# Non-perennial segments in river networks

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## Abstract

Non-perennial river segments—those that recurrently cease to flow or frequently dry—occur in all river networks, and are globally more abundant than perennial (always flowing) segments. However, research and management have historically focused on perennial river segments. In this Review, we outline how non-perennial segments are integral parts of river networks. Repeated cycles of flowing, non-flowing and dry phases in non-perennial segments influence biodiversity and ecosystem dynamics at different spatial scales, from individual segments to entire river networks. Varying configurations of perennial and non-perennial segments govern each river network's physical, chemical and ecological responses to changes in flow regimes, especially in response to human activities. The extent of non-perennial segments in river networks has increased due to warming, changing hydrological patterns and human activities, and this increase is expected to continue. Moreover, the dry phases of flow regimes are expected to be longer, drier, and more frequent, albeit with high regional variability. These changes will likely impact biodiversity, potentially tipping some ecosystems to compromised stable states. Effective river network management must recognize ecosystem services (such as flood risk management and groundwater recharge) provided by non-perennial segments and ensure their legislative and regulatory protection, which is often lacking.

## [H1] Introduction

Rivers cover less than 2% of the Earth’s surface but contain approximately 13% of all described species and provide key ecosystem services such as provision of drinking water and food, regulation of climate and opportunities for recreation[1,2]. Despite their importance, rivers are among the world’s most threatened ecosystem types; one out of three riverine species in these biodiversity hotspots is threatened with extinction[3]. River science and management have historically focused on perennial segments **[G]**, which flow year-round, but rivers are increasingly being conceptualized as spatially variable networks in which hydrological connections between perennial and non-perennial segments **[G]** enable exchanges of water, materials and organisms that support network-scale biodiversity and ecosystem functioning[4,5] (**Figure 1a**).

Non-perennial river segments (hereafter NPRs[4]) recurrently experience flow cessation **[G]** and lose most or all surface water (**Figure 1b**). There is no global consensus in terminology[6–9] owing to the high temporal and spatial variability of flows within and among NPRs[10,] but here they are classified generally as ‘ephemeral’ **[G]**, which only flow in response to rainfall, or 'intermittent’ **[G]**, whose flows are longer and more predictable. When flowing (Figure 1c), NPRs supply water, biota, energy, nutrients and other materials to connected waters, influencing their water quality, biodiversity and ecological integrity. These pulsed hydrological connections are often irregular in time and space yet generate dynamic transition zones between aquatic and terrestrial habitats that extend longitudinally down river channels, laterally onto floodplains and vertically into the underlying groundwaters[11].

Every river network encompasses NPRs, particularly in the headwaters (**Figure 1a**), but sometimes also in substantial lengths of the lower segments and often in braided sections and alluvial floodplains. NPRs naturally constitute more than half of the global river network length[4] (**Figure 1c**), a proportion that is expected to rise in some regions because of climate change, land-use alteration and increased water abstraction[12,13]. Despite the ubiquity of NPRs and the ecological importance of the hydrological connectivity they provide, almost all policies and management practices for river networks are tailored for rivers that are perennial. The omission of NPRs from river management seriously risks undermining effective protection of biodiversity and ecological integrity of entire river networks and their ecosystem services. For example, rubbish dumped into unmanaged headwater NPRs when surface water is absent will impact receiving perennial waters when flow resumes and carries contaminants downstream[14]. Scientists and managers need greater awareness of the importance of NPRs to biodiversity and ecosystem processes to protect entire river networks.

In this Review, we explore key insights from research on NPRs in the context of network-scale riverine connectivity. For brevity, we focus on aquatic responses to drying from segment to river network scale but acknowledge that interactions with terrestrial ecosystems are also crucial in NPRs, especially during dry phases. We conclude by exploring the drawbacks of excluding NPRs from river network management. River management strategies must treat river networks as arrays of co-occurring perennial segments and NPRs, and must integrate NPRs into actions that maintain and, where possible, enhance network-scale biodiversity, ecosystem processes and ecosystem services.

# [H1] Characterizing non-perennial segments

This section discusses NPR flow regimes, the types of connections between perennial segments and NPRs in river networks, their distribution within different networks, and how such connections can alter fluxes of water, materials and organisms across river networks.

## *[H2] Typology and connections*

### *[H3] Flow regimes*

The flow regime **[G]** governs river geomorphology, water quality and ecology[15] and, thus, is crucial to the understanding and management of river networks. In NPRs, the flow regime encompasses alternating flowing phases **[G]**, non-flowing phases **[G]** and, in many cases, dry phases **[G]** (**Figure 1c**). The frequency, duration and timing of each phase are powerful determinants of biodiversity, ecological integrity and ecosystem services, both at local scales within NPRs[16,17] and at the river-network scale[18,19].

Drying is a gradual process whose effects are separated by hydrological thresholds[20]. Early in the drying phase **[G]**, while flow declines, surface water contracts and lateral aquatic habitats become disconnected. As drying progresses, riffles and other flowing surface habitats disappear, leaving the riverbed as disconnected pools (**Figure 1c**). Eventually, the riverbed dries, although subsurface flow can continue in saturated sediments beneath the dry channel (the hyporheic zone)[20–22] (**Figure 1c**). This loss of surface water is governed by the type of surface–groundwater interactions occurring at the segment scale[23–25]. In losing segments **[G]** surface water, the water table of the underlying aquifer is generally deep and the hyporheic zone usually dries quickly[21,25], whereas in gaining segments **[G]** , upwelling groundwater can maintain a saturated hyporheic zone throughout the dry phase[21,25].

During the rewetting phase **[G]**, surface water returns to inundate the dry channels, sometimes quickly as flash floods[26,27] or slowly as a rise in water table. Like all components of flow regimes, the characteristics of drying and rewetting transitional phases are driven by both natural climatic and geological factors and by human activities[28–30] and vary greatly within and between river networks[31,32]. The consequences of such variability remain poorly understood but are likely to be an important determinant of a river network's biodiversity and ecological integrity[19,33].

