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Biological invasions in intermittent rivers and streams: current knowledge and future frontiers

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Biological invasions in intermittent rivers and streams: current knowledge and future frontiers

Abstract: Intermittent rivers and ephemeral streams (IRES) have been overlooked in invasion science as the characteristic drying - wetting regimes are assumed to be a barrier to invasion processes. Flow contraction/cessation limits the persistence and success of water-dependent invasive alien species (IAS) in most IRES, while flash floods may restrict limnophilic and strictly terrestrial ones. However, IRES are subject to multiple anthropogenic stressors that could ultimately favour the arrival and spread of IAS and their mosaic of dynamic habitats may theoretically support both terrestrial and aquatic IAS. Successful IAS are characterised by adaptations, traits and life histories which facilitate rapid, opportunistic exploitation of habitats and resources. Here, the potential invasibility of IRES is discussed along with a summary of current knowledge gaps, examples and challenges across different continents. IAS in IRES should be considered a cause for concern but also an intriguing study system to understand the mechanics of biological invasions under global change.

Keywords: fluvial ecosystems; global change; invasive alien species; non-perennial waterways

Invasiones biológicas en ríos y arroyos intermitentes: conocimiento actual y fronteras futuras

Resumen: Los ríos intermitentes y los arroyos efímeros (IRES en inglés) han sido escasamente estudiados por la ciencia de las invasiones biológicas ya que los regímenes de secado e inundación pueden actuar como barrera para los procesos de invasión. La contracción/cese del flujo limita la persistencia y el éxito de las especies exóticas invasoras (EEI, IAS en inglés) dependientes del agua, mientras que las inundaciones pueden restringir las especies limnófilas y estrictamente terrestres. Sin embargo, los IRES están sujetos a múltiples factores de estrés antropogénicos que, en última instancia, podrían favorecer la llegada y propagación de EEI y su mosaico de hábitats dinámicos puede teóricamente sostener EEI tanto terrestres como acuáticas. Las EEI exitosas se caracterizan por adaptaciones, rasgos e historias de vida que facilitan la explotación rápida y oportunista de hábitats y recursos. En esta revisión se analiza el potencial de invasibilidad de IRES junto con un resumen de las lagunas de conocimiento, ejemplos y desafíos actuales en diferentes continentes. Las EEI en IRES deben considerarse un motivo de preocupación, pero también un sistema de estudio interesante para comprender la mecánica de las invasiones biológicas bajo el cambio global.

Palabras claves: cambio global; cursos de aguas no perennes; ecosistemas fluviales; especies exóticas invasoras

Introduction

Intermittent rivers and ephemeral streams (IRES) occur within all climates and biomes, and on every continent representing a huge part of the river network length worldwide (Messager et al. 2021). Flow intermittency, with lack of superficial water flow, may be natural or due to anthropogenic alteration of the hydrological dynamics (e.g., flow regulation, Belmar et al. 2019). Regardless, intermittent flow regimes should be considered as part of the suite of multiple stressors on freshwater environments. Biological invasions by invasive alien species (IAS) are another major driver of ecological change and are recognised as among the most important features of the Anthropocene (IPBES 2023). Despite the co-occurrence and severity of both stressors, there has been relatively little interdisciplinary work which truly addresses both topics, as IRES research has been historically geochemistry and hydrology-based (but see Datry et al. 2017; Bruno et al. 2022 and references inside) whereas IAS research is mostly dominated by ecological approaches (Francis and Chadwick 2012; Guareschi and Wood 2022).

