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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 physical, chemical and ecological responses to changes in the flow regimes of each river network, especially in response to human activities. The extent of non-perennial segments in river networks has increased owing to warming, changing hydrological patterns and human activities, and this increase is predicted 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

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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.

Introduction

Rivers cover less than 2% of the surface of the Earth 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 most threatened ecosystem types in the world; one out of three riverine species in these biodiversity hotspots is threatened with extinction³. River science and management have historically focused on perennial segments, which flow year-round, but rivers are increasingly being conceptualized as spatially variable networks in which hydrological connections between perennial and non-perennial segments enable exchanges of water, materials and organisms that support network-scale biodiversity and ecosystem functioning^{4,5} (Fig. 1a).

Non-perennial river segments (NPRs)⁴ recurrently experience flow cessation and lose most or all surface water (Fig. 1b). There is no global consensus in terminology^{6–9} owing to the high temporal and spatial variability of flows within and among NPRs¹⁰, but here they are classified generally as ‘ephemeral’, which only flow in response to rainfall, or ‘intermittent’, whose flows are longer and more predictable. When flowing (Fig. 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 groundwaters¹¹.

Every river network encompasses NPRs, particularly in the headwaters (Fig. 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 length⁴ (Fig. 1c), a proportion that is predicted 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 the 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 downstream¹⁴. 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.

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.

Typology and connections

Flow regimes.: The flow regime governs river geomorphology, water quality and ecology¹⁵ and, thus, is crucial to the understanding and management of river networks. In NPRs, the flow regime encompasses alternating flowing phases, non-flowing phases and, in many cases, dry phases (Fig. 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 thresholds²⁰. Early in the drying phase, 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 (Fig. 1c). Eventually, the riverbed dries, although subsurface flow can continue in saturated sediments beneath the dry channel (the hyporheic zone)^{20–22} (Fig. 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, the water table of the underlying aquifer is generally deep and the hyporheic zone usually dries quickly^{21,25}, whereas in gaining segments, upwelling groundwater can maintain a saturated hyporheic zone throughout the dry phase^{21,25}.

During the rewetting phase, surface water returns to inundate dry channels, sometimes quickly as flash floods^{26,27} or slowly as a rise in the water table. Similar to 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 the biodiversity and ecological integrity of a river network^{19,33}.

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 floodplain³⁴) (Fig. 1a), reflecting their ubiquitous co-occurrence in river networks globally (Fig. 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 ecosystems³⁵. 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 (Fig. 1a).

The spatial arrangements of NPRs and perennial river segments and their connections are diverse, complex and dynamic (Fig. 2a,b). Most river networks have naturally non-perennial headwaters that span the interface between terrestrial and aquatic domains³⁶. 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 occur in the downstream parts of river networks (Fig. 2b). Typically, river networks that flow out onto porous alluvial plains and recharge the underlying groundwater have downstream NPRs, such as the Tagliamento River (Italy²⁶) and the Albarine River (France³⁸). Other causes of downstream NPRs include excessive evaporation such as in the Diamantina River (Australia³⁹) and human activities such as damming and water abstraction cause artificial drying, for example, in the Colorado River (USA) and Yellow River (China⁴⁰). 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 Zealand⁴¹). In arid regions, whole river networks are often non-perennial, such as many rivers in northern and southwestern Africa⁴² and the Nordeste region in Brazil⁴³. 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.

Functional connections among river segments.: The different functional roles played by the varying connections between perennial segments and NPRs in space and time can be classified by the general mechanisms by which stream segments influence fluxes to downstream waters⁴⁵ (Fig. 2c). 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 (Fig. 2c). These contrasting effects occur because the fluxes can cease, increase, decrease or be stored when they pass through NPRs before entering downstream waters⁴⁵.

Connections between perennial segments and NPRs can act as sources of material, notably when the organic material that accumulates during dry phases is leached during rewetting, causing high nutrient fluxes to downstream waters⁴⁶ (Fig. 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 material⁴⁷ (Fig. 2c). As dry phases progress, terrestrial leaf litter from riparian zones is retained in NPRs and gradually accumulates on the streambed³³ (Fig. 2c). Upon rewetting, this organic material is flushed downstream, sometimes en masse²⁷, with NPRs functioning to delay its release and processing (Fig. 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} (Fig. 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.

Global distribution and temporal trends—NPRs are prevalent on all continents, representing more than half of the global river network⁴ (Fig. 1b). For example, 94% of river lengths in the southwestern USA⁴⁹ and more than 70% of river lengths in Australia are non-perennial⁵⁰. NPRs typically dominate in arid, semi-arid and dry subhumid regions, which represent up to half of the land surfaces of the Earth⁴⁰. 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}.

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 segments 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.

Non-perennial segment scale—Biotic groups respond locally to recurrent shifts between flowing, non-flowing and dry conditions in NPRs (Fig. 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 10-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 zone³⁸. An increase in the duration of the non-flowing phase from 0 (perennial flow) to 78 days reduced the survival rate of Coho salmon (*Oncorhynchus kisutch*) populations from 59% to 11% in tributaries of the Russian River in California, USA⁵².