### *[H3] Perennial and non-perennial segment connections*

Most NPRs are structurally connected to perennial segments by the spatial continuity of the river corridor (the channel, hyporheic zone and floodplain[34]) (**Figure 1a**), reflecting their ubiquitous co-occurrence in river networks globally (**Figure 1b**). This connectivity is well captured by the meta-ecosystem perspective that considers river networks as mutually dependent arrays of perennial river segments and NPRs that are connected to nearby aquatic and terrestrial ecosystems[35]. The connected terrestrial ecosystems range from riparian zones and uplands in the headwaters to floodplains downstream, and the connected aquatic ecosystems encompass nearby wetlands, lakes, subsurface groundwaters, reservoirs, estuaries and coastal waters (**Figure 1a**).

The spatial arrangements of NPRs and perennial river segments and their connections are diverse, complex and dynamic (**Figure 2 a&b**). Most river networks have naturally non-perennial headwaters that span the interface between terrestrial and aquatic domains[36]. Flow in headwater segments is driven by a combination of surface runoff, groundwater inputs and/or meltwater and is often seasonal[18,37]. NPRs can also be in the downstream parts of river networks (**Figure 2b**). Typically, river networks that flow out onto porous alluvial plains and recharge the underlying groundwater have downstream NPRs, such as the Tagliamento River (Italy[26]) and the Albarine River (France[38]). Other causes of downstream NPRs include excessive evaporation such as in the Diamantina River (Australia[39]) and human activities such as damming and water abstraction cause artificial drying, for example in the Colorado River (USA) and Yellow River (China[40]). In other river networks, the upper and lower segments are perennial but the mid-segments are non-perennial, such as in the Selwyn River (New Zealand[41]). In arid regions, whole river networks are often non-perennial, such as many rivers in northern and southwestern Africa[42] and the Nordeste region in Brazil[43]. Most braided sections of rivers comprise NPRs, which can also be prevalent across large, alluvial floodplains[26,44]. The varying physical settings (such as channel shape and size, streambed permeability, groundwater influence and large wood deposits), flow regimes and catchment land-uses of these different network configurations drive physical, chemical and ecological responses to the connections between NPRs and perennial segments.

### *[H3] Functional connections among river segments*

The different functional roles played by the varying connections between perennial and NPRs in space and time can be classified by the general mechanisms by which stream segments influence fluxes to downstream waters[45] (**Figure 2c, Supplementary 1**). Fluxes of water, sediments, material and organisms from perennial to NPRs and *vice versa* are often altered, which can have contrasting effects on downstream river segments (**Figure 2c**). These contrasting effects occur because the fluxes can cease, increase, decrease or be stored when they pass through NPRs before entering downstream waters[45].

Connections between perennial segments and NPRs can act as sources of material, notably when the organic material accumulated during dry phases is leached during rewetting, causing high nutrient fluxes to downstream waters[46] (**Figure 2c**). When NPRs dry, exchanges of water cease, both vertically between surface and groundwaters and longitudinally from upstream to downstream waters, transforming NPRs into sinks of material[47] (**Figure 2c**). As dry phases progress, terrestrial leaf litter from riparian zones is retained in NPRs and gradually accumulates on the streambed[33] (**Figure 2c**). Upon rewetting, this organic material is flushed downstream, sometimes en masse[27], with NPRs functioning to delay its release and processing (**Figure 2c**). Connections between NPRs and perennial river segments can also transform spatial patterns in chemical parameters such as dissolved oxygen when anoxic or hypoxic pulses of water from remnant pools or rewetting fronts are carried downstream to connected aquatic ecosystems by rewetting flows[19,48] (**Figure 2c**). The types and direction of processes that are altered are likely to reflect flow regime characteristics such as dry phase duration and the longitudinal sequence of perennial segments and NPRs.

### *[H2] Global distribution and temporal trends*

NPRs are prevalent on all continents, representing more than half of the global river network[4] (**Figure 1b**). For example, 94% of river lengths in the southwestern USA[49] and more than 70% of river lengths in Australia are non-perennial[50]. NPRs typically dominate in arid, semi-arid, and dry sub-humid regions, which represent up to half of the Earth’s land surfaces[40]. These segments are also common across alpine, boreal, continental, Mediterranean, oceanic, polar and tropical regions[16,51]. Every river network on Earth includes NPRs, especially in their headwaters. Headwaters are estimated to represent more than 70% of the total river network length and are typically prone to drying[4,36].

## [H1] The ecology of non-perennial segments

Drying in NPRs controls local biotic communities, ecosystem processes and ecosystem services. In addition, the spatial arrangement and type of connections between perennial and NPRs at the river-network scale shape the ecological integrity of river networks. This section discusses how drying influences the ecology of NPRs at the segment scale and how these effects propagate across the entire river network.

### *[H2] Non-perennial segment scale*

Biotic groups respond locally to recurrent shifts from flowing to non-flowing and dry conditions in NPRs (**Figure 1c**). Aquatic biodiversity declines steadily in response to non-perenniality as taxa lacking adaptations promoting resistance or resilience to drying are lost[16,17]. The extent of these declines is governed by hydrological parameters such as the duration of non-flowing and dry phases, with longer dry phases resulting in greater declines[38,52,53]. For example, a ten-day increase in the dry phase in the Albarine River, France, led to an additional loss of six invertebrate taxa from the benthic community and four invertebrate taxa from the hyporheic zone[38]. An increase in the duration of the non-flowing phase from 0 (perennial flow) to 78 days reduced the survival rate of Coho salmon populations from 59 to 11% from tributaries of the Russian River in California (USA)[52].

Concurrent increases in terrestrial species richness occur as colonizing species arrive from riparian and wider terrestrial habitats[54]. For example, 22 and 12 invertebrate taxa colonized the dry riverbeds of the Albarine River (France) and Oaky Creek (Australia), respectively, within two months of the onset of the dry phase[54]. Although aquatic species richness during the flowing phase at the site-scale can be considerably lower in NPRs than perennial segments[55], their contribution to regional biodiversity can exceed those of perennial segments because of the inherently high beta diversity **[G]** (regional variability in community composition) in space and time and the presence of specialized species adapted to non-perennial conditions[51,56].