Riverine invasion dynamics are generally related to connectivity, disturbance, propagule pressure, anthropogenic modification, and landscape position (Francis and Chadwick 2012; Woodford et al. 2013; Chapman et al. 2020). Characteristics of IRES may include all of these factors. For instance, connectivity dynamics may be through natural hydrological networks (e.g., from headwaters to lowland areas, or from main axis to tributaries, and *vice versa*) or human mediated via inter-basin water transfers (Woodford et al. 2013; Ollero et al. 2022), where the latter occurs mostly in semi-arid/arid agricultural areas but is expected to increase due to climate change driven water scarcity (van Wilgen et al. 2022). Moreover, being historically neglected by social perspectives, and mostly excluded from management plans (Rodríguez-Lozano et al. 2020; Cottet et al. 2023), IRES are prone to suffer multiple anthropogenic modifications and pressures, for example: occupation of the channel and elimination of the fluvial space; dumping of rubbish; uncontrolled urban development; resection of the banks, that will ultimately favour the arrival and spread of generalist alien species (Ollero et al. 2022).

The aim of this paper is to synthesise aspects of the scarcely investigated invasibility of IRES through identifying knowledge gaps, examples and features from different continents in order to support a future interdisciplinary agenda on the topic. Intermittently freezing streams (Tolonen et al. 2019) fall outside of the scope of this research as they can also face interruptions and loss of water flow, but they do not usually experience partial or complete streambed drying.

IRES as aquatic and terrestrial habitats

IRES are characterised by alternating flowing, drying, and dry reaches that generate a mosaic of dynamic and different habitats (e.g., flowing, standing, terrestrial, see **Figs. 1** and **2**) throughout the year (Datry et al. 2014). Presenting both terrestrial and aquatic habitats, IRES may be theoretically subject to double invasions from both terrestrial and aquatic IAS in different phases. During the aquatic, or wet phase, intermittence dynamics impose an environmental filter on aquatic biota which favours species with traits related to desiccation resistance or recovery traits that confer resilience to stochastic conditions (e.g., Belmar et al. 2019). For this reason, IRES biological communities are usually highly specialised with similar traits, such as insects with fast life cycle, organisms exhibiting resistance stages or displaying opportunistic dispersion (Arthington and Balcombe 2011; Kerezsy et al. 2017; Pařil et al. 2019). The physiological barriers related to habitat availability, high temperature and conductivity during flow contraction/cessation limit the persistence of strictly aquatic IAS in most IRES. In this framework, species with traits related to drought tolerance should be prioritised as potentially problematic new arrivals in IRES (van Wilgen et al. 2022).

Terrestrial invasive plants often colonize riparian areas along rivers, especially those which have been heavily modified and degraded. This is a particular issue in IRES and systems with seasonally exposed sediments (Bolpagni and DallaVecchia 2022). Riparian habitats may host high proportions of IAS plants in general (24–30% for systems in France and USA, Planty-Tabacchi et al. 1996), the roots, fragments and seeds of which may proliferate with fluvial corridors and dry riverbeds as pathway for invader dispersal through the basin (Williams 2006). Beyond dry periods, IRES may also be subject to short flash floods that may drastically and temporally change the habitat conditions, exacerbating downstream spread of taxa (e.g., riparian vegetation) while allowing new connectivity into upstream and lateral ecosystems (see **Figs. 1** and **2**).

Winners and Losers in IRES: a matter of connectivity

The cessation of water flow and the absence of superficial water represent a clear challenge for strictly water-dependent organisms including IAS (from microorganisms to vertebrates) which are at risk from habitat shrinkage. In this instance, mobile species which are able to seek temporary refugia, either in the perennial stretches or in the mainstem, are more likely to migrate out of the drying reach as the drying period can be considered a ramp disturbance (Pařil et al. 2019). At the same time flash flooding events disfavour strictly terrestrial invaders (Chiu et al. 2017) but may indirectly help dispersion of taxa able to survive submersion (Corti and Datry 2012; Steward et al. 2017).