Concurrent increases in terrestrial species richness occur as colonizing species arrive from riparian and wider terrestrial habitats⁵⁴. For example, 22 and 12 invertebrate taxa colonized the dry riverbeds of the Albarine River (France) and Oak Creek (Australia), respectively, within 2 months of the onset of the dry phase⁵⁴. Although aquatic species richness during the flowing phase at the site scale can be considerably lower in NPRs than in perennial segments⁵⁵, NPRs contribution to regional biodiversity can exceed those of perennial segments because of the inherently high β -diversity (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 organisms including invertebrates 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 dispersal abilities of species. Communities in NPRs connected to upstream perennial waters are soon replenished by colonists⁶², 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 segments⁶⁴. 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. By 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 production 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 favour denitrification, reducing nitrate concentrations²⁵. During dry phases, the microorganisms that make up biofilms coating the surfaces of sediment particles emit large quantities of CO₂ (ref. 66) and upon rewetting, large CO₂ pulses can occur from NPRs. Accounting for the global prevalence of NPRs, a single rewetting event contributes up to 10% of the daily carbon dioxide emissions from all perennial rivers and streams, particularly in temperate climates³³. When water returns, ecosystem processes such as respiration⁶⁷, nitrification and denitrification⁶⁸ and decomposition of leaf litter⁶⁹ 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 assessments⁷⁰.

Owing to drying-driven decreases in the functional diversity of their aquatic communities, NPRs can collectively perform fewer ecosystem functions than perennial ones during flowing phases⁷¹. These declines can be mitigated by functional redundancy⁷² (multiple species sharing traits), making the drying-induced loss of individual species functionally inconsequential⁷³. 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 collapse⁷⁴. Similarly, the loss of desiccation-sensitive microorganisms and invertebrate detritivores reduces decomposition rates of particulate organic matter that fuels food webs⁷⁵, altering the quantity, quality and timing of energy sources transported downstream to perennial segments after flow resumes^{46,76}.

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} (Fig. 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, which is likely to lead to ‘hotspots’ and ‘hot moments’ of material processing along a river network²⁵. For example, terrestrial plant litter accumulates in dry and non-flowing segments and this litter decomposes very slowly³³ (Fig. 3). When flow resumes in these segments, it can trigger rapid microbial decomposition of the labile plant litter³³ and flush the decomposing litter downstream²⁷ to perennial segments, providing a delayed subsidy of a resource that may be limiting to downstream consumers⁷⁹ (Fig. 3). However, the network-scale effects of non-perenniality largely depend on the spatial arrangement of NPRs within the river network (Fig. 3). Where NPRs are concentrated in the headwaters, particularly in deciduous forested areas³⁶, the downstream effects of non-perenniality will include high seasonal inputs of unprocessed litter (Fig. 3) that can reduce downstream water quality⁸⁰ or cause technical problems for dam intakes⁸¹. By 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 (Fig. 3).

Synchrony 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 segments⁸². 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 fluctuations¹⁹ or the recovery of biological communities during flowing phases¹⁸. When flow resumes in NPRs, hydrological connectivity is restored, promoting network-scale synchronization of such fluctuations and processes¹⁹.

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 segments and NPRs contributes to the persistence of regional biodiversity and, thus, stable ecosystem functioning and associated availability of ecosystem services⁸⁴.

At the river-network scale, NPRs increase the β -diversity of aquatic communities because of the simultaneous coexistence of different successional stages at the river-network scale^{18,40,87} (Fig. 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 organisms¹⁶ (Fig. 4). Alternatively, when non-perenniality is concentrated upstream, their biological communities can be more variable in space and time compared with their downstream perennial counterparts^{87,88} (Fig. 4). This variability is because recolonization from downstream perennial segments is limited by the unidirectional

flow of water along river networks and by topographic barriers, particularly for weak aquatic dispersers, increasing the role of 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 that can dominate over the local process of species-sorting during rewetting phases^{18,89,90}. The spatial extent of drying influences access to and from refuges in the network during dry phases 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 zones⁵⁶, hyporheic zones and groundwaters⁹³, and downstream ecosystems⁹⁴.

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.

Widespread and increasing non-perennial flow—The spatial extent of NPRs in global river networks has increased^{12,95,96} owing to shifts in flow regimes (Fig. 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 (refs. ^{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 KS, 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 resumes⁸⁶.

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} (Fig. 5a,b), there is high confidence that changes will intensify in the near future. These predicted changes include increases in dry-phase durations, frequency, severity⁹⁹ and rates of onset of both dry phases and flow resumption¹⁰⁵. 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^{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 latitudes⁴³.

