Africa (Wishart, 2000), and high abundances of ants and springtails in New Zealand (Larned, Datry & Robinson, 2007). Wishart (2000) found that the invertebrate composition in dry riverbeds was diverse, with 19 invertebrate orders identified from just three sites. Lalley *et al.* (2006) sampled invertebrates in a Namibian desert and reported that

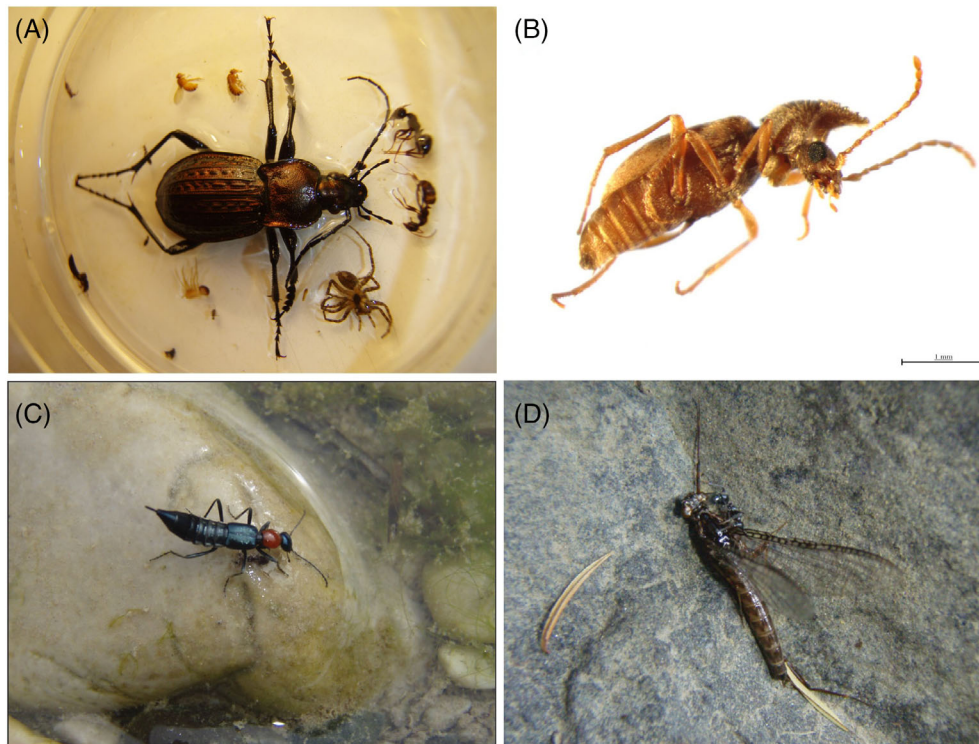


Fig. 2. Examples of terrestrial and semi-aquatic invertebrates (TSAIs). (A) Specimens from a sample collected from a dry channel in the Tagliamento River, Italy, with ants (Formicidae), beetles (Coleoptera), and spiders (Araneae) among others. (B) Beetle from the genus *Mecynotarsus*, showing the pronotal horn used for digging in sand. (C) Beetle (Staphylinidae) at the shoreline of the Tagliamento River, Italy. (D) Ant dragging a recently emerged mayfly from Wild Cattle Creek, Australia. Photographs by Alisha Steward.

the highest number of species occurred in a temporary river channel with shrub patches compared to six other habitat types they sampled.

(b) *Functional diversity*

TSAIs are involved in diverse ecosystem functions in IRES thanks to a high functional diversity derived intrinsically from the dual aquatic–terrestrial nature of IRES. IRES support a wide range of feeding groups, including predators, scavengers, herbivores, detritivores, and parasites (Williams, 1993), some of which may be able to switch between feeding strategies. Predators and scavengers are often the dominant functional classes of ground-dwelling invertebrates in IRES, especially in rivers with extensive areas of exposed gravel bars such as braided rivers (Steward, 2012; Steward *et al.*, 2017; R. Corti and T. Datry, unpublished data). Ground-dwelling predators and scavengers are the dominant feeding groups along river shorelines due to the presence of aquatic subsidies with high energy value. Terrestrial riparian predators inhabiting river banks such as wolf spiders (Lycosidae) and ground beetles (Carabidae) (Steward, 2012; Steward *et al.*, 2017) typically prey on emerging aquatic insects, which can make up 85% of their diets (Boumezzough & Musso, 1983; Paetzold, Schubert & Tockner, 2005; Greenwood & McIntosh, 2010). Consumption may also include pupal skins. Emerging insects

are susceptible to desiccation and physical injury, and some experience failed emergence and die due to unfavourable wind conditions or by using unsuitable substrates (Jakob & Suhling, 1999). Aquatic insects probably represent a crucial link for IRES food webs, but effects resulting from the loss of these invertebrates as IRES dry up have not yet been explored.

Detritivorous species are likely to be attracted by stranded organic matter such as dead and dying fish and aquatic invertebrates, with substantial consequences for nutrient cycling (Steward, 2012; von Schiller *et al.*, 2017) and trophic food webs (Boersma *et al.*, 2014; McIntosh *et al.*, 2017). An experimental study by Steward *et al.* (2012) using dead fish placed on dry riverbeds in Italy and Australia found that the fish were actively consumed or foraged by ants (Formicidae), beetles (Coleoptera), European wasps (*Vespula germanica*; Vespidae), fly larvae (Diptera) and slugs (Gastropoda). Other taxa associated with, but not actively consuming, the fish included ground beetles (Carabidae), Scarabaeoidea beetles, rove beetles (Staphylinidae) and adult flies (Diptera). Some taxa found on carcasses are, in fact, predators or parasites of the scavenging taxa (Catts & Goff, 1992).

Herbivores can be abundant in IRES. Many herbivorous species such as pygmy grasshoppers (e.g. *Paratettix aztecus* and *P. mexicanus*; Tettigidae) inhabit the shoreline of rivers and are likely to colonise the riverbed as it progressively dries. Algal-mat development (Steward, 2012; Steward *et al.*, 2017;

Fig. 3) and vegetation growth may constitute valuable energy sources for these herbivores.

Globally, TSAI assemblages in IRES share similar patterns, such as the dominance of predators and scavengers at the shoreline, and the composition of the ‘clean-up crew’ consisting of opportunistic predators and scavenging taxa during the drying phase (e.g. Williams & Hynes, 1977; Wishart, 2000; Lalley *et al.*, 2006; Langhans, 2006; Larned *et al.*, 2007; Steward, 2012; Dell, Alford & Pearson, 2014; Langhans & Tockner, 2014a; Corti & Datry, 2016; Sánchez-Montoya *et al.*, 2016). Beetles, ants, and spiders, for example, are common to IRES in most of the countries that have been sampled (Steward *et al.*, 2012, 2017; Fig. 2), with many shared taxonomic groups even at the family level. Ground beetles (Carabidae) were noted from Australia, France, Greece, Italy, Portugal, and South Africa; rove beetles (Staphylinidae; Fig. 2C) from Australia, Canada, France, New Zealand, Portugal, and Italy; and wolf spiders (Lycosidae) from Australia, Canada, France, and South Africa. These data represent a wide range of climatic zones – wet–dry tropical, subtropical, semi-arid, arid, humid continental, Mediterranean, and temperate – and suggest that a similar suite of functional groups (at the family level, at least) is found in IRES habitats worldwide, regardless of the local climate experienced.

TSAIs also play significant functional roles in IRES by processing organic matter and altering the structural complexity of the substrate. TSAIs such as earthworms (Oligochaeta) can recycle nutrients within the riverbed during the dry phase. Earthworms also enhance water infiltration through tunnelling and burrowing (Pimentel *et al.*, 1995). *Mecynotarsus* (Anthicidae) beetles use their pronotal horn to dig through sand (Hashimoto & Hayashi, 2012; Steward, 2012; Fig. 2B), and it is expected that these beetles and other TSAI taxa that tunnel, burrow, or dig into riverbeds have similar effects to those of earthworms.