Overall, adaptation to local hydrological regimes is a key predictor in the establishment success of non-native fish (Moyle and Light 1996). In desert rivers of Morocco alien fish were associated with reservoirs, colonising the regulated downstream reaches, while unregulated upstream reaches tended to be free of non-natives (Clavero et al. 2015). In South Africa, Mediterranean-climate streams in the Cape Fold Ecoregion are prone to intermittency and heavy drought conditions, the frequency and duration of which are predicted to increase under current climate projections (van Wilgen et al. 2022; Broom et al. 2023). The fragmented streams are a freshwater biodiversity hotspot, for endemic and vulnerable minnow species (Broom et al. 2023). Two common invasive species across these systems are the African sharptooth catfish *Clarias gariepinus* - introduced via aquaculture and inter-basin water transfer (e.g. the Orange-Fish River, Petitjean and Davies (1988)), and black basses (*Micropterus* spp.) - introduced for food fisheries, that tend to colonise the lower reaches and invade upstream during times of riverine connectivity (Ellender et al. 2018; Weyl et al. 2020; Broom et al. 2023). During times of drought, black bass are then either restricted to the lower reaches or trapped in isolated pools in the headwaters until flood events facilitate re-colonisation and potential spread (Ellender et al. 2011, 2018; JS unpublished data). African sharptooth catfish *Clarias gariepinus* on the other hand is able to breathe air, move over land and create crude burrows in wet mud (Bruton 1979). These traits are related to adaptation to the seasonal afro-tropical flood pulse (Van der Waal 1997) and allow migration back into the mainstem during harsh climatic periods which result in episodic invasions of headwaters (Ellender et al. 2015). In the desert streams of Arizona (USA), similar natural dynamics can be observed where extremely short episodic flows can facilitate the rapid colonisation of previously fragmented water bodies through “normally dry” reaches (fish assemblage: Stefferud and Stefferud 2007). However, the same isolated upper reach pool habitats may also be a crucial refugia for threatened native species (e.g., *Psuedobarbus afer* - forest redfin) so long as predatory IAS (e.g., black bass *Micropterus* spp., see **Fig. 3**) are not also confined to the pool (Ellender et al. 2011, 2018; Firmat et al. 2013; JS unpublished data). Management tools such as downstream barriers can be effective when threatened native species and invasive species occupy different stream stretches or if isolated upstream populations of invasive species are eradicated prior to barrier implementation and so long as barriers are sufficient to withstand heavy and high-water flash flooding (Stefferud and Reinthal 2005; Stefferud and Stefferud 2007). However, if invasive species dominate upstream, eradication may become particularly challenging and alternative spread management measures are necessary.