When flow resumes, aquatic organisms recolonize from various refuges, including upstream pools, moist sediments and leaf litter[57–59]. Some aquatic macroinvertebrates and diatoms have desiccation-tolerant forms that can survive in moist riverbed sediments[60,61]. Recovery rates and trajectories vary depending on connectivity to refuges and on species' dispersal abilities. Communities in NPRs connected to upstream perennial waters are soon replenished by colonists[62], whereas community recovery in isolated NPRs can be slow and more stochastic[58,63]. Recovery can be modified by anthropogenic influences such as fragmentation by instream barriers that sever links between NPRs and sources of colonists in perennial segments[64]. Despite well-developed recovery mechanisms, differences persist between communities in perennial and non-perennial segments[38,55]. These differences can be particularly pronounced and long-lasting when unprecedented dry phases occur during drought events. In contrast, communities can recover rapidly, generally within a few weeks, after 'normal' seasonal dry phases[63,65].

Aquatic species control fundamental ecosystem processes such as primary productivity and organic matter decomposition, and changes in aquatic biodiversity related to non-perenniality therefore alter ecosystem functioning. For example, desiccation-tolerant microorganisms in natural NPRs mediate biogeochemical cycling. When flow decreases, hypoxic conditions that develop in disconnected pools favor denitrification, reducing nitrate concentrations[25]. During dry phases, the microorganisms that make up biofilms coating the surfaces of sediment particles emit large quantities of $CO_2$[66] and upon rewetting, large $CO_2$ pulses can occur from NPRs. Accounting for the global prevalence of NPRs, a single rewetting event contribute up to 10% of the daily carbon dioxide emissions from all perennial rivers and streams, particularly in temperate climates[33]. When water returns, ecosystem processes such as respiration[67], nitrification and denitrification[68] and decomposition of leaf litter[69] quickly resume to previous levels. Recognizing the active contribution of NPRs to carbon cycling – during both wet and dry phases – could improve the accuracy of local-to-global-scale assessments[70].

Due to drying-driven decreases in the functional diversity of their aquatic communities, NPRs can collectively perform fewer ecosystem functions than perennial ones during flowing phases[71]. These declines could be mitigated by functional redundancy[72] (multiple species sharing traits), making the drying-induced loss of individual species functionally inconsequential[73]. However, as losses accumulate, the risk of losing functionally unique species increases, potentially representing a tipping point that drives the ecosystem to an alternative state. For example, by eliminating pivotal species, especially predators, drying can alter the structure and functioning of food webs, potentially leading to partial food-web collapse[74]. Similarly, the loss of desiccation-sensitive microorganisms and invertebrate detritivores reduces decomposition rates of particulate organic matter that fuels food webs[75], altering the quantity, quality and timing of energy sources transported downstream to perennial segments after flow resumes[46,76].

### *[H2] River-network scale*

River network-scale responses to drying are unlikely to be simple additive effects of segment-scale responses but arise from complex, interacting effects of segment-scale drying with other drivers  For example, spatial and temporal patterns of drying vary among river networks[32,77,78] (**Figure 2b**). Longitudinal trends related to elevation and channel form are superimposed on idiosyncratic drying patterns, thwarting efforts to extrapolate segment-scale patterns or assume that ‘river continuum’ predictions are realistic[18,19,41].

Complex responses to drying also result from the propagation of biogeochemical and ecological influences downstream by surface and subsurface flows. These transfers can slow, cease or be amplified by functional connections across hydrological phases that are likely to lead to ‘hotspots’ and ‘hot moments’ of material processing along a river network[25]. For example, terrestrial plant litter accumulates in dry and non-flowing segments and this litter decomposes very slowly[33] (**Figure 3**). When flow resumes in these segments, it can trigger rapid microbial decomposition of the labile plant litter[33] and flush the decomposing litter downstream[27] to perennial segments, providing a delayed subsidy of a resource that may be limiting to downstream consumers[79] (**Figure 3**). However, the network-scale effects of non-perenniality largely depend on the spatial arrangement of NPRs within the river network (**Figure 3)**. Where NPRs are concentrated in the headwaters, particularly in deciduous forested areas[36], the downstream effects of non-perenniality will be high seasonal inputs of unprocessed litter (**Figure 3**) that can reduce downstream water quality[80] or cause technical problems for dam intakes[81]. In contrast, where NPRs are in downstream segments of river networks, which are typically less dependent on terrestrial litter inputs from riparian zones, lower fluxes of unprocessed litter are expected in downstream river network segments. Meanwhile, periods of disconnectivity retain leaf litter in the headwaters, which can thus become hotspots of carbon cycling (Figure 3).

Synchrony **[G]** can describe how local responses propagate at the river network scale and can be enhanced by connectivity (upstream dispersal, advective transport) between segments or by a driver such as drying that simultaneously affects multiple segments[82]. By reducing longitudinal connectivity of flowing water, the effects of non-perenniality of river segments can reverberate throughout a river network and desynchronize, for example, diel dissolved oxygen fluctuations[19] or the recovery of biological communities during flowing phases[18]. When flow resumes in NPRs, hydrological connectivity is restored, promoting network-scale synchronization of such fluctuations and processes[19].

The dynamics of aggregate stream systems are typically less variable than their individual contributing segments[83,84] because combining asynchronous contributions from many segments has a stabilizing effect (the ‘portfolio concept’[83]). However, widespread non-perenniality in river networks can synchronize dynamics across populations, increasing the risk of regional species extinctions[85,86]. Therefore, when aggregated in river networks, the variation in flow regimes between perennial and NPRs contributes to persistence of regional biodiversity and, thus, stable ecosystem functioning and associated availability of ecosystem services[84].