(2) Micro-habitats used by TSAIs

IRES are dynamic ecosystems, with aquatic and terrestrial habitats expanding, contracting, and fragmenting through time (Stanley *et al.*, 1997; Datry *et al.*, 2016, 2017; Boulton *et al.*, 2017; Fig. 4). TSAIs can inhabit intermittent rivers and ephemeral streams during all hydrological phases, including floods (Corti & Datry, 2012; Steward *et al.*, 2017; Fig. 4). They can be found taking refuge in emergent vegetation or on higher ground (Fig. 5), drifting in floodwaters, and ‘rafting’ on debris in the advancing wetted fronts (Corti & Datry, 2012). When surface water is present, they can be found at the edge, or ‘shoreline’, of rivers, streams, and isolated pools (Figs 2 and 3), on the surface of exposed gravel

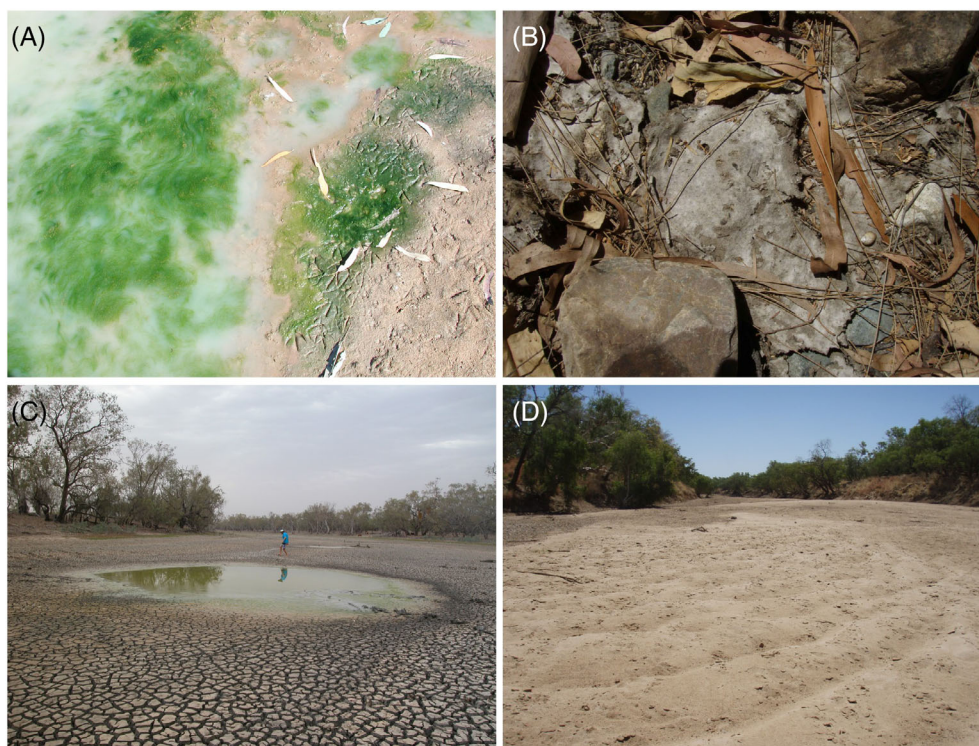


Fig. 3. Examples of terrestrial and semi-aquatic invertebrate (TSAI) habitats in intermittent rivers and ephemeral streams (IRES). (A) The shoreline of Warranee Waterhole in Cooper Creek, Australia, showing stranded algae. (B) Dried algal mat, leaf litter, and cobbles in the dry riverbed of Oaky Creek, Australia. (C) Cracking clay around an isolated pool in Cooper Creek, Australia. (D) Dry, sandy riverbed in the Cloncurry River, Australia. Photographs A and C by Jonathan Marshall; photographs B and D by Alisha Steward.

bars, and within the unsaturated gravel of the channel (Langhans & Tockner, 2014b). When rivers and streams are dry, TSAIs can inhabit the surface and interstitial spaces of dry riverbeds (Steward *et al.*, 2011). At any time, TSAIs can inhabit riparian zones and floodplains (Steward *et al.*, 2011).

The progression from wet to dry is sometimes gradual, although in the wide channels of some desert rivers entire riffles, runs, and pools can dry rapidly in a day (Stanley *et al.*, 1997). Similarly, 100–300 m sections of gravel-bed rivers in New Zealand have been observed to dry in a day (Davey, Kelly & Biggs, 2006). TSAIs can use riverbeds once surface water has disappeared, but also for many months, or even years, following drying (Steward, 2012). TSAIs can inhabit coarse and fine riverbed substrates (Fig. 3), and substrates that are a combination of the two (Steward *et al.*, 2011, 2017). Coarse substrates such as boulders, cobbles, gravels, woody debris, and leaf litter have larger interstitial spaces available for invertebrates to inhabit than finer substrates such as sand and silt. Moring & Stewart (1994) found that the abundance of prey for streamside and riparian wolf spiders (Lycosidae) was higher in coarser (rock-cobble) than finer (sand-cobble) substrates and, as a result, the coarser substrates supported a higher abundance and higher species richness of wolf spiders. Fine substrates, however, can be preferred by taxa capable of digging. For example, beetles from the anthicid genus *Mecynotarsus* may dig to avoid predators, extreme temperatures, or humidity, or to forage (Hashimoto & Hayashi, 2012; Fig. 2B). The deep furrows provided by cracking clays can also provide habitat for TSAIs (Fig. 3C).

Large, wide, dry riverbeds can be harsh, exposed places devoid of vegetation that experience higher fluctuations in air temperature and solar radiation, and lower humidity, than that provided by shaded riparian zones (Steward, 2012; Langhans & Tockner, 2014a). Therefore, TSAIs may need to withstand extreme environmental conditions in such habitats; however, the nature of the river margin, the distance from the river channel, and the pattern of drying can influence this. For most eukaryotic organisms, 60°C is their upper thermal tolerance (Tansey & Brock, 1972). A study of Australian dry riverbeds found that ground temperatures exceeded 60°C more frequently and for a longer duration than in adjacent riparian zones, and that dry riverbeds were sometimes up to 20°C hotter than riparian zones (Steward *et al.*, 2017). Similarly, smaller diel temperature ranges have been recorded from riparian zones than from exposed riverbed gravels in Italy and Switzerland (Tonolla *et al.*, 2010). Ground temperatures of over 60°C have also been recorded in the dry riverbed of the Kuseb River, Israel (Holm & Edney, 1973).

Dry riverbeds are physically harsher places for biota than riparian zones (Steward *et al.*, 2017), and are physical pressures that may influence the activity of TSAIs. Invertebrates may have behavioural adaptations that involve the use of daytime refuges; for example, some desert beetles can find tolerable temperatures by retreating underground or moving to the base of vegetation during the hottest times of the day

(Holm & Edney, 1973). Langhans & Tockner (2014b) found terrestrial arthropods inhabiting the unsaturated sediments of a gravel-bed river down to 1.1 m all year round, and they suggest that temperatures within the sediment are more stable throughout the year than those at the surface. Riverbed sediments, therefore, may act as a temperature refuge for TSAIs. It is also likely that humidity is more favourable within the sediments than above them.

Large mats of stranded algae can cover the dried beds of IRES (Strandine, 1941; Steward *et al.*, 2017; Fig. 3A, B). The microhabitat underneath such algal mats can remain cool and moist and may act as a temperature and/or humidity refuge for TSAIs, prolonging the survival of aquatic and semi-aquatic invertebrates lacking physiological or morphological adaptations to resist desiccation (Strandine, 1941). A study by Strandine (1941) found that algal mats were inhabited by an average of 6600 living aquatic snails per m² of algae; however, the extent to which algal mats are used by TSAIs remains unknown.