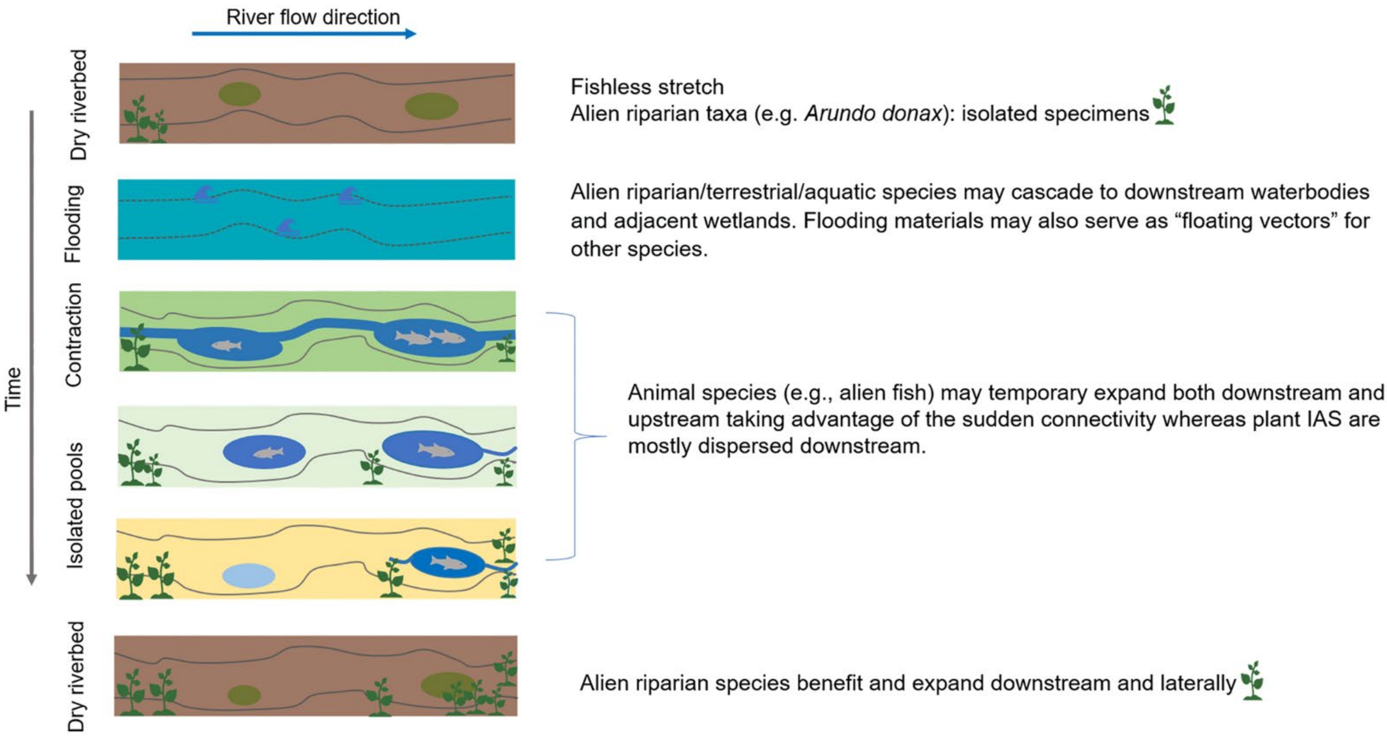

Figure 1. *Example of spread of terrestrial and aquatic alien taxa along an intermittent water way and adjacent systems during flooding and contraction events. Flood episodes can unintentionally spread alien taxa downstream and in adjacent riparian wetlands temporally connected. Similarly, exposed sediments can be colonized from the lateral areas toward the centre zone of the riverbed. Results will be visible weeks/months after the event. Inverse route can be used by alien fish (if able to persist in some permanent reaches downstream or actively introduced during the wet phase) that take advantage from flash floods to temporary colonize the upstream section. After a further cycle of contraction and drying, fish without specific drought-resistance traits, risk to remain trapped in isolated drying pools. Modified from: Chiu et al. (2017).*

Figura 1. *Ejemplo de propagación de taxones exóticos terrestres y acuáticos a lo largo de un curso de agua intermitente y sistemas adyacentes durante eventos de inundación y contracción. Los episodios de inundación pueden involuntariamente propagar taxones exóticos río abajo y en humedales adyacentes conectados temporalmente. De igual manera, los sedimentos expuestos pueden ser colonizados desde las áreas laterales hacia la zona central del cauce. Los resultados serán visibles semanas/meses después del evento. La ruta inversa puede ser utilizada por peces exóticos (si pueden persistir en algunos tramos permanentes aguas abajo o se introducen activamente durante la fase húmeda) que aprovechan las inundaciones repentinas para colonizar temporalmente la sección río arriba. Después de un nuevo ciclo de contracción y sequía, los peces sin rasgos específicos de resistencia corren el riesgo de quedar atrapados en pozas aisladas en desecación. Modificado de Chiu et al. (2017).*

Figure 2. *Baganza stream (Northern Italy). Example of intermittent stretch with **a**) dry riverbed (late summer 2021) and **b**) wet channel (early summer 2023), with exposed sediments (undergoing riparian/terrestrial taxa colonization) and dense riparian vegetation. Red circles stressed thickets of IAS Arundo donax (often combined with Amorpha fruticosa) that may benefit from flooding events to spread downstream (toward the upper part of the photo). Photo credits: Guareschi & Pederzani.*