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 sediments⁶⁰. Similarly, an increase in dry-phase duration and frequency could eliminate desiccation-sensitive species without enabling colonization by tolerant equivalents⁷² (Fig. 5c). Faster wet-to-dry transitions could shorten the time between environmental cues that trigger insect metamorphosis and its completion, reducing the emergence of adults¹¹³. 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 desiccation¹¹³. Prolonging the dry phase could prevent egg-laying behaviours by species that oviposit on water¹¹⁷. 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, because 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 drift¹¹⁹. 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 phases 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 markedly affected by increasing drying, such as the decomposition of terrestrial leaf litter, because they are more dependent on macroorganisms¹⁰¹. 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 multiple 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 decomposition¹²³.

In most cases, a reduction in aquatic biodiversity is likely to be 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}. By 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}.

Managing NPRs in river networks

The effects of alternating flowing, non-flowing and dry phases on water quality, biodiversity, ecosystem processes 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 segments 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 segments and NPRs.

Management implications of non-perenniality—Understanding the connections between perennial segments 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 posed by 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 Oregon¹³³ and in tributaries of the Russian River⁵² during dry phases provide refuges that promote the survival of juvenile Coho salmon (Fig. 6a). In the Russian River tributaries, the mean cumulative survival of salmon in these pools reached 50% (ref. 52). The deterioration or loss of these habitats, together with the lack of access to them owing to fragmentation by anthropogenic barriers¹³⁴, reduces fish populations, which, in turn, affects subsistence fishers⁵². 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 (Fig. 6b). For example, the dry channel of the ephemeral river Rambla de Nogalte, southeastern Spain efficiently absorbs flash flood waters and sediments except where walls and embankments have been built¹³⁷. Infiltration potential (the extent to which water can enter the sediments) in NPRs should be integrated into 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 (Fig. 6c). For example, flooding after a rain event in the ephemeral Sand River, Kenya, recharged the groundwater level in only 1.5 h (ref. 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 reservoir⁴⁷. The resultant availability of water can be a major benefit for people living and depending on these 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 (Fig. 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 available¹³⁹ (Fig. 6d).

Non-perenniality has major consequences for the 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 supply¹⁴⁰. However, in many regions, a substantial fraction of public water supply comes from sources that include NPRs¹⁴¹ or their underlying groundwater sources¹⁴². Surface water loss is also likely to reduce fish populations that support subsistence fishers⁵². Regulating services such as water purification, flood mitigation and climate regulation are all compromised by drying¹⁴³. For example, drying eliminates desiccation-sensitive microorganisms from biofilms and slows assimilation of inorganic nutrients (including anthropogenic pollutants) after flow resumes¹⁴⁴. Drying also affects the cultural services provided by 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 how people perceive drying^{147,148}, which greatly affects how river networks with extensive NPRs are likely to be managed.

Improving river-network management—Human activities alter flow regimes in NPRs, with major implications for functional connections and nearby perennial segments. However, compared with 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} (Fig. 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 segments 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 the biodiversity and ecosystem functions of river networks and their connected ecosystems (Fig. 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 1999¹⁵⁰).

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 biomonitoring¹⁵³. 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 France¹⁵⁴, the UK⁵¹ and the Czech Republic¹⁵⁵, river typologies used to implement the WFD do not distinguish between perennial segments and NPRs. In some cases, such as France, there are attempts to remove NPRs from national legislation and regulations (Fig. 7h). In the USA, 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 plans¹⁴⁸ 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 accepted¹⁵⁷, there is limited appreciation of the importance of connectivity between perennial segments 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 Europe¹⁵⁸ 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 regimes¹⁵⁹. 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^{164,165} model

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 multiplatform remote sensing technology could be combined with modelling approaches that target stream gauging or field observations to reduce bias and fill gaps. Such approaches 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 multispectral 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 interpretation¹⁶⁸, could support better integration of NPRs in distributed hydrological models¹⁶⁹.

Another major obstacle to more effective management of connected perennial segments 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 traits¹⁷³, metaclassification approaches¹⁷⁴, molecular tools¹⁷⁵ 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 segments and NPRs could encourage river managers to include both types of segments in river-network biomonitoring.

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 NPRs¹⁷⁸, 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 inherent intermittence and resilience of these systems 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 revegetation¹⁷⁹. 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 degradation¹⁸⁰. 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 must prioritize recovery of lost functional connections between NPRs and perennial segments (such as through removal of instream barriers such as 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.

Similar to restoration, targeted conservation of NPRs at the river-network scale is rare, with most protected NPRs occurring in areas conserved for other reasons. For example, conservation actions targeting the endangered Coho salmon in the Russian River consisted of fish rescues during the non-flowing phase¹⁸¹. In NPRs in Texas, USA, local habitat restoration increased populations of the endangered desert pupfish (*Cyprinodon bovinus*)¹⁸². In Australia, standard methods have been developed to classify disconnected pools (riverine waterholes)^{183,184}, informing actions taken to protect pools that act as refuges for biodiversity during drought^{58,184}. However, connectivity is required among individual refuges to maintain metapopulation and metacommunity dynamics⁵, 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 Marxan¹⁸⁵ 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 species¹⁸⁶.