At the river-network scale, NPRs increase the beta diversity of aquatic communities because of the simultaneous coexistence of different successional stages at the river network scale[18,40,87] (**Figure 4**). Depending on the spatial arrangement of NPRs and perennial segments within the river network, communities in NPRs can comprise a subset of the taxa inhabiting perennial segments, notably when NPRs are downstream of perennial segments acting as a source of colonizing organisms[16] (**Figure 4**). Alternatively, when non-perenniality is concentrated upstream, their biological communities can be more variable in space or time compared to their downstream perennial counterparts[87,88] (**Figure 4**). This variability is because recolonization from downstream perennial segments is limited by the unidirectional flow along river networks and by topographic barriers, particularly for weak aquatic dispersers, promoting alternative sources of colonists in the landscape such as perennial waterbodies and the underlying hyporheic zone.

Including NPRs in the study of biodiversity dynamics within river networks demonstrates the importance of dispersal, a regional process which can dominate over the local process of species-sorting during rewetting phases[18,89,90]. The spatial extent of drying influences the access to and from refuges in the network during the dry periods and thus controls the dispersal of organisms and overall metacommunity dynamics[18,91,92]. However, the relative contribution of species dispersal in shaping riverine biodiversity patterns is highly context-dependent, as well as being taxon-specific and extends to nearby habitats such as riparian zones[56], hyporheic zones and groundwaters[93] and downstream ecosystems[94].

# [H1] The future of river networks

This section discusses the future changes predicted for NPR flow regimes, the likely responses by aquatic biota and how management strategies for entire river networks could be tailored to incorporate these changes. Currently, perennial river segments are potentially vulnerable to the lack of protection or restoration of NPRs elsewhere in the river network.

## *[H2] Widespread and increasing non-perennial flow*

The spatial extent of NPRs in global river networks has increased[12,95,96] due to shifts in flow regimes (**Figure 5a & b**). This increase is predicted to continue[13,43,97], driven in part by climatic trends such as rising temperatures and associated increases in evaporation, changing precipitation patterns, and the increasing occurrence of drought in many parts of the world[98–100]. For example, previously perennial rivers in Europe and China dried for the first time during the severe droughts that began in 2022[101,102]. In addition, intensifying use of water resources, including surface and groundwater abstraction, storage and diversion, are driving shifts from perennial to artificially non-perennial flow[40,101]. In Kansas (USA), for example, widespread irrigation from the High Plains aquifer since the mid-1900s has lowered the regional water table, sometimes by more than 50 m, shifting rivers and streams from naturally gaining and perennially flowing to artificially losing and non-perennial flow[103,104].

The predicted increase in the spatial extent of NPRs represents a network-scale decline in aquatic habitat availability and hydrological connectivity which will alter riverine biodiversity, with consequences for ecosystem functioning and services. For example, a decrease in the availability and quality of wet refuges that support aquatic organisms during dry phases will synchronize biological responses to drying, reducing metacommunity resilience and local community recovery after flow resumes[86].

### *[H2] Longer, drier and more frequent dry phases*

Flow regime characteristics such as the frequency, duration, severity and timing of flowing, non-flowing and dry phases are changing, as is the rate of change during transitional drying and rewetting phases. Despite considerable regional variability in the evidence for such changes[12,96] (**Figure 5a & b**), there is high confidence that changes will intensify in the near future. These predicted changes include increases in dry-phase duration and in dry-phase frequency, severity[99] and rates of onset of both dry phases and flow resumption[105]. Inherent within the predicted increase in dry-phase duration is the earlier onset and/or later cessation of dry phases in NPRs with seasonal flow regimes, as well as an increased co-occurrence of dry phases and extreme climatic events, particularly heatwaves[106–108].

In the context of megadroughts **[G]** [109,110], dry phases could continue uninterrupted for years in NPRs that currently have seasonal flow regimes. Deglaciation and snow loss are expected to reduce summer flows, resulting in shifts to non-perennial flow[111,112]. Conversely, warmer winters with greater snowmelt and glacial melting could cause NPRs to become perennial at higher elevations and northern latitudes[43].

### *[H2] Biological responses to future changes*

Biological communities in NPRs are expected to respond to future changes in flow regime characteristics. An increase in dry-phase duration and severity (caused by a lack of precipitation, water abstraction, and/or high temperatures and manifesting as reduced in-channel water availability) is likely to reduce the survival of desiccation-tolerant life stages of aquatic organisms within the riverbed sediments[60]. Similarly, an increase in dry-phase duration and frequency in NPRs could eliminate desiccation-sensitive species without enabling colonization by tolerant equivalents[72] (**Figure 5c**). Faster wet-to-dry transitions could shorten the time between environmental cues that trigger insect metamorphosis and its completion, reducing the emergence of adults[113]. Rapid-onset rewetting phases that wash insects, crustaceans, amphibians or fish straight from refuges to downstream segments could reduce local community recovery rates[114–116]. Both earlier dry-phase onset and later dry-phase termination could reduce successful completion of aquatic stages of life cycles by riverine animals. For example, earlier onset of drying could reduce the proportion of aquatic juvenile insects that emerge as terrestrial adults in time to avoid desiccation[113]. Prolonging the dry phase could prevent egg-laying behaviors by species that oviposit on water[117]. Distances and connectivity to perennial refuges in the landscape may determine post-drying community composition[86,118]. In cases of shifts from perennial to non-perennial flow regimes, biological responses might be particularly dramatic where species lack adaptations to drying. However, if NPRs are abundant in a river network, they could provide colonists adapted to the newly non-perennial conditions[86,101].

In terms of ecosystem processes, biofilms generally recover within a few days upon flow resumption, from dormant forms and through drift[119]. Some ecosystem processes, such as primary production and ecosystem respiration, are therefore highly resilient to drying. As such, natural NPRs experiencing longer or more frequent dry periods might not be severely affected in the near future, although shifts towards greater reliance on external energy sources could occur[120,121]. Other processes could be more dramatically affected by increasing drying, such as the decomposition of terrestrial leaf litter, because they are more dependent on macroorganisms[101]. Where once-perennial segments become non-perennial, biodiversity is predicted to respond strongly, with multiple cascading effects on ecosystem processes, although these effects will depend on the functional redundancy of a community and the types of organisms involved[101,120,122]. Finally, increasing non-perenniality is likely to occur in streams affected by other anthropogenic stressors, such as pollution and water abstraction, that interact to cause complex changes to ecosystem processes. For example, mesocosm experiments suggest that flow reductions and fine sediment pollution have synergistic effects on both algal biomass and thus primary production, and on invertebrate abundance and thus leaf litter decomposition[123].