Figura 2. *Arroyo Baganza (norte de Italia). Ejemplo de tramo intermitente con **a**) cauce seco (finales del verano de 2021) y **b**) canal activo (principios del verano de 2023), con sedimentos expuestos (en procesos de colonización por taxones riparios/terrestres) y densa vegetación de ribera. Los círculos rojos resaltan los matorrales de Arundo donax (a menudo en combinación con Amorpha fruticosa) que pueden beneficiarse de las inundaciones para extenderse río abajo (hacia la parte superior de la foto). Créditos fotográficos: Guareschi y Pederzani.*

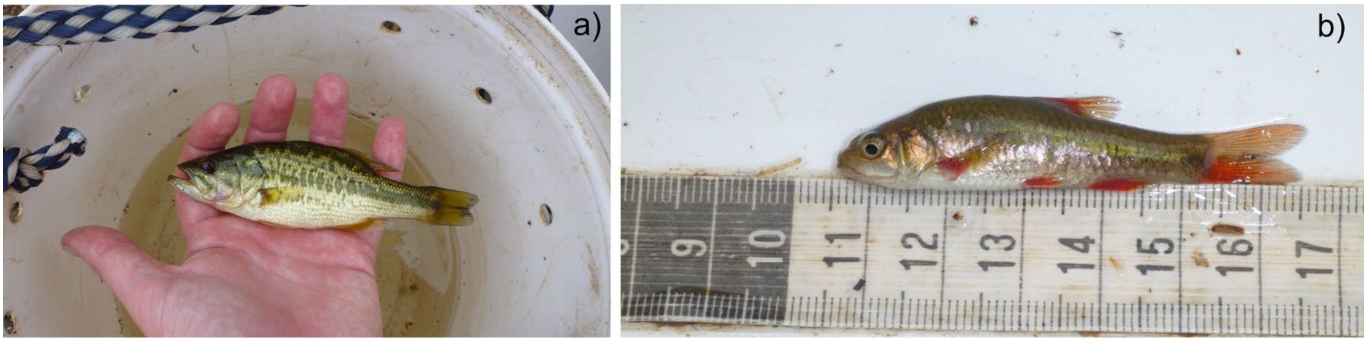

Figure 3. *Invasive and native threatened fish species from the Cape Fold Ecoregion IRES.* ***a****) Example of invasive fish in South Africa: juvenile* *Micropterus* *sp. (15 cm size);* ***b****) Native South African species:* *Pseudobarbus afer* *(Peters, 1854) (IUCN Red list status: endangered). Photo credits: D.J. Woodford.*

Figura 3. *Especies de peces invasoras y nativas amenazadas de la ecorregión de Cape Fold IRES.* ***a****) Ejemplo de pez invasor en Sudáfrica: juvenil* *Micropterus* *sp. (tamaño 15 cm);* ***b****) Especie nativa sudafricana:* *Pseudobarbus afer* *(Peters, 1854) (Estado en la Lista Roja de la UICN: en peligro de extinción). Créditos de las fotos: D.J. Woodford.*

Similarly, intermittent reaches can act as refugia for native invertebrate species and in some specific cases they may represent the only portions of the river network which are free from IAS (e.g., intermittent stretches only parts not invaded by New Zealand mudsnail *Potamopyrgus antipodarum* in Californian creeks, Abramson 2009). In both perennial and intermittent rivers, the most common invertebrate IAS are crustaceans and molluscs, whereas aquatic insects are extremely rare IAS in both systems (Fenoglio et al. 2016; Burgazzi et al. 2018). The multi-dimensionality and dynamism of IRES habitat form an extra factor where fine scale spatial attributes are important as they provide fractal micro-refugia which support even species with no desiccation resistance traits (Burgazzi et al. 2018; Pardil et al. 2019). For instance, *Procambarus clarkii* tends to use complex microhabitats (e.g., vegetated sections or under boulders) in ephemeral water bodies of Portugal (Aquiloni et al. 2005) and Kouba et al. (2016) emphasised the evasive capacity of invasive crayfish (e.g., *Procambarus virginalis* and *P. clarkii*) to dig vertical burrows into the hyporheic zone under drought conditions.