We suggest that the most effective approaches 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 dry phases and thus provide a more nuanced and comprehensive perspective of ecological responses to the management strategies¹⁷⁶.

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 segments 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 should identify 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 owing to their likely interacting effects.

Second, the influence of physical and hydrological features on different types of fluxes must be characterized. For example, fluxes and their effects should be compared in small ephemeral NPRs and larger intermittent ones, as well as in 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 analyse 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 in river networks worldwide.

Sustaining the integrity of entire river networks and the quality of downstream waters, including rivers, lakes, reservoirs, groundwaters, estuaries and 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 river networks as they adapt to global change.

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Glossary

β -Diversity

Spatial and temporal variability in community composition

Dry phases

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 phases

In a non-perennial river segment, the periods of time in which water flows from upstream to downstream

Flow regime

The temporal variability in the quantity and timing of discharge

Gaining segments

Stream segments in which flow increases owing to the upwelling of groundwater into the surface channel

Intermittent

A non-perennial flow regime, often seasonal, that is typically characterized by long flowing phases (usually multiple months) and short dry phases

Losing segments

Stream segments in which flow decreases owing to the infiltration of surface water into the streambed towards the groundwater

Megadroughts

Droughts that exceed the duration of most droughts in the instrumental record

Non-flowing phases

In a non-perennial river segment, the periods of time in which spatially continuous non-flowing (still or lentic) surface water is present

Non-perennial segments

Stream segments in which surface water recurrently stops flowing. These segments lose all or most of their surface water

Perennial segments

Stream segments 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

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Key Points

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

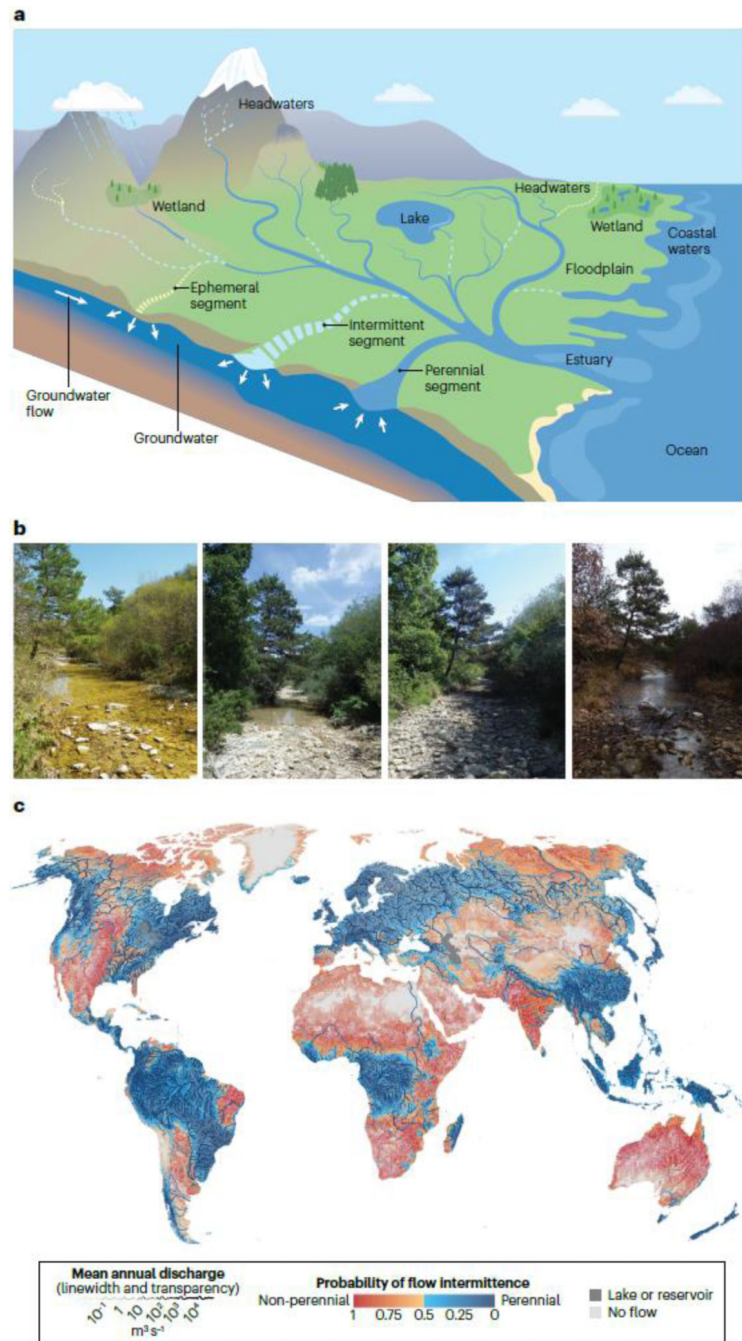


Figure 1. Non-perennial river segments: definition, abundance and flow regimes. a, An idealized river network, indicating the different types of non-perennial (ephemeral and intermittent) river segment and their linkages with nearby waters. b, A typical hydrological sequence of a non-perennial segment: 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 with permission from ref. 4, Springer Nature Limited.