TSAIs can also inhabit leaf litter and woody debris, including flood debris, branches, and logs (Steward *et al.*, 2017; Fig. 3B). TSAIs such as beetles and ants have even been found to inhabit fish carcasses on dry riverbeds – some invertebrates consuming the dead fish, whilst others were predators of these consumers (Steward, 2012). Carcasses can provide nutrients to different assemblages of terrestrial consumers through time (including necrophages, omnivores and parasites), depending on the stage of breakdown.

(3) Adaptations of TSAIs to inundation and drying

While drying of surface water is a primary driver of the assemblage composition of aquatic invertebrates (Datry *et al.*, 2014b), inundation is arguably a strong driver of the composition of TSAIs in IRES, as reported in riparian zones (Lambeets *et al.*, 2008), alluvial forests (Bonn & Schröder, 2001), floodplains (Junk, Bayley & Sparks, 1989; Ballinger, MacNally & Lake, 2005; Datry *et al.*, 2014a) and wetlands (Plum, 2006). During the first flush of river rewetting, flow velocities can be as high as 3 m s⁻¹, with most values in the range of 1–2 m s⁻¹ (Jahns, 1949; Sharma, Vangani & Choudhari, 1984; Reid, Laronne & Powell, 1998; Jacobson *et al.*, 2000; Doering *et al.*, 2007). Terrestrial invertebrates can be entrained by swiftly advancing wetted fronts (Jacobson *et al.*, 2000; Larned *et al.*, 2010) during these sudden terrestrial–aquatic transitions, as water may move too fast to allow terrestrial invertebrates to escape to adjacent riparian areas (Boumezzough & Musso, 1983). These events are catastrophic for local TSAI communities if they are not followed promptly by drying, because non-aerial TSAIs often have poor dispersal capacities in aquatic environments, and some TSAI taxa may have a relatively low resistance to submersion (Bogan *et al.*, 2017), although some taxa such as the ground beetle *Cicindela togata* have been found to survive submersion and anoxia after more than 6 days (Hoback *et al.*, 1998).

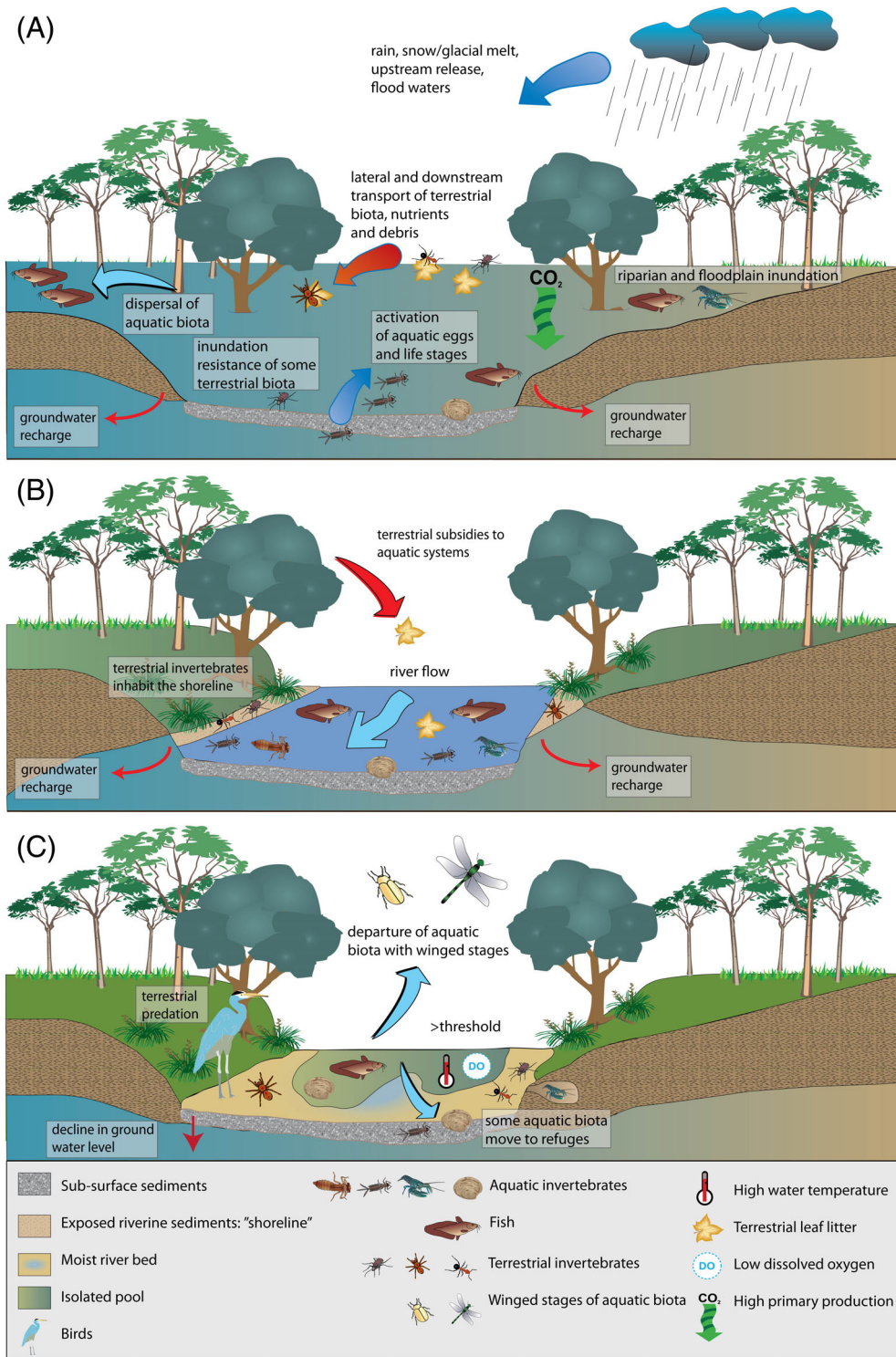


Fig. 4. Conceptual diagrams of aquatic-dominated stages of intermittent rivers and ephemeral streams (IRES): (A) an overbank flood; (B) a flow event; (C) cessation of flow; (D) loss of surface water; (E) short-term dry; and (F) long-term dry. Note that the transition between stages can be gradual through time.

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Rewetting is not necessarily catastrophic for all TSAIs, however, and semi-aquatic taxa are likely to survive rewetting better than fully terrestrial taxa. Resilience and

resistance traits to flooding have been identified for many terrestrial taxa from riparian habitats such as spiders (Araneae), ground beetles (Carabidae), and true bugs (Hemiptera), and