In most cases, a reduction in aquatic biodiversity is the initial ecological effect of predicted future increases in drying. These taxonomic changes have functional consequences, altering ecosystem processes and associated ecosystem services. Although biological communities have proven resilient to drying, recovering within weeks to a few years even from rare dry phases in NPRs[124,125], predicted future changes in riverine flow regimes have increasing potential to tip ecosystems to new, functionally compromised stable states. For example, decreases in flowing-phase duration and frequency could interact with concurrent stressors such as artificial enrichment by inorganic nutrients to shift aquatic vegetation communities from habitat-forming plants to filamentous algae. This change would alter basal food resources and habitat availability for invertebrates and fish, triggering trophic cascades that extend through food webs. In addition, plants act as ecosystem engineers that alter sediment dynamics, and therefore their loss could alter river shape[126,127]. In contrast, the ecological consequences of region-specific shifts towards perenniality could increase network-scale hydrological connectivity, promoting biotic dispersal and thus homogenizing communities[90,128,129].

## [H1] Managing NPRs in river networks

The effects of alternating flowing, non-flowing and dry phases on water quality, ecosystem processes, biodiversity and ecosystem services at the river network scale mean that management expectations of natural NPRs must differ from those of perennial segments[93,130,131]. In particular, to be effective, management, conservation and restoration of river networks must explicitly recognize perennial and NPRs and their multifaceted connections. This section discusses the management implications of the presence of NPRs in river networks and of the connections between perennial and NPRs.

## *[H2] Management implications of non-perenniality*

Understanding the connections between perennial and NPRs, and with other connected waters (lakes, reservoirs, wetlands, aquifers, estuaries and in coastal areas), is a crucial step towards integrated management of river networks. The processes mediated by these connections have major network-scale implications for biodiversity conservation, water quality management, mitigation of risks such as floods and droughts, and the provisioning of ecosystem services.

Dry-phase refuges located in NPRs are crucial to maintaining freshwater biodiversity at the river network scale[52,132]. For example, disconnected pools maintained in intermittent streams in coastal Oregon[133] and in tributaries to the Russian River in California[52] during dry phases provide refuges that promote the survival of juvenile Coho salmon (*Oncorhynchus kisutch*) (**Figure 6a**). In the Russian River tributaries, the mean cumulative survival of salmon in these pools reached 50%[52]. The deterioration or loss of these habitats, together with the lack of access to them due to fragmentation by anthropogenic barriers[134], reduces fish populations which, in turn, affects subsistence fishers[52]. Therefore, management strategies for biodiversity conservation of entire river networks should prioritize the identification and protection of these refuges[135,136].

NPRs can attenuate floods and act as flood protection zones in the catchment (**Figure 6b**). For example, the dry channel of the ephemeral river Rambla de Nogalte, SE Spain, efficiently absorbs flash flood waters and sediments except where walls and embankments have been built[137]. Infiltration potential (the extent to which water can enter the sediments) in NPRs should be integrated in flood risk management at the river network scale by identifying priority zones where this function is maximized. The high infiltration capacity of dry riverbeds in NPRs can also limit evaporative losses and facilitate groundwater recharge (**Figure 6c**). For example, flooding after a rain event in the ephemeral Sand River, Kenya, recharged the groundwater level in only 1.5 hours[138]. Similarly, 49% of the monsoon flood volume from the ephemeral Río Puerco basin in New Mexico, USA, recharged the aquifer and the rest entered a downstream reservoir[47]. The resultant availability of water resources can be a major benefit for people living and depending on these water resources in arid and semi-arid regions.

Nutrients released from NPRs during flowing phases can subsidize downstream connected waters and support biodiversity and ecosystem functioning downstream, enhancing services provided by freshwater and marine fisheries (**Figure 6d**). For example, the timing of a nutrient pulse from the ephemeral Santa Clara River (California, USA) to at least 20 km offshore during the 1998 floods was key to supporting marine productivity at a time when nutrient inputs from oceanic upwelling were less available[139].

Non-perenniality has major consequences for provisioning, regulating and cultural ecosystem services made available by river networks. River drying prevents surface water abstraction for uses such as crop irrigation and public water supply[140]. However, in many regions, a substantial fraction of public water supply comes from sources that include NPRs[141] or their underlying groundwater sources[142]. Surface water loss is also likely to reduce fish populations that support subsistence fishers[52]. Regulating services such as water purification, flood mitigation and climate regulation are all compromised by drying[143]. For example, drying eliminates desiccation-sensitive microorganisms from biofilms and slows assimilation of inorganic nutrients (including anthropogenic pollutants) after flow resumes[144]. Drying also affects cultural services of river networks by limiting water-associated activities such as boating while creating opportunities for new activities such as rambling[140,145,146]. These impacts on cultural services depend on people's perceptions of drying[147,148], which greatly affects how river networks with extensive NPRs are likely to be managed.

## *[H2] Improving river network management*

Human activities alter flow regimes in NPRs, with major implications for functional connections and nearby perennial segments. However, compared to perennial segments, these NPRs are seldom as well-protected by legislation and associated regulations from the impacts of human activities that might alter their flow[101,149] (**Figure 7**). Indeed, management practices have yet to be adapted to match new conceptual developments in river science[4,5,101] that recognize the ecological importance of non-perenniality. Such adaptations in management practices would necessarily extend to other connected waters, such as floodplains, lakes and alluvial groundwaters, as well as the estuaries and near-shore coastal waters associated with river networks that drain to the sea.