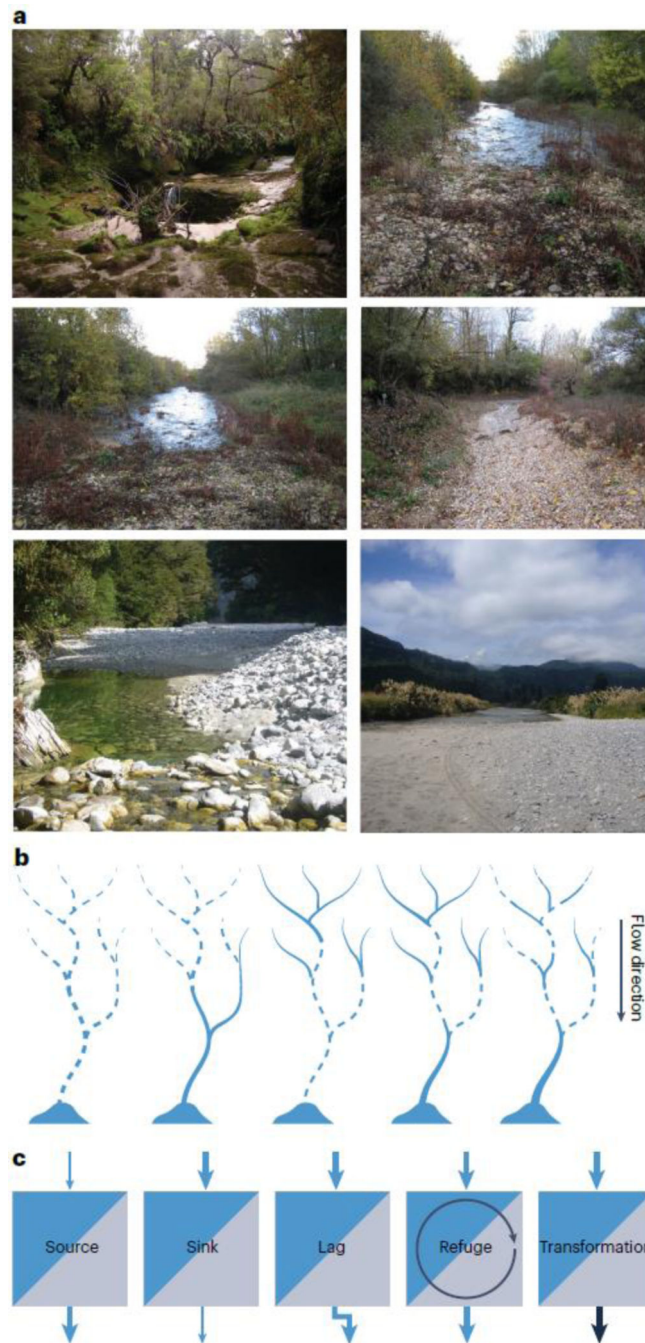


Figure 2. The connections between non-perennial and perennial river segments. a, Examples of connections between perennial and non-perennial segments. b, River-network patterns of co-occurring non-perennial (dashed lines) and perennial (solid lines) segments. c, Functions affecting fluxes of water, materials and organisms through non-perennial segments (blue triangles) before entering downstream waters (grey triangles), as in ref. 45. Changes in arrow thickness reflect changes in the fluxes through the functional connections. Changes in arrow

colour reflect conversion of material or energy form. Changes in arrow shape reflect delayed delivery of material or energy.