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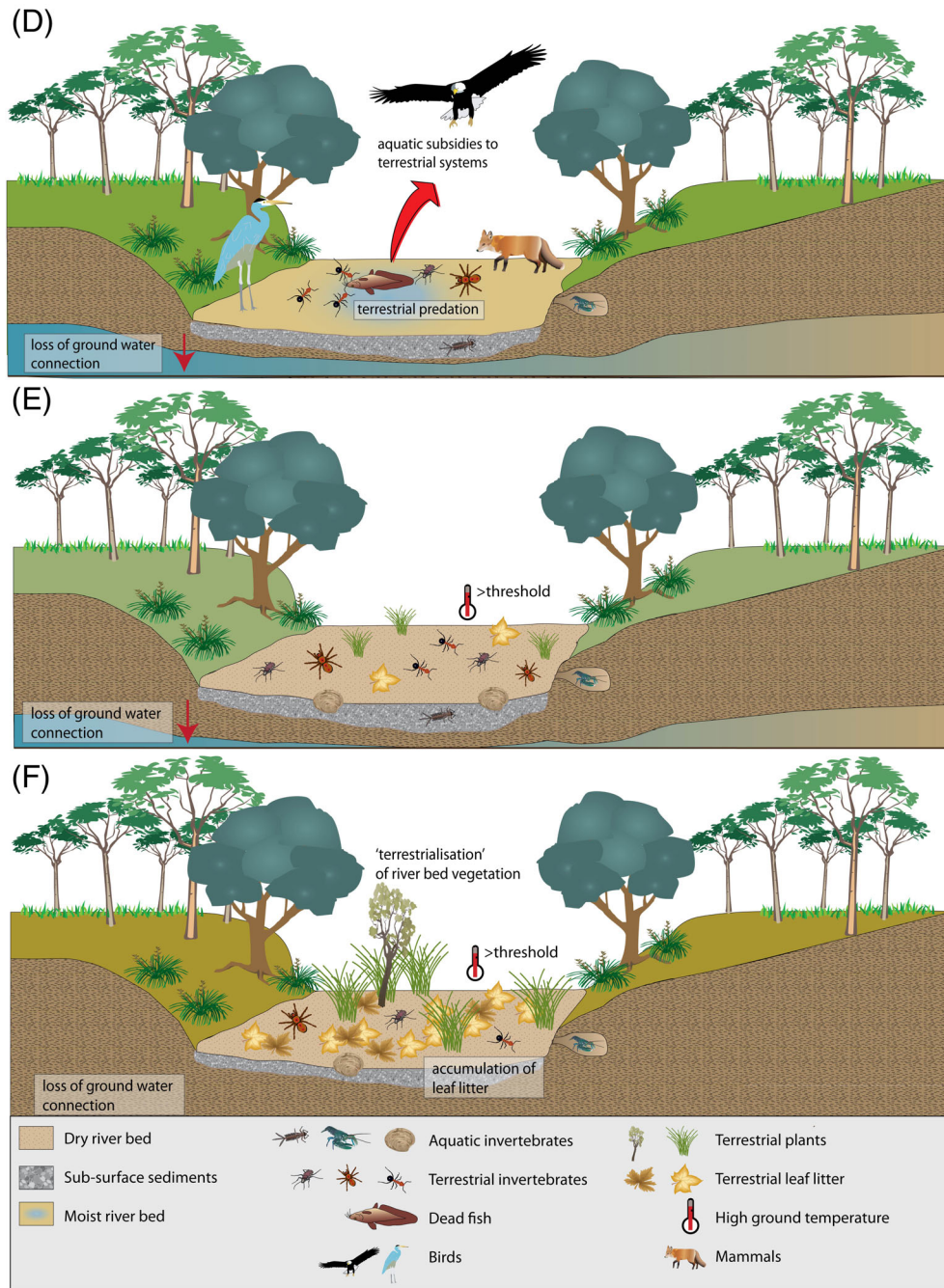


Fig. 4 (Continued)

these traits appear to also apply in IRES. Resistance traits include mechanisms such as flight, swimming, flotation, climbing onto floating organic matter, and respiration through air bubbles (Andersen, 1968; Boumezzough & Musso, 1983; Lytle & White, 2007; Lamberts *et al.*, 2008). Some ground beetles (Carabidae) can survive completely submerged for more

than 20 h (Boumezzough & Musso, 1983; Lamberts *et al.*, 2008; Kolesnikov, Karamyan & Hoback, 2012). At least one third of the 71 terrestrial taxa washed downstream in an advancing wetted front in the Albarine River in France survived submersion and could therefore potentially colonise downstream habitats (Corti & Datry, 2012).



Fig. 5. Ants, spiders, and other terrestrial biota seeking higher ground during a flood in the Bokhara River, an intermittent river in north-western New South Wales, Australia. Photograph used under licence © Stuart McEvoy/Newspix.

Resistance can also involve behavioural mechanisms. For example, some hemipterans in desert streams use rainfall cues to anticipate and escape flash floods (Lytle, 1999; Lytle & Smith, 2004). In addition, many terrestrial taxa are strong fliers (Bonn, 2000) – most ground beetles (Carabidae) can fly (Boiteau, Bousquet & Osborn, 2000), some for distances exceeding 1 km (Meijer, 1974; Kotze, 2008). Re-establishment of terrestrial communities upon drying may therefore be rapid (Hering *et al.*, 2004). In the Selwyn River in New Zealand, for instance, a steady fivefold increase was seen in the density of ground-dwelling invertebrates during the 90 days following complete riverbed drying, and taxonomic richness rapidly increased 1.5-fold within the first 7 days of drying (R. Corti and T. Datry unpublished data).

River drying and decreasing soil moisture have predictable consequences for TSAI behaviour (Davis & DeNardo, 2009) and physiology (Hadley, 1994), and may particularly influence communities in dryland regions (McCluney & Sabo, 2012). For instance, drying altered the composition and reduced the diversity of riparian terrestrial communities in a desert stream, primarily because of decreasing water availability (McCluney & Sabo, 2012).

Drying also affects TSAIs by reducing aquatic prey availability. As aquatic prey became rarer during flow cessation in IRES in southern New Zealand, for example, there was increased competition and presumably cannibalism, decreases in daily prey consumption, as well as a subsequent change in size class and spatial structures of populations of pisaurid spiders (*Dolomedes aquaticus*) (Greenwood & McIntosh, 2010). TSAIs may switch to a diet composed mainly of terrestrial prey during dry periods (Sabo & Power, 2002; Briers *et al.*, 2005). River regulation of the Rio Grande, New Mexico, led to a twofold decrease in aquatic invertebrate

densities, and this subsequently resulted in terrestrial communities being less diverse and less abundant along riparian zones of regulated compared with unregulated sections (Kennedy & Turner, 2011). It is likely that direct and indirect effects of drying interact synergistically. Drying directly reduces the number of terrestrial riparian predators and prey, and indirectly reduces the number of terrestrial predators through the reduction of aquatic prey (Hagen & Sabo, 2012; Allen *et al.*, 2014). Hence, the effects of drying may be particularly significant for predaceous species.

The effects of river drying on TSAIs are likely to depend on climate. In the temperate Albarine River in France, only weak effects of river drying were found on riparian arthropods at the assemblage level (Corti & Datry, 2014), and taxonomic richness was even higher at intermittent sites compared to perennial sites. Hot summer temperatures in the Albarine River, combined with sufficient inputs of rainwater, may stimulate a pulse in riparian primary production, which could in turn support riparian primary consumers (Marczak, Hoover & Richardson, 2007; Klemmer & Richardson, 2013). Abundant primary consumers could allow some predators to be less dependent upon aquatic prey, or to shift their diet from aquatic to terrestrial prey as surface water disappears (Paetzold *et al.*, 2005). Furthermore, during the dry phase, rain, dew, and vegetation cover can provide sufficient moisture and drinking water for riparian arthropods.

Life-history characteristics may be another possible reason for the weak effect of river drying in the Albarine River. Activity patterns of TSAIs may align with unfavourable seasonal conditions, where species may have completed their seasonal life cycle in preparation for subsequent diapause before the dry phase (Lovei & Sunderland, 1996). Life-history characteristics may thus favour the resistance of TSAIs to the decline in aquatic resources and changes in environmental conditions when the river dried.

Unlike aquatic invertebrates (Stubbington *et al.*, 2009, 2017; Schriever & Lytle, 2016), TSAIs may not have strong relationships with the spatial or temporal variability of drying events. This difference is due to resilience and resistance traits of TSAIs, which enable the invertebrates to seek refuge in, and recolonise from, relatively stable upland habitats. Nonetheless, flow cessation and rewetting events affect TSAI assemblages in predictable ways. For example, long flow durations may eliminate TSAIs that lack inundation resistance, whereas rewetting and drying events interrupt and reset terrestrial taxa succession.