River network management can be improved by recognizing and protecting the functional connections between perennial and NPRs. For example, if the legislative and regulatory protection of perennial segments in many countries were to be automatically extended to NPRs and their catchments, it would likely reduce the impacts of human activities that threaten biodiversity and ecosystem function of river networks and their connected ecosystems (**Figure 7**). Some nations already have limited legislative protection for NPRs. In Australia, independent scientific assessment of the potential environmental impacts of large coal mining and coal seam gas developments on water-dependent biota and ecosystems in both perennial and non-perennial segments in the disturbance footprint is expressly required under legislation (the 2013 'water trigger' amendment of the *Environment Protection and Biodiversity Conservation Act 1999*[150]).

Major obstacles need to be overcome to extend legislative protection for NPRs[149,151]. In Europe, the Water Framework Directive (WFD)[152] largely omits NPRs from conservation, restoration and biomonitoring[153]. For example, the WFD only recognizes NPRs in one 'river type' in some countries in the Mediterranean region. Elsewhere, where NPRs are less prevalent but nonetheless diverse and extensive, such as in France[154], the UK[51] and the Czech Republic[155], river typologies used to implement the WFD do not distinguish between perennial and NPRs. In some cases, such as France, there are attempts to remove NPRs from national legislation and regulations (**Figure 7h**). In the US, under implementation of the Clean Water Act, some NPRs are not included as Waters of the United States, potentially exposing them to impacts from activities such as dredging and waste dumping.

Another obstacle is the public perception of NPRs in river networks as less valuable than perennially flowing waters[147,148,156]. Consequently, NPRs are often overlooked in restoration and conservation plans[148] and there is little appreciation of their ecosystem services[143,146]. Even in Australia, where the need for separate water quality guidelines for NPRs is accepted[157], there is limited appreciation of the importance of connectivity between perennial and NPRs in influencing water quality. Scientists need to communicate the importance of ecosystem services provided by NPRs to the general public, river managers, politicians, policy makers and other stakeholders. Such evidence-informed actions could include producing fact sheets and policy briefs, using social media and conducting collaborative research projects with citizen scientists, river managers and stakeholders. For example, the open-source smartphone application DryRivers enables both citizen and professional scientists to map NPRs throughout Europe[158] and has substantially increased public appreciation of the nature and extent of NPRs.

Logistically, there are serious limitations in fundamental hydrological data and hydrographic mapping for NPRs in river networks. Stream gauges that quantify flow and describe flow regime components of a stream segment are typically placed along larger perennial streams and fail to capture NPR flow regimes[159]. Most available maps are based on static, low-resolution surveys and cartography that omit many headwater NPRs[36,160]. Despite increasing efforts at various scales to statistically[4,161–163] and mechanistically model[164,165] the distribution and flow regimes of NPRs, such efforts are hampered by the scant stream gauge and groundwater-level data, which amplifies uncertainty over large areas[4,163].

Further development and refinement of multi-platform remote-sensing technology could be combined with modeling approaches that target stream gauging or field observations to reduce bias and fill gaps. The approach would enable the production of hydrographic maps that better reflect the dynamic connections between all segments in river networks. Remote-sensing platforms with synthetic aperture radar (SAR) are better able to capture surface water blocked by clouds, vegetation or shadows than multi-spectral platforms such as LandSat or CubeSat[166,167]. Future use of high spatial and temporal resolution SAR datasets (for example, from NASA-ISRO SAR) to map NPRs, in tandem with advances in data interpretation[168], could support better integration of NPRs in distributed hydrological models[169].

Another major obstacle to more effective management of connected perennial and NPRs in river networks is the limited availability of monitoring tools and approaches that perform equally well in both segment types. Most river management tools have been developed primarily or exclusively for perennial segments[131,170,171] and typically perform poorly in NPRs. For example, biomonitoring indices used to indicate river health can rarely disentangle the effects of drying from those of stressors associated with human activities[131,170,172,173]. Functional traits[173], metasystem approaches[174], molecular tools[175] and data on composition of terrestrial and semi-aquatic assemblages[176,177] all have the potential to enhance assessment of NPR health. Developing common tools and approaches that are applicable in both perennial and NPRs could encourage river managers to include both types of segments in river network biomonitoring.

## *[H2] Restoration and conservation of NPRs*

Many NPRs are severely degraded by human activities, and thus require restoration to recover lost biodiversity and ecological integrity. NPRs that are not degraded are seldom adequately protected yet many urgently need conservation to preserve their current values. However, ignorance of these values, especially in ephemeral NPRs[178], and of the importance of NPRs to connected perennial segments has meant that efforts to restore or conserve NPRs are rare. It is likely that the same tools and approaches used for conserving and restoring perennial segments are equally applicable to NPRs. However, expectations of the outcomes, especially rates and trajectories of responses to restoration, need to consider these systems' inherent intermittence and their resilience to different types of impacts (such as altered flow regimes versus altered water quality).

The few attempts at targeted restoration of NPRs have focused on riparian revegetation[179]. Of these attempts, even fewer have sought to evaluate restoration success or investigate pathways and mechanisms of ecological recovery. An experiment assessing ecosystem responses to reach-scale riparian replanting and livestock exclusion in three degraded NPRs in southeastern Australia found no differences in water quality, organic matter or aquatic invertebrate community composition between paired treatment and control sites after 6–8 years, ascribing the lack of response to a drought and pervasive effects of catchment-scale degradation[180]. The effectiveness of NPR restoration activities could also be enhanced by recovering natural flow regimes, reducing pollutant inputs, remediating degraded catchments, controlling invasive species and repairing damaged channels and streambeds. These multiple restoration activities must be implemented at appropriately broad spatial scales, and prioritize recovery of lost functional connections between NPRs and perennial segments (such as through removal of instream barriers like weirs or dams). As responses to restoration in NPRs are likely to be slower than in equivalent-sized perennial segments because of their inherent intermittence and often-arid or semi-arid climatic setting, expectations must be modified to reflect these key differences.