Further, the drying regime and habitat mosaic increase entrance of terrestrial invertebrate species into the community in a manner that can transport propagules both downstream, and laterally, with flow resumption (e.g., Rosado et al. 2015; Steward et al. 2017; Sánchez-Montoya et al. 2020; Sánchez-Montoya et al. 2023). Therefore, the incursion and timing of terrestrial and semi-aquatic IAS is a topic which requires further research.

Encroachment of terrestrial IAS into IRES is mostly characterised by vegetation which spreads along the riparian zone and expands into newly available habitats formed in the emerging dry channels and exposed riverbeds. During prolonged drought periods this may involve the entire riverbed, with colonisation from the lateral riparian zone to the main riverbed by generalist, pioneer and fast spreading vegetation on the exposed sediments (e.g., Bolpagni and DallaVecchia 2022). Drought resistant and flood-adapted flora are then particularly favoured and the hydrologic dynamism of IRES may assist spread through hydrochory. For instance, the Giant reed *Arundo donax*, common IAS in numerous European and North American regions, reproduce via asexual fragments (vegetative reproduction), and its spread is accelerated through flooding events which transport fragments downstream whereupon establishment occurs (Calazans et al. 2023; Ollero et al. 2022; Saltostall et al. 2017, see **Figs. 1** and **2**).

Riparian ecosystems of ephemeral streams in some areas of southern Africa (e.g., Namibia) have been affected by severe infestations of *Prosopis* spp. that tend to form dense thickets. These are in some cases perceived as useful for fodder and shade by farmers, but considered a critical threat to the riparian forests displacing native vegetation and thus affecting the animal taxa which utilise these habitats (Joubert 2009). Plant invasions (e.g., early stage) may tend to go unnoticed in arid areas (Milton and Dean 2010) also because of the close resemblance between arid-adapted alien and some indigenous species (i.e., cryptic invasion processes: Morais and Reichard 2018). For instance, Australian *Atriplex nummularia* and Asian *Tamarix ramosissima* are well adapted for dispersal in flooding rivers to mud banks and floodplains, as are their indigenous congeners in Africa (Milton and Dean 2010). Moreover, alien riparian species like *Tamarix* spp., in the USA and South Africa, are highly salt and desiccation tolerant which promotes their capacity to colonise and stabilise floodplain soils, while their traits ultimately affect channel morphology and hydrology (e.g., USA: Birken and Cooper 2006; Africa: Grenfell and Dube 2022). Establishment of these species can shift community traits from deciduous to evergreen species and may exacerbate the drying phase by increasing transpiration rates (Zedler and Kercher 2004).

Knowledge to date, gaps and new frontiers

A literature review using the Web of Science publication database (April 25, 2023) combining terms related to biological invasions and intermittent streams [(invas* OR alien OR non-native OR exotic) AND (intermittent river OR ephemeral stream OR non-perennial water way)] on the topic section ("title", "abstract" and "keywords") provided 112 results in English (110) and non-English (2) languages in a period from 1992 to 2023 (details in **Tables S1-S2**). Of these publications 57 somehow focussed on IAS and IRES and were mostly published after the year 2000. Approximately half of the publications concerned the fish community

(47.4%: 27 out of 57), followed by studies on vegetation (15) and invertebrates (8). North America (32) and Europe (10) were the regions more explored, with few publications based on Asia, Africa or South America. These outputs stress that Global South and some target organisms (i.e., invertebrates and microorganisms) are still underrepresented in the current international scientific literature. This geographic pattern appears common in river science, as seen in a recent review of stream communities and ecosystem functioning (Colls et al. 2024).