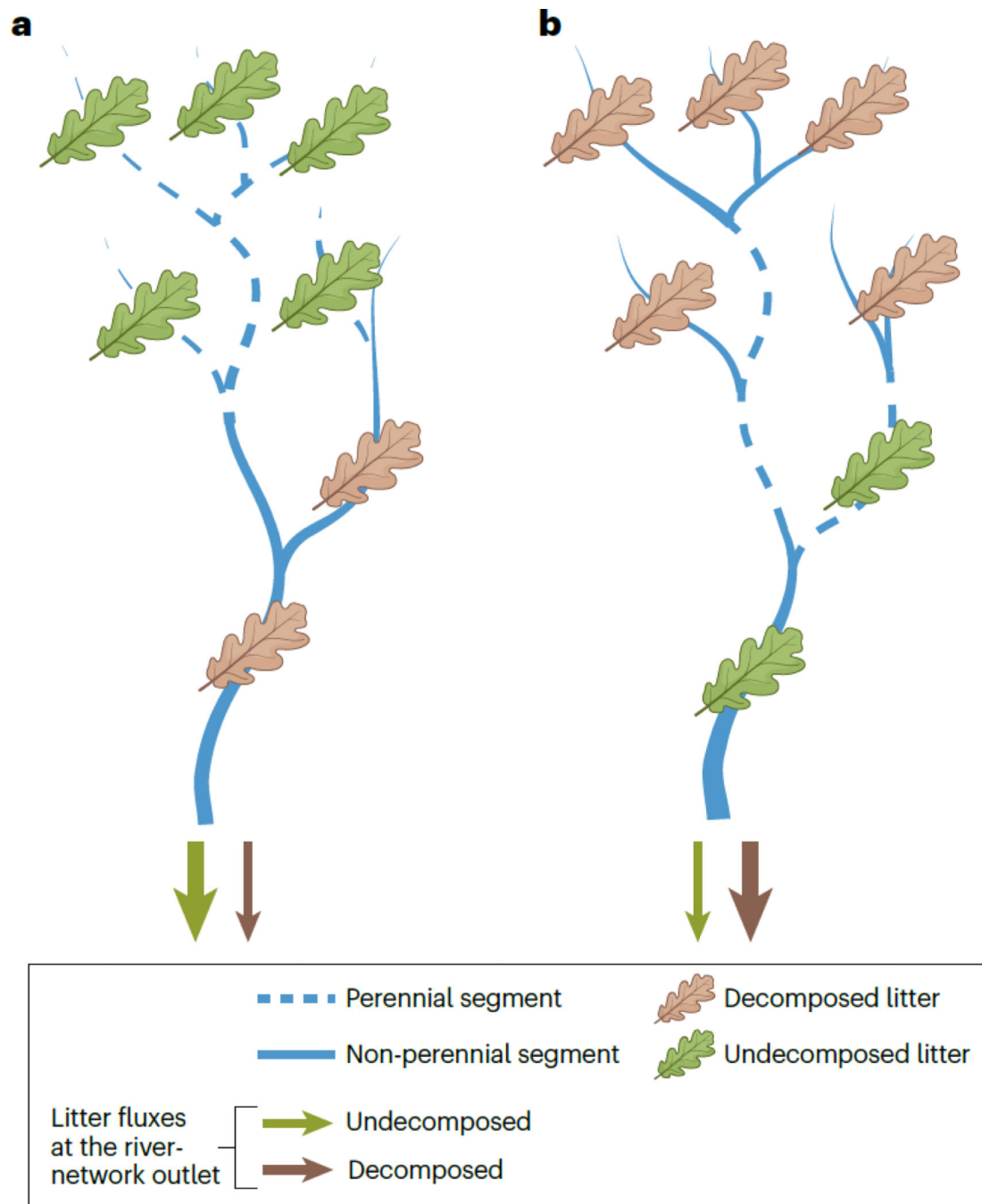


Figure 3.

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.