Like restoration, targeted conservation of NPRs at the river-network scale has been rare, with most protected NPRs occurring in areas conserved for other reasons. For example, conservation actions targeting the endangered Coho salmon (*Oncorhynchus kisutch*) in the Russian River, California consisted of fish rescues during the non-flowing phase[181]. In NPRs in Texas, local habitat restoration increased populations of the endangered desert pupfish (*Cyprinidon bovinus*)[182]. In Australia, standard methods have been developed to classify disconnected pools (riverine waterholes)[183,184], informing actions taken to protect refuges that act as drought refuges for biodiversity during drought[58,184]. However, connectivity is required among individual refuges to maintain metapopulation and metacommunity dynamics[5], thus achieving effective network-scale conservation. In addition, effective network-scale conservation should seek to identify and protect key NPRs and their riparian zones. Systematic conservation planning tools such as Marxan[185] are powerful approaches for identifying priority sites acting as refuges for fish across entire river networks[135,136], and for evaluating the conservation value of NPRs considering both their aquatic and terrestrial species[186].

We suggest the most effective approach for river network management will be multifaceted, integrating targeted conservation and restoration strategies in an appropriate legislative context and explicitly acknowledging the importance of functional connections between NPRs and perennial segments. Although some biomonitoring approaches developed for perennial segments are effective in NPRs during flowing phases, biological indicators should include terrestrial communities to encompass the dry phases and provide a more nuanced and comprehensive perspective of ecological responses to the management strategies[176].

## [H1] Summary and future perspectives

Repeated cycles of flowing, non-flowing and, in particular, dry phases govern the biodiversity and ecosystem processes of NPRs, in turn influencing ecosystem dynamics in connected perennial segments and downstream waters. NPR can function as sources, sinks and refuges for water, energy, materials and organisms, and can delay and transform such ecosystem components, thus governing their fluxes across these connections. We contend that scientific recognition of the importance of these hydrological connections between perennial and NPRs in spatially variable river networks must be matched with a shift in river management. To facilitate such a shift, policy developments are needed to extend the legislation and regulations that protect perennial rivers to include NPRs.

There are five specific and actionable research domains within the next 3-5 years to further characterize how NPRs influence connected perennial segments and what this means for effective management at the river network scale. First, researchers shouldidentify how different functional connections affect fluxes of water, materials and organisms from NPRs to perennial segments at different locations within river networks (for example, upstream versus downstream segments). One approach is to use experimental manipulations to identify causal mechanisms. Such experiments should explore multiple fluxes concurrently due to their likely interacting effects.

Second, the influence of physical and hydrological features on different types of fluxes must be characterized. For example, how different are fluxes and their effects in small ephemeral NPRs should be compared to larger intermittent ones, as well as between single-thread and braided NPRs. Third, along these lines, the collective effects of different functional connections on ecosystem services provided by whole river networks must be evaluated and understood. For example, lagged connections could nullify or delay the influence of other types of connections upstream and alter the types, timing and location of ecosystem services contributed by NPRs.

These three points largely relate to improving our knowledge of NPRs and their role in river networks, but understanding how human impacts and management actions alter NPRs is equally important. Therefore, fourth, researchers must analyze how human activities modify functional connections in different river networks and, in particular, impact the provision of multiple ecosystem services. For example, the clearance – or restorative planting – of riparian vegetation along NPRs could change downstream functional connections and fluxes of organic matter. Finally, the scientific evidence provided by such research must be used to inform management actions as well as policy developments that enhance holistic legislative and regulatory protection for NPRs within river networks, to stop ongoing losses of biodiversity and ecological functions occurring in river networks worldwide.

Sustaining the integrity of entire river networks and the quality of downstream waters, including rivers, lakes, reservoirs, groundwaters, estuaries and in coastal areas, requires integrated management strategies that consider NPRs and their interconnections with perennial waters. Neglecting the important roles of NPRs compromises effective river management and could ultimately undermine actions taken to support the resilience of entire river networks as they adapt to global change

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## Author contributions

**TD, AJB, KF**: Conceptualization, Writing- Original draft preparation. **JC, KT, NC, RS**: Writing- Original draft preparation. **All**: Writing- Reviewing and Editing.

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## Key points

1. Non-perennial segments comprise over half the global river network. Ongoing climate change and human activities will further increase the occurrence of river drying.

2. Recurrent cycles of flowing, non-flowing and dry phases influence exchanges of water, energy, nutrients and organisms between non-perennial segments and connected perennial waters.

3. Physical, chemical and biological processes in non-perennial segments affect water quality and quantity, and ecological integrity in downstream receiving waters and entire river networks.

4. Historically, river science and management have focused on perennial river segments, neglecting the ubiquity and importance of non-perennial segments. This imbalance has often led to environmental problems such as poor water quality, loss of biodiversity and alteration of natural flow regimes at the river network scale.

5. Sustaining the water quality and ecological integrity of entire river networks and associated downstream waters requires integrated management strategies that explicitly consider non-perennial segments and their connections with perennial ones.

**Figure 1. Non-perennial river segments: definition, abundance and flow regimes.**

a| An idealized river network, indicating the different types of non-perennial (ephemeral and intermittent) river segments and their linkages with nearby waters. b| A typical hydrological sequence of a non-perennial segment, from flowing, non-flowing, dry and rewetting phases in the Calavon River, France. c| Global prevalence of non-perennial river networks. Panel b images courtesy of Bertrand Launay. Panel C reprinted from Ref[4] Springer Nature Limited.

**Figure 2. The connections between non-perennial and perennial river segments.**

a| Examples of connections between perennial and non-perennial segments. b| River-network patterns of co-occurring non-perennial (dashed lines) and perennial (solid lines) segments. c| Functions affecting fluxes of water, materials and organisms through non-perennial segments (blue triangle) before entering downstream waters (gray triangle), as in Ref[45]. Changes in arrow thickness reflect changes in the fluxes through the functional connections. Changes in arrow color reflect conversion of material or energy form. Changes in arrow shape reflect delayed delivery of material or energy.

**Figure 3. Effects of non-perenniality on river-scale leaf litter decomposition and transport.** Two theoretical river networks with contrasting spatial arrangement of non-perennial segments, upstream (panel a) and downstream (panel b). Leaf litter is poorly decomposed during dry phases in non-perennial segments. Instead, it accumulates and is then transported downstream en masse when flow resumes. As such, fluxes of decomposed and undecomposed litter vary substantially between the two river networks.