(4) Interactions of TSAIs with aquatic biota

As a riverbed dries and loses surface water, aquatic biota such as fish, invertebrates, macrophytes, and algae (Fig. 3) can become stranded if they cannot migrate to other waters or find drought refugia. Stranding and mortality of aquatic biota can occur during natural, seasonal drying of surface waters, or droughts (Larimore, Childers & Heckrotte, 1959; Lowe-McConnell, 1964; Chapman & Kramer, 1991; Stanley *et al.*, 1997), or by anthropogenic means, such as the

intentional cessation of flow downstream of dams or weirs (Bishop & Bell, 1978). The assemblage of TSAIs scavenging this aquatic food source has been collectively described as the ‘clean-up crew’ (Abell, 1984), and can comprise invertebrates, reptiles, birds, and mammals (Larimore *et al.*, 1959; Williams & Hynes, 1976; Abell, 1984; Boulton & Lake, 1992; Stanley *et al.*, 1994; Williams, 2006). The drying phase of IRES therefore represents one of the mechanisms for the aquatic subsidy of terrestrial food webs.

Aquatic subsidies from rivers and streams can flow into adjacent terrestrial ecosystems *via* the movement of aquatic biota. For example, many insects with aquatic larvae or nymph stages emerge as winged adults and are preyed upon by terrestrial consumers (Fig. 2D). They can contribute significantly to the diets of web-weaving spiders (Collier, Bury & Gibbs, 2002; Sanzone *et al.*, 2003), ground-dwelling spiders (Collier *et al.*, 2002; Sanzone *et al.*, 2003; Paetzold *et al.*, 2005), ground beetles (Hering & Plachter, 1997; Paetzold *et al.*, 2005), and rove beetles (Paetzold *et al.*, 2005). Stranded algae at the shoreline of rivers and streams (Fig. 3A, B) are another form of aquatic subsidy utilised by terrestrial invertebrates. Shoreline pygmy grasshoppers graze almost exclusively on stranded filamentous algae during summer, with 80–100% of the carbon content of their tissues derived from this source (Bastow *et al.*, 2002).

TSAIs can influence the diet of the aquatic fauna after rewetting. The large number of terrestrial invertebrates washed downstream in the advancing wetted fronts probably also influences the diet of downstream fish by providing important energy subsidies and by cascade chains, which could affect river food-web dynamics (Nakano, Miyasaka & Kuhara, 1999; McIntosh *et al.*, 2017). For example, during flow pulses and submersion of riverine habitats, fish move towards the inundated floodplain and seasonal tributaries, benefiting from the higher densities of terrestrial invertebrate prey (Limm & Marchetti, 2009; Eberle & Stanford, 2010). In IRES, fish survive drying periods by migrating towards perennial refugia, from which they can recolonise surrounding habitats upon rewetting (Davey & Kelly, 2007). Importantly, the quantity of terrestrial invertebrates and particulate organic matter swept by advancing wetted fronts may constitute valuable food resources for aquatic food webs at downstream confluences and reservoirs, as well as a feeding bonanza for birds, reptiles, and mammals (Sánchez-Montoya *et al.*, 2017), potentially providing a substantial transfer of energy into the adjacent riparian and terrestrial zones. Thus, the exchanges of material and organisms across aquatic and terrestrial ecosystems may occur far away from the zones where they originated. From a management perspective, the terrestrial invertebrates and particulate organic matter in advancing wetted fronts represent a concern for mitigating eutrophication of downstream waters.

(5) Space–time dynamics of TSAI communities

Rivers and their surrounding terrestrial environment are intimately linked. The margins of rivers are aquatic–terrestrial ecotones: that is, they are dynamic, transitional zones, which

are neither spatially nor temporally stable; nor are they simply static zones where aquatic and terrestrial communities join (Pinay *et al.*, 1990; Naiman, Décamps & Pollock, 1993). The boundaries of these ecotones are constantly changing as the shoreline expands and contracts due to fluctuating flow conditions (Stanley *et al.*, 1997; Tockner, Malard & Ward, 2000; Doering *et al.*, 2007), and the distribution of aquatic and terrestrial biota changes as a result. The transition of a temporary riverbed from an aquatic habitat to a terrestrial one represents an important, but poorly explored, temporal aquatic–terrestrial ecotone.

Following the alternating wet and dry phases in IRES, TSAI assemblages are dynamically organised within river networks. First, succession occurs locally as the riverbed dries and rewets. A study by Steward *et al.* (2012) showed that semi-aquatic invertebrate taxa, such as velvet water bugs (Hebridae), are typically present until the bed undergoes complete drying. As the dry spell continues, the assemblage composition becomes more ‘terrestrial’ with fewer or no semi-aquatic taxa present in an active stage, although aquatic and semi-aquatic taxa may persist as desiccation-resistant life stages (Datry, 2012; Bogan *et al.*, 2017; Stubbington *et al.*, 2017). The invertebrates of drying riverbeds do not always appear to be a subset of those in the riparian zone, and some riverbed communities remain unique from adjacent riparian forest communities (Lalley *et al.*, 2006; Steward *et al.*, 2011; Steward, 2012; Corti & Datry, 2014). The resumption of flow in the study by Steward *et al.* (2012) coincided with the loss of some ant, beetle, bug, mite, and springtail taxa.

Although less explored, these local successions are embedded within regional-scale population dynamics of TSAIs, which could define spatial differences in local successions. This is because rewetting events might act as downstream dispersal paths for many species that are able to survive inundation temporarily (Corti & Datry, 2012). However, very few attempts to explore the metacommunity dynamics of TSAIs are available and results are still unclear (Corti & Datry, 2016; Sánchez-Montoya *et al.*, 2020). Lateral mass dispersal from adjacent terrestrial habitats could outweigh longitudinal dispersal along the river networks, except during rewetting events which would redistribute TSAIs downstream. Thus, depending on the location and timing of drying, sources of colonists of dry riverbeds could strongly differ spatially.

Dry riverbeds may provide suitable habitats that allow for the dispersal of terrestrial and semi-aquatic invertebrates, if they are cooler and more humid than the surrounding landscapes due to the presence of riparian trees. This may be particularly important in arid zones. Marshall *et al.* (2006) suggest that it is unlikely that adult aquatic insects could survive for long away from waterholes and the areas immediately fringing them in Cooper Creek, Australia – an arid, dryland river system. In this system, Marshall *et al.* (2006, p. 72) suggest that ‘overland movement of aquatic taxa is unlikely to be a major form of dispersal because of the hot, arid nature of the surrounding landscape, which has a high evaporative potential and is likely to represent an insurmountable barrier to many aquatic and riparian insects’.

III. VALIDATION OF THE CONCEPTUAL MODEL

Conceptual models can be qualified through targeted data collection. TSAIs are ideal for testing predictions as they are common, ubiquitous, taxa-rich, cheap and easy to sample in terms of sampling effort and laboratory processing, and can inhabit IRES at every hydrological stage – from floods and flow events to long-term dry periods. We tested our predictions about the responses of terrestrial and semi-aquatic invertebrates to wetting and drying as presented in Fig. 1 using two case studies: Oaky Creek, a subtropical stream in Australia; and the Albarine River in France. The studies investigated the temporal changes in taxon richness and abundance, with the expectation that these metrics would decline as the dry period progressed. We then used the findings to validate our model.