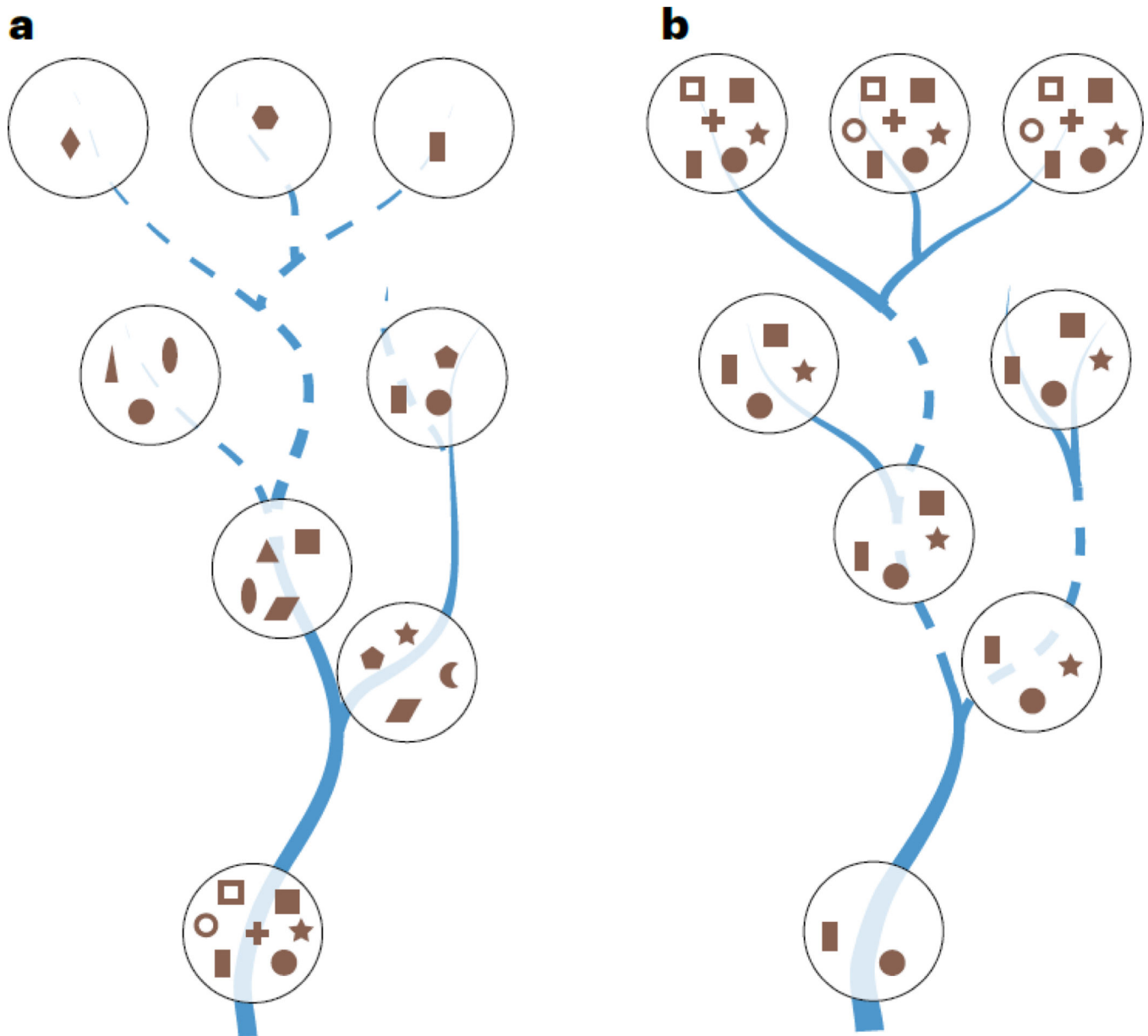


Figure 4. Non-perenniality impacts on biodiversity patterns at the river network scale. Predicted diversity patterns in two hypothetical river networks in which non-perennial sections are located upstream (panel a) and downstream (panel b). Circles represent communities hosting different species (shapes). 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.

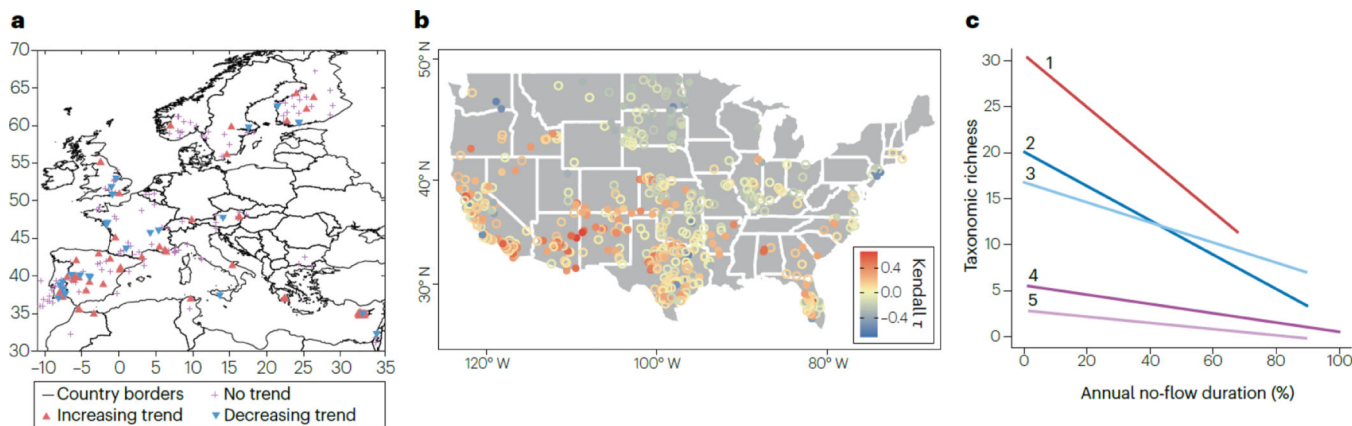


Figure 5. The future hydrological and biological fate of non-perennial rivers. a, Increasing or decreasing trends at the European scale (crosses indicate no trend) at the 10% significance level for the annual mean number of zero-flow days⁹⁶. b, Mann–Kendall trends in annual no-flow days across the USA; red and blue indicate longer and shorter no-flow durations, respectively¹². Unfilled circles indicate there was no significant trend. c, Relationships between annual no-flow duration (as a percentage) and the taxonomic richness (as the number of taxa) of aquatic communities. Labels mark (1) benthic invertebrates in the Albarine River, France³⁸; (2) benthic invertebrates in the Selwyn River, New Zealand⁴¹; (3) hyporheic invertebrates in the Selwyn River¹⁸⁷; (4) riparian plants in the San Pedro River, Arizona¹⁸⁸; and (5) fish in the Selwyn River¹⁸⁹. The lines are based on regression models published in the original studies. Panel a reprinted with permission from ref. 96, Taylor & Francis Group. Panel b is reprinted with permission from ref. 12, CC BY 4.0. Panel c is adapted with permission from ref. 16, Oxford University Press.

