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2 **Non-perennial segments in river networks**

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20 **Abstract**

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

36

37 **[H1] Introduction**

38 Rivers cover less than 2% of the Earth's surface but contain approximately 13% of all described
39 species and provide key ecosystem services such as provision of drinking water and food, regulation
40 of climate and opportunities for recreation^{1,2}. Despite their importance, rivers are among the world's
41 most threatened ecosystem types; one out of three riverine species in these biodiversity hotspots is
42 threatened with extinction³. River science and management have historically focused on **perennial**

43 segments [G], which flow year-round, but rivers are increasingly being conceptualized as spatially
44 variable networks in which hydrological connections between perennial and non-perennial segments
45 [G] enable exchanges of water, materials and organisms that support network-scale biodiversity and
46 ecosystem functioning^{4,5} (Figure 1a).

47 Non-perennial river segments (hereafter NPRs⁴) recurrently experience flow cessation [G] and lose
48 most or all surface water (Figure 1b). There is no global consensus in terminology⁶⁻⁹ owing to the
49 high temporal and spatial variability of flows within and among NPRs¹⁰, but here they are classified
50 generally as ‘ephemeral’ [G], which only flow in response to rainfall, or ‘intermittent’ [G], whose
51 flows are longer and more predictable. When flowing (Figure 1c), NPRs supply water, biota, energy,
52 nutrients and other materials to connected waters, influencing their water quality, biodiversity and
53 ecological integrity. These pulsed hydrological connections are often irregular in time and space yet
54 generate dynamic transition zones between aquatic and terrestrial habitats that extend longitudinally
55 down river channels, laterally onto floodplains and vertically into the underlying groundwaters¹¹.

56 Every river network encompasses NPRs, particularly in the headwaters (Figure 1a), but sometimes
57 also in substantial lengths of the lower segments and often in braided sections and alluvial
58 floodplains. NPRs naturally constitute more than half of the global river network length⁴ (Figure
59 1c), a proportion that is expected to rise in some regions because of climate change, land-use
60 alteration and increased water abstraction^{12,13}. Despite the ubiquity of NPRs and the ecological
61 importance of the hydrological connectivity they provide, almost all policies and management
62 practices for river networks are tailored for rivers that are perennial. The omission of NPRs from
63 river management seriously risks undermining effective protection of biodiversity and ecological
64 integrity of entire river networks and their ecosystem services. For example, rubbish dumped into
65 unmanaged headwater NPRs when surface water is absent will impact receiving perennial waters

66 when flow resumes and carries contaminants downstream¹⁴. Scientists and managers need greater
67 awareness of the importance of NPRs to biodiversity and ecosystem processes to protect entire river
68 networks.

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

76 **[H1] Characterizing non-perennial segments**

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

80 *[H2] Typology and connections*

81 *[H3] Flow regimes*

82 The **flow regime [G]** governs river geomorphology, water quality and ecology¹⁵ and, thus, is crucial
83 to the understanding and management of river networks. In NPRs, the flow regime encompasses
84 alternating **flowing phases [G]**, **non-flowing phases [G]** and, in many cases, **dry phases [G]** (**Figure**
85 **1c**). The frequency, duration and timing of each phase are powerful determinants of biodiversity,

86 ecological integrity and ecosystem services, both at local scales within NPRs^{16,17} and at the river-
87 network scale^{18,19}.

88 Drying is a gradual process whose effects are separated by hydrological thresholds²⁰. Early in the