**Figure 4. Non-perenniality impacts on biodiversity patterns at the river network scale.**

Expected diversity patterns of two hypothetical river networks in which non-perennial sections are located upstream (panel a) and downstream (panel b). Circles represent communities hosting different species (symbols). For the two river networks, the magnitude of the effect of drying on biodiversity is the same (the same number of species disappears along a longitudinal gradient of drying). When non-perenniality is concentrated in the headwaters, the species-poor communities are composed of species not found in species-rich communities in downstream perennial segments. Conversely, when non-perenniality occurs downstream, the species-poor communities of these segments are subsets of species-rich communities from upstream perennial segments. These network patterns emerge because recolonization is faster from upstream to downstream, following the directionality of river flow. Adapted with permission from Ref[10], Elsevier.

**Figure 5. The future hydrological and biological fate of non-perennial rivers.**

a. Increasing (upward triangle) or decreasing (downward triangle) trends at the European scale (crosses indicate no trend) at the 10% significance level for the annual mean number of zero-flow days[96]. b. Mann–Kendall trends in annual no-flow days across the USA; red indicates longer no-flow duration, blue indicates a shorter flow duration[11]. Unfilled circles indicate there was not a significant tren. c. Relationships between annual no-flow duration (as a percentage) and the taxonomic richness (as the number of taxa) of lotic communities. The letter labels mark (1) benthic invertebrates in the Albarine River, France[38]; (2) benthic invertebrates in the Selwyn River, New Zealand[41]; (3) hyporheic invertebrates in the Selwyn River[187]; (4) riparian plants in the San Pedro River, Arizona[188]; and (5) fish in the Selwyn River[189]. The lines are based on regression models published in the original studies. Panel a reprinted with permission from ref 96, Taylor & Francis Group. Part b is reprinted from ref 11, CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Part c reprinted with permission from ref 16, Oxford University Press.

**Figure 6 Examples of ecosystem processes and services occurring in non-perennial segments and management opportunities.**

a| Residual and disconnected pools in a non-perennial river segment from Oregon (USA)[133] and Coho salmon juveniles in a non-perennial segment from the Russian River in California (USA). b| Rambla de Nogalte (SE Spain) during a flood in 2012, and an example risk inundation map. c| The Puerco River, a tributary of Río Grande (USA) during the flowing period, and the comparison of flood hydrographs and well response during floods in 2003[47]. d| Satellite image of Santa Clara ephemeral river inputs to the Channel Islands in California (USA) during flooding in 1998. Nutrients and chlorophyll-a were carried out from the river to the coastal waters during these floods[139]. Arrows show the river mouth. Panel a schematic is adapted from ref 190 CC BY 4.0

(https://creativecommons.org/licenses/by/4.0/). Panel a image courtesy of the Russian River Monitoring Program. Part b image is reprinted from ref 190, CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Part c, d photo reprinted with permission from the USGS. Part d adapted with permission from Ref 139, Elsevier.

**Figure 7. Examples of threats on non-perennial river segments.**

Garbage in the dry riverbed of the Hodgsons Creek, Victoria (panel a) and in Madura gully, West Australia (panel b). A non-perennial segment of the Chitterne Brook flows through an intensively grazed cow pasture in England, UK (panel c). Sheep in the non-flowing segments of the Barranc del Carraixet, Spain (panel d). Sewage effluent turning the non-perennial segment of the Sant Miquel River artificially perennial in Spain (panel e). Gravel extractions from dry riverbeds in France (Albarine River) (panel f) and Bolivia (Janq'u Qala) (panel g). An example of a map showing in red, the NPRs to be removed from protection by legislation in France, on the basis of their non-perenniality (panel h). The perennial segment in blue is the only part of the river network under protection by law. Sewage effluent discharge generates a permanent pool in a non-perennial segment of the Albarine River, France (panel i). Example of an NPR that is no longer under protection in eastern France, le Ruisseau des Tendasses (panel j). Photos courtesy of T. Sykes (panel c, h), H. Pella (panel j).

**TOC Summary:**

Non-perennial segments of rivers undergo cycles of flowing, non-flowing and dry phases, influencing ecosystem dynamics and services across the river network. This Review describes the occurrence, ecology, and future of these intermittent and ephemeral flows, and highlights the importance of protecting these segments.

## Glossary

**Beta diversity.** Spatial and temporal variability in community composition.

**Dry phase.** In a non-perennial river segment, a period of time with no spatially continuous flowing or non-flowing surface water, although disconnected surface-water pools and subsurface water can be present.

**Drying phase.** In a non-perennial river segment, the transitional period between a flowing or non-flowing phase and a dry phase, during which most or all surface water is lost.

**Ephemeral.** A non-perennial flow regime in which water only flows in response to rainfall events, and flowing phases are thus unpredictable and typically short (hours to weeks).

**Flow cessation.** The point in time at which surface water ceases to flow from upstream to downstream in a non-perennial segment.

**Flowing phase.** In a non-perennial river segment, a period of time in which water flows from upstream to downstream.

**Flow regime.** The temporal variability in the quantity and timing of discharge

**Gaining segment.** A stream segment in which flow increases due to the upwelling of groundwater into the surface channel.

**Losing segment:** A stream segment in which flow decreases due to the 'loss' of surface water that infiltrates the streambed towards the groundwater.**Intermittent.** A non-perennial flow regime, often seasonal, that is typically characterized by long flowing phases (usually multiple months) and short dry phases.

**Megadrought**. A drought that exceeds the duration of most droughts in the instrumental record.

**Non-flowing phase.** In a non-perennial river segment, a period of time when spatially continuous non-flowing (still or lentic) surface water is present.

**Non-perennial segments.** Those in which surface water recurrently stops flowing. These segments lose all or most of their surface water.

**Perennial segments.** Those in which surface water never stops flowing.

**Rewetting phase.** In a non-perennial river segment, the transitional period between a dry phase and a flowing or non-flowing phase.

**Synchrony**. The degree of concurrent change across spatially distinct segments or populations.