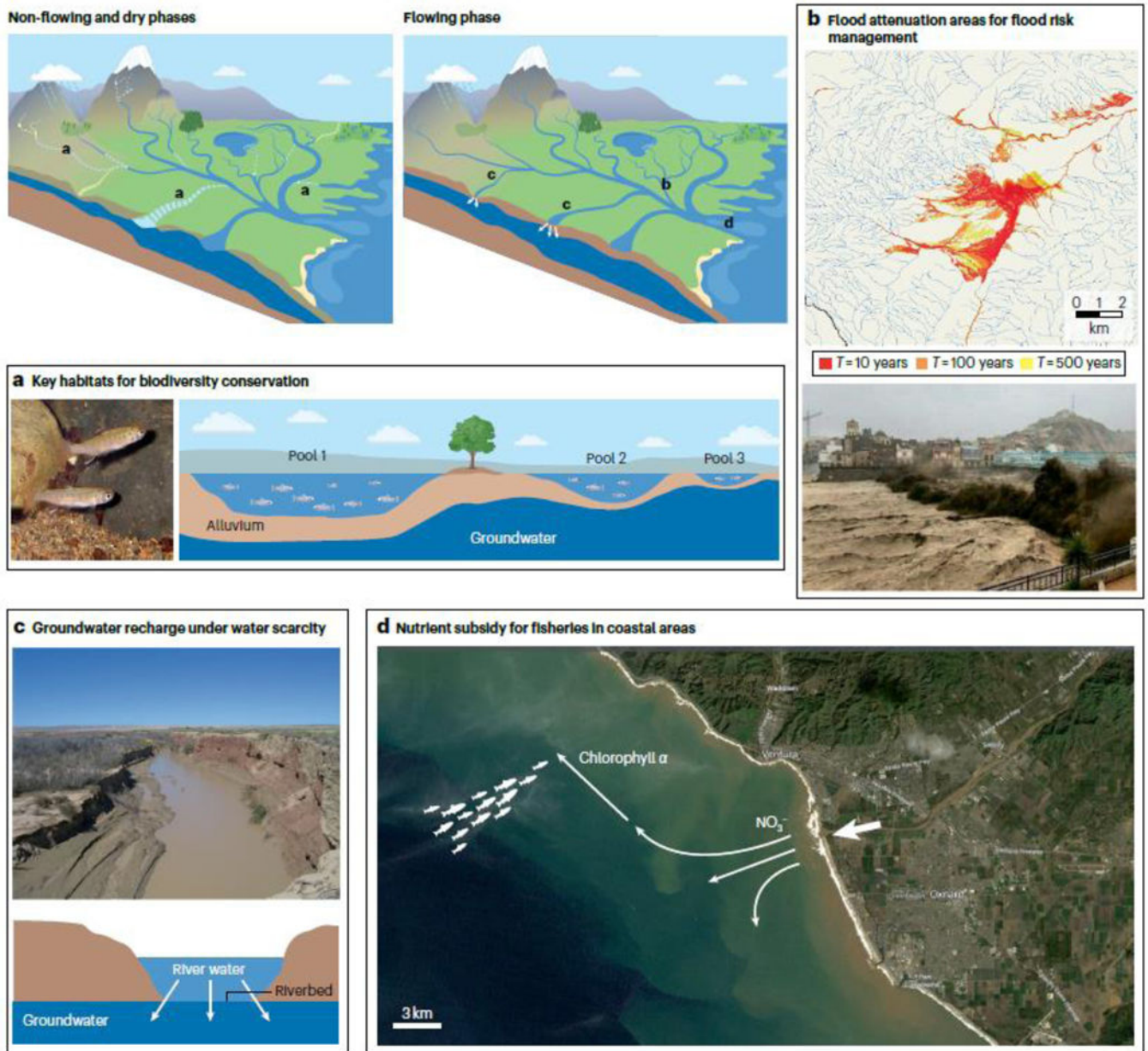


Figure 6. Examples of ecosystem processes and services occurring in non-perennial segments and management opportunities. a, Disconnected pools in a non-perennial river segment and Coho salmon juveniles in a non-perennial segment from the Russian River in California, USA. b, Rambla de Nogalte (southeastern Spain) during a flood in 2012, and an example of map showing inundation risks. c, The Río Puerco, a tributary of Río Grande, USA, during the flowing period and diagram showing groundwater recharge⁴⁷. 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 floods¹³⁹. The big white arrow shows the river mouth. Panel a schematic is adapted from ref. 190 CC BY 4.0. Panel a image courtesy of the Russian River Monitoring

Program. Panel b image is reprinted with permission from ref. 190, CC BY 4.0. Panels c and d photo reprinted with permission from the USGS.



Figure 7. Examples of threats on non-perennial river segments. Rubbish 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). A map showing the non-perennial river segments to be removed from protection by legislation in France (white; one of which is shown in panel j), on the basis of their non-perenniality (panel h); the perennial segment (yellow) is the only legally protected part of the river network. Sewage effluent generates a permanent pool in a non-perennial segment of the Albarine River, France (panel i). Non-perennial river segment that is no longer under protection in

eastern France, le Ruisseau des Tendasses (panel j). Photos courtesy of T. Sykes (panel c) and H. Pella (panels j and h).