(1) Case study of TSAIs from a subtropical stream in Australia

We sampled Oaky Creek (−27.1611, 152.2818) in subtropical Queensland, Australia, for TSAIs as the riverbed dried and rewetted over 1 year (Steward, 2012). Rainfall in the area is mostly associated with subtropical lows and storms, resulting in an unpredictable flow regime. The active channel is less than 5 m wide, and the site has a dense riparian canopy of native species. The riverbed substrate is coarse and dominated by cobbles, pebbles, and gravel. For more information on site details and the sampling method see Steward *et al.* (2012).

TSAIs were collected as the riverbed dried in July, August, September, and December of 2009, and then in August of 2010 after flow resumed. Samples were collected using pitfall traps set into the dry riverbed, and within the riparian zone at 0, 5, 10, 15 and 20 m from the edge of the riverbed, along three replicated transects. Pitfall traps were used to sample TSAIs during flowing stages by deploying the traps into dry ‘islands’ or exposed riverine sediments where available in the channel. Traps were set for approximately 24 h.

The loss of aquatic habitat as Oaky Creek dried resulted in a gain of terrestrial habitat and increased TSAI taxon richness and abundance (Fig. 6A, B). These increases could initially be due to the increased availability of aquatic resources for consumption by predators and scavengers as surface water disappeared, such as dead fish and aquatic invertebrates, or as a result of the expansion of the terrestrial habitat into the riverbed making new terrestrial habitats available, such as filamentous algal mats and riverbed cobbles. This was supported by our data – as the riverbed dried, the first taxa to be collected largely comprised predators, such as wolf spiders (Lycosidae), ants (Formicidae), bugs (e.g. Hebridae), and wasps (Hymenoptera). These predators may have been consuming dead and dying aquatic biota, aquatic biota actively searching for drought-refuges, or TSAIs colonising the newly available terrestrial habitat. Drying may also have provided a cue for the hatching of eggs or the emergence of terrestrial life stages that prefer dry conditions.

The lowest abundance of TSAIs was recorded in August 2010, which could be explained by the reduced area of dry bed habitat available, as flow had resumed, and dry bed habitat was only represented by exposed riverine sediments as ‘islands’ within the channel and along the edges (Fig. 6B).

(2) Case study of TSAIs from a temperate stream in France

We sampled the Albarine River in temperate France for TSAIs as the riverbed dried, rewetted, and dried again over 1 year (Corti & Datry, 2016). The Albarine River is in eastern France and drains a 313 km² catchment. The river flows for 45 km through the Jura Mountains, then 15 km across an alluvial plain to its confluence with the Ain River. On the alluvial plain the river is 1–14 m above the regional water table, and the river loses flow to the underlying vadose zone and aquifer at an average rate of 0.4 m³ s^{−1} km^{−1}. The entire alluvial plain reach is intermittent due to the rapid seepage loss. Descriptions of the climate, geology and geomorphology of the Albarine River catchment are given in Datry (2012). Flow ceases during spring of most years at the confluence with the Ain River, and the terminus of flow moves upstream over the summer. Flow resumption along the entire intermittent reach generally occurs in late autumn/early winter. Flow intermittence and average annual dry-event duration and frequency all increase with distance downstream. At the downstream end of the intermittent reach, annual flow intermittence (the percentage of the year without water) ranges from 50 to 90%. For more information on site details and the sampling method see Corti & Datry *et al.* (2016).

TSAIs were collected in April and June of 2010 before all the sites dried, and then when all the sites were dry without rewetting events occurring in between – in August and October of 2010 (Corti & Datry, 2016). Samples were then collected in December 2010 when flow had resumed. The final samples were collected in February 2011 within the first weeks of dry conditions after ~1 month of flowing conditions. Samples were collected from four reaches using pitfall traps set into riverbed habitats, and within the riparian zone (Spence & Niemelä, 1994; Corti, Larned & Datry, 2013). At each reach, sampling took place at three transects, and seven pitfall traps were installed at each transect. This design resulted in three pitfall traps in dry riverbeds and four pitfall traps in riparian zones distributed on either side of the riverbed. As for the Australian case study, pitfall traps were used to sample TSAIs during flowing stages by deploying the traps into dry sections of the channel where available. Traps were set for 7 days.

Before the riverbed dried, taxonomic richness and abundance declined between the first two sampling periods (Fig. 6C, D). Once the riverbed dried, both taxonomic richness and abundance increased. This pattern was also seen in the riparian zone TSAI assemblages; however, in both habitats, richness and abundance declined 2 months after drying, but not below the levels recorded during flowing conditions. Once flow had returned to all riverbed sites,

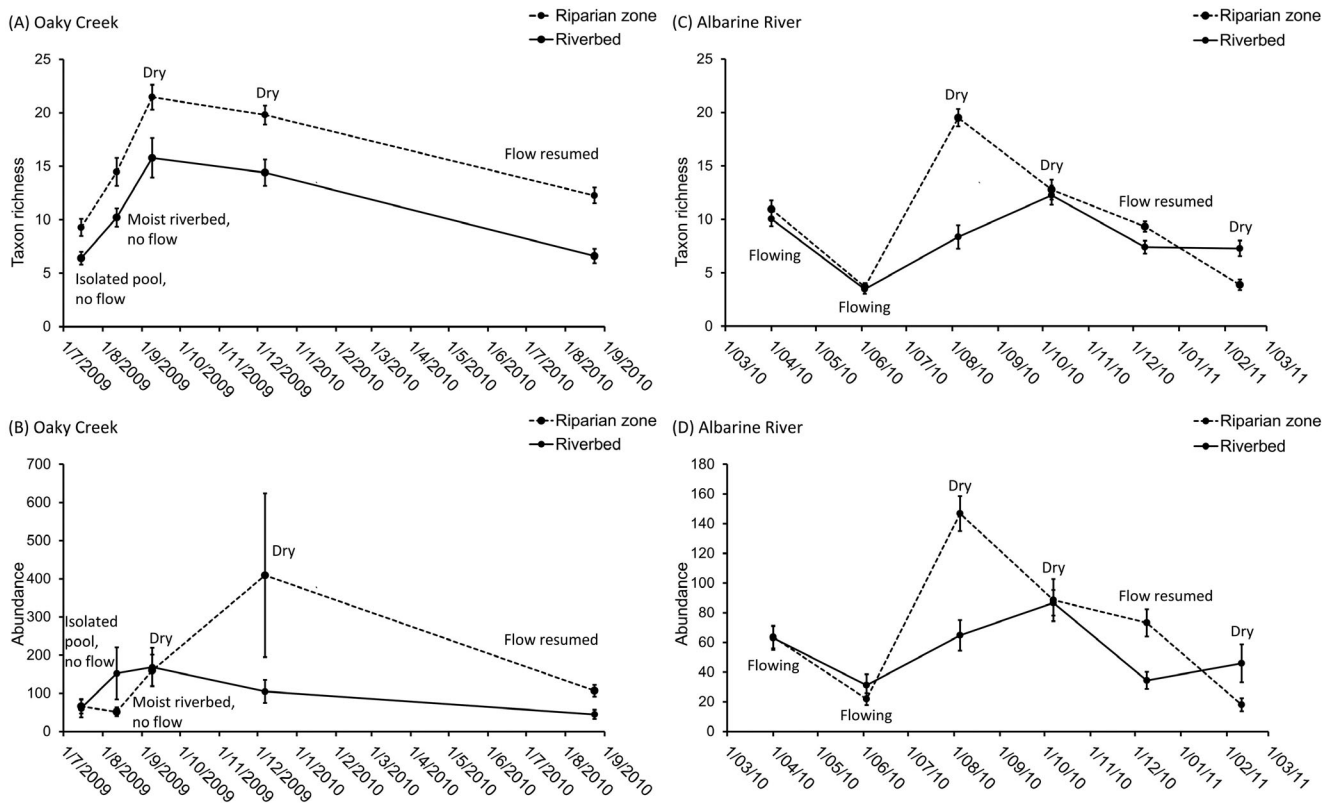


Fig. 6. Taxon richness and abundance of terrestrial and semi-aquatic invertebrates in riverbeds (solid lines) and riparian zones (dashed lines) over time during drying and rewetting in (A, B) Oaky Creek, Australia (A, taxon richness; B, abundance), and (C, D) Albarine River, France (C, taxon richness; D, abundance). Error bars are ± 1 standard error.

taxonomic richness and abundance continued to decline. Once the riverbed had completely dried again, both taxonomic richness and abundance increased.