In this context, there has been relatively little direct focus on the interplay between IRES and IAS due to a lack of interdisciplinary research and quite likely as a result of unpredictable / rapid wetting-drying events which are a barrier to extensive field expeditions and to realistic/representative mesocosm experiments on large temporal and space scale. A general trend, however, is that during wet periods animal IAS (e.g., fish) may migrate both downstream and upstream taking advantage of the sudden connectivity whereas plant IAS (but theoretically also animals without active dispersal) are mostly dispersed downstream in the flood period. Overall, extreme persistent drought events prevent the arrival and spread of water-dependent alien taxa. In fact, desiccation and water level management are part of the aquatic IAS management toolbox, having been proposed to eradicate/limit populations in artificial water bodies or channels (e.g., Paukstis et al. 1999).

Context specific approaches specifically designed to consider communities and ecosystem services in riverine systems are highly necessary to improve and enhance research of biological invasions in flowing waters (Guareschi et al. 2022; Mathers et al. 2022), this approach ought to be implicitly extended to IRES (e.g., biological invasion hypotheses). There are various opportunities to exploit in developing the interdisciplinary study of IAS and IRES as multiple stressors on biological communities to understand and predict outcomes of global change, as well as forming “natural arenas” for testing hypotheses in the field. For example, the role of ecological matching and environmental filtering, where species with broad physiological tolerances, fast generational turnover, life histories linked to flood pulses or over-land linked dispersal traits, and generalist consumers may be hypothesised to be more likely to invade IRES. In numerous contexts most IAS (both plants and animals) already showed adaptations and life histories which facilitate rapid, opportunistic exploitation of habitats and resources (e.g., Zedler and Kercher 2004; Drown et al. 2011; Coverdale et al. 2013). Similarly, the nature of IRES as transitional, ‘blank slate’, ecosystems may allow pioneering species to colonise faster and restrict native species re-colonisation through predation and niche exclusion. At the same time, the biotic resistance hypothesis (Kennedy et al. 2002) can be also tested in IRES where the native assemblage is pre-adapted to the local hydrology to understand the mechanisms of invasion. In this context, it can be hypothesized that the focal invasive species would exploit a gap in an ecological niche specific to IRES rather than competitively excluding pre-adapted native species from a given niche. Interdisciplinary ventures which predict drying-wetting events can be used to target specific locations for monitoring to jointly understand the drivers and processes behind colonisation succession in invaded and uninvaded IRES, which can aid understanding of poorly documented phenomena such as invasion meltdown (e.g. Braga et al. 2020). A further aside of interest is an assessment of the structure of interspecific interactions and trophic pathways considering the shifts between terrestrial dominated and aquatic dominated habitats in the same mosaic. These systems should be also studied comparatively at a global scale to understand the linkages in systems adapted to a flood pulse, such as Afro and Neo tropical wetlands. However, there are considerable challenges in the successful implementation of before-after-control-impact approaches due to their high hydrological dynamism.

Physiological preference and desiccation resistance should be further investigated, ideally at different population levels, especially for successful IAS (e.g., Guareschi and Wood 2020) to increase our knowledge and understanding on future potential invaders in IRES. At the same time emerging monitoring approaches like eDNA-based species detections showed promising outputs from isolated pools in IRES, especially for fish communities (Bylemans et al. 2016). Nonetheless, technical development and standardised methodology needs to be completed to fully understand and exploit eDNA detection in hydrologically variable systems. For example, the degradation of eDNA and downstream transport of eDNA during a flash drying or flooding event, and the capacity to detect historical communities from dry reach sediment. Finally, the implications of biological invasions and naturally intermittent hydrological regimes should be used to predict outcomes of climate induced changes to flow regimes in historically perennial systems now threatened by drought and abstraction (e.g., Alpine streams: Piano et al. 2019). Further advances in trait based predictive ecology, combined with international cohesion, has the potential to advance the knowledge regarding management of IAS and IRES at a global scale.

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Contribution of the authors

Simone Guareschi, Josie South: Conceptualisation, Methodology, Writing - Review and editing.

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