(3) Summary of model validation

Our results from both a sub-tropical and a temperate stream support our conceptual model presented in Fig. 1, showing that IRES continuously provide habitat for terrestrial and semi-aquatic invertebrates over time, regardless of whether the channel is dry or wet, acknowledging that the quality and quantity of this habitat can vary substantially. At both sites we saw an increase in the taxon richness and abundance of TSAIs with riverbed drying, with values of these metrics decreasing as flow resumed. This pattern was also true of TSAI assemblages from riparian zones.

We acknowledge that when streams cease flowing, vegetation in the riparian zone could become a food source for terrestrial invertebrates. We might have expected riparian invertebrate abundance and richness to decline over the dry period when food resources could be most scarce. However, at both sites, we saw increases in invertebrate abundance and richness in both dry riverbeds and riparian zones. This increase coincided with warmer seasons, and warmer times of year could be associated with increased

growth of invertebrates and plants. We acknowledge that this might not be the case if we were working in other climates, such as Mediterranean climatic zones, and the availability of food sources is a knowledge gap that could be investigated.

In addition to TSAIs, we also recognise that other suites of biota can colonise and inhabit IRES – from the obvious aquatic biota during wet phases, such as fish, aquatic macro-invertebrates, amphibians, and algae, to terrestrial and semi-aquatic biota during dry phases, such as mammals and terrestrial vegetation. However, there is much overlap between wet and dry stages, and many biota that utilise IRES habitats have life-history, behavioural, and/or physiological strategies to survive inundation or desiccation. Some biota can persist in IRES at any hydrological stage, whereas others need to migrate or disperse to more suitable habitats. This is a knowledge gap that needs to be verified with data.

IV. PERSPECTIVES

(1) Managing IRES to preserve TSAI diversity and their ecological functions

Recognition of the conservation significance of IRES is limited (Acuña *et al.*, 2014), even though IRES currently

comprise more than half of river networks worldwide (Datry *et al.*, 2014c) and provide unique habitats that support TSAI species of high conservation value (Sadler, Bell & Fowles, 2004; Bates *et al.*, 2009; Langhans & Tockner, 2014a). As a consequence, examples of catchment-scale conservation and adequate management of IRES are rare (Leigh *et al.*, 2016; Kingsford *et al.*, 2017; Lake, Bond & Reich, 2017). Neither the diversity of habitats nor the associated fauna (aquatic, semi-aquatic and terrestrial) of IRES are currently recognised in most protective legislations and policies (Acuña *et al.*, 2014; Fritz, Cid & Autrey, 2017). For instance, the European Water Framework Directive (WFD; European Commission, 2000) ignores the existence of IRES altogether, as it does not discriminate between intermittent and perennial rivers. The set of river types in the WFD needs to be extended explicitly to include IRES as a first step towards acknowledging the value of IRES and their characteristics, in particular the dry phases, and adaptive assessment methods need to be developed that consider hydrological variability (Nikolaidis *et al.*, 2013; Prat *et al.*, 2014).

IRES are typically ignored in ecological river assessment and monitoring programs (Steward *et al.*, 2018). Consequently, determining their natural or ‘reference’ conditions has not received much attention and remains difficult (Prat *et al.*, 2014), as does assessing their ecological condition (Datry, Arscott & Sabater, 2011a). This may also explain the current lack of knowledge of how to differentiate between the effect of natural and anthropogenic causes of intermittent flow on biodiversity (Boulton, 2014; Mazor *et al.*, 2014; Lake *et al.*, 2017). In turn, the poor understanding of how TSAIs respond to human activity makes it difficult to identify reference sites. Many researchers stress the need for new or modified assessment methods to address these challenges (Boulton *et al.*, 2000; Sheldon, 2005; Dallas, 2013). TSAIs have been listed as promising bioindicators of ecological condition for IRES by Leigh *et al.* (2016), as well as hyporheic invertebrates (Leigh *et al.*, 2013) and microbial biomarkers (Wilkes *et al.*, 2013).

Together with assessing the tolerance and preferences of aquatic invertebrates (Chessman & Royal, 2004), TSAIs may be the most promising avenue for the future biological assessment of IRES, since TSAIs persist long after hyporheic refuges cease to exist. Andersen (1999) suggests that criteria for selecting appropriate biological indicators should relate to an indicator’s (i) distribution, abundance, and richness; (ii) functional importance in ecosystems; (iii) sensitivity to environmental change; (iv) ability to be sampled, sorted and identified; and (v) responses to change. TSAIs meet most of these criteria as they are distributed in IRES worldwide, can be found in high abundances, are taxonomically diverse, and can be easily and cheaply sampled and sorted (Steward *et al.*, 2018). Andersen (1999, p. 61) argues that ‘a primary challenge with indicator taxa consequently lies in distinguishing anthropogenic perturbation (i.e., an ecologically meaningful “signal”) from natural variability (background “noise”)’. It is therefore necessary to investigate whether TSAIs respond to anthropogenic disturbance to meet the fifth criterion above. Recent research shows that this is the

case, with TSAIs responding negatively to the impacts of livestock and feral mammals (Steward *et al.*, 2018).

Gathering spatial data on the distribution of TSAIs across different biomes is one step towards their use as biological indicators. These data can be used to analyse the relationships between the occurrence of TSAIs and the ecological health of IRES. The water quality, flow regime, and catchments of many IRES have been subjected to intense, long-term human modification (Chiu *et al.*, 2017), and the ecosystems that we assess now and into the future will most likely have the characteristics of ‘novel’ ecosystems (Hobbs, Higgs & Harris, 2009), differing substantially from their unmodified or ‘natural’ condition. As restoring such systems back to their ‘natural conditions’ is usually impossible, Leigh *et al.* (2016) suggest establishing realistic policy goals that recognise this fact. Nonetheless, managing IRES appropriately will benefit TSAIs. Efforts should concentrate on improving or maintaining local and regional habitat heterogeneity through the promotion of natural flow and sediment regimes (Bonn & Kleinwächter, 1999; Eyre, Luff & Phillips, 2001; Manderbach & Framenau, 2001; Adis & Junk, 2002; Eyre, Woodward & Luff, 2002; Sadler *et al.*, 2004). Meta-populations of IRES specialists will only be sustainable if unconstrained floodplain segments, multiple gravel bars and associated ecotones are available – a catchment-level approach is critical (Sadler *et al.*, 2004).

The ecological functions that TSAIs provide should be preserved by the successful management of IRES. In addition to contributing to the biological diversity of IRES, TSAIs have been shown to play other important roles such as providing food for terrestrial mammals, reptiles, amphibians, and birds during the dry phase, and food for aquatic biota once the riverbed has rewetted. TSAIs, therefore, underpin crucial trophic linkages between the wet and dry phases of IRES. TSAIs can transfer energy from aquatic systems to the adjacent riparian zones by consuming emerging and stranded aquatic biota. TSAIs can also enhance water infiltration through tunnelling, burrowing and digging, and they can recycle nutrients within the riverbed substrate. Anthropogenic impacts on IRES that reduce the taxonomic diversity and abundance of TSAIs will, therefore, alter the linkages between aquatic and terrestrial food webs, as well as limit the availability of TSAIs as food for terrestrial animals. Steward *et al.* (2018) investigated the consequence of anthropogenic alterations to TSAI communities, finding that the impacts of cattle and feral mammals reduced the taxonomic richness and abundance of terrestrial invertebrate assemblages in dry riverbeds.

(2) Knowledge gaps and research questions: ecosystem services of TSAIs

Due to their high functional diversity, arthropods, in general, play a significant role in the provision of a range of ecosystem services (ESs). However, current knowledge is relatively scarce and shows large gaps for some functional and taxonomic groups (Noriega *et al.*, 2018; Schowalter, Noriega &

Table 1. Knowledge gaps and research questions relating to terrestrial and semi-aquatic invertebrates (TSAIs) and the habitat continuum model

Knowledge gaps and research questions	Example topics for further research
What ecosystem services are provided by TSAIs?	<ul style="list-style-type: none"> • Recycling of organic matter • Aeration of soil due to digging • Biological control of pests in crops planted adjacent to river channels • Provision of food to aquatic and terrestrial consumers, contributing to both aquatic and terrestrial food webs
How does the habitat continuum model apply to other regions of the world?	<ul style="list-style-type: none"> • How might the habitat continuum model look in IRES from different climatic regions?
What are the effects of human activities on TSAIs, including climate change?	<ul style="list-style-type: none"> • How might climate change impact TSAIs in IRES, in particular the taxa that may only be able to tolerate short-term drying? How might this affect the habitat continuum model? • How do TSAIs respond to prolonged dry or wet conditions and higher temperatures? • Are perennial rivers that have recently dried due to human activities (including climate change) similar to naturally dry IRES, with respect to TSAI features?
How does hydrology affect TSAIs?	<ul style="list-style-type: none"> • Can the relationships between IRES biota and hydrological stages be measured to improve the model further? IRES are often ungauged, resulting in a lack of hydrological data • Can future research on this biota be linked adequately with hydrology? • Can the habitat continuum model be used to identify stages of the hydrograph where biota are most vulnerable to anthropogenic stressors, such as water abstraction or water releases? • What are the flow–ecology relationships for the terrestrial biota of IRES and how these could be used to set up flow management (e.g. environmental flows)?
Aquatic–terrestrial linkages need to be explored further – are there reciprocal subsidies in IRES?	<ul style="list-style-type: none"> • Aquatic–terrestrial linkages and TSAIs
Are there hot spots/hot moments of subsidies in IRES?	<ul style="list-style-type: none"> • Hot spots are patches of high biogeochemical reaction rates, and hot moments are short periods of time that exhibit high biogeochemical reaction rates
What are the key functional roles of TSAI in the ecological integrity of IRES?	<ul style="list-style-type: none"> • Functional roles of TSAIs
What patterns/processes can be explored at a large scale?	<ul style="list-style-type: none"> • Metacommunity perspectives of TSAIs
How does the habitat continuum model apply to other biotic groups?	<p>Expand the habitat continuum model to include:</p> <ul style="list-style-type: none"> • Animals: birds, reptiles, mammals, amphibians, fish • Terrestrial vegetation: grasses, herbs, trees, shrubs • Aquatic vegetation: phytoplankton, macroalgae, aquatic macrophytes • Fungi • Bacteria

IRES, intermittent rivers and ephemeral streams.

Tscharntke, 2018) and ecosystems, including IRES. Comparing knowledge of how specific taxonomic groups contribute to ESs in other ecosystems allows speculation that the same taxonomic and functional TSAIs promote ESs such as biological control, food provision, organic matter decomposition and nutrient recycling in IRES. Native herbivores, such as grasshoppers, which were found to influence nutrient cycles, increase soil fertility and regulate primary production in prairie ecosystems (Belovsky & Slade, 2000), might also regulate riparian vegetation and play a role in plant richness, since herbivore diversity and herbivory were positively linked to plant diversity (Ebeling *et al.*, 2018). TSAIs that reside in soil likely improve soil texture and water-holding capacity

in IRES, as shown within a Chihuahuan Desert watershed for two ant species whose nests affected hydrology and soil chemistry (James *et al.*, 2008). Bark and wood-boring TSAIs might indirectly accelerate decomposition by facilitating colonisation of woody debris by fungi, a process that has been studied in managed mature conifer forests in Southeast Sweden (Strid *et al.*, 2014). They were also found to build suitable habitats for other insects (e.g. Zuo *et al.*, 2016), contributing to habitat provision. Finally, TSAIs can be food for either terrestrial organisms preying along the shoreline or subsidies for aquatic organisms when they fall into the water, adding carbon, nitrogen and phosphorus to the dry or wet part of the IRES habitat continuum, and thus affect respective assemblage

dynamics (Paetzold *et al.*, 2005; Paetzold & Tockner, 2005; Menninger *et al.*, 2008). Possible ESs of TSAIs in IRES for further research are presented in Table 1.

(3) Expanding the habitat continuum model

The habitat continuum model needs to be expanded to ensure its relevance to other biotic groups, such as vertebrate animal taxa, as well as plant, fungal, and bacterial taxa (Table 1). Birds, reptiles, mammals, amphibians, and fish can inhabit IRES (Sánchez-Montoya *et al.*, 2017) and use them as movement corridors (Sánchez-Montoya *et al.*, 2016). Some species of crocodiles, turtles, and snakes can aestivate in dry riverbeds (Sánchez-Montoya *et al.*, 2017). Fish are obviously more abundant when surface water is present, but several species can persist in dry riverbeds (Fishman *et al.*, 1986) or in the hyporheic zone (Rodríguez-Lozano, Leidy & Carlson, 2019).

Of the remaining biotic groups, grasses, herbs, trees, shrubs, phytoplankton, macroalgae, aquatic macrophytes, fungi, and bacteria can inhabit IRES (Romani *et al.*, 2017), and could be included in an expanded habitat continuum model. A loss of surface water can result in the stranding of aquatic plants, such as macrophytes and phytoplankton. Some of these biota can persist in the drying stage through desiccation-resistant forms such as seeds, tubers or stems (Brock & Rogers, 1998). Terrestrial vegetation can colonise the riverbed once surface water disappears (Steward, 2012).

V. CONCLUSIONS

- (1) Terrestrial and semi-aquatic invertebrates (TSAIs) are important components of intermittent rivers and ephemeral streams (IRES) ecosystems that have previously been overlooked. Many knowledge gaps exist (Table 1).
- (2) Our case studies from Australia and France demonstrate that IRES continuously provide habitat for TSAIs, regardless of hydrological stage.
- (3) IRES should be recognised as supporting a unique mix of aquatic, semi-aquatic, and terrestrial biota. The IRES habitat continuum model proposed here is relevant to ecologists, but also water managers and policy makers, ensuring that both wet and dry phases are considered in the management and protection of IRES.
- (4) We call for collaboration among aquatic and terrestrial ecologists to explore these dynamic ecosystems further, and to improve the relevancy of our model to all biotic groups of IRES.

VI. ACKNOWLEDGEMENTS

Part of this research was conducted while A.L.S. was a PhD student at Griffith University and was supported by funding from the Queensland Government and the TRACK

(Tropical Rivers and Coastal Knowledge) program. T.D. was supported by the DRYvER project, which has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 869226. S.D.L. was supported through the Spanish Government's María de Maeztu excellence accreditation 2018-2022 (Ref. MDM-2017-0714). We thank Roland Corti for his data on TSAIs from the Albarine River, France, and the landowners for access to the sampling sites.

Open access publishing facilitated by Griffith University, as part of the Wiley - Griffith University agreement via the Council of Australian University Librarians.

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(Received 10 March 2021; revised 18 February 2022; accepted 21 February 2022; published online 28 February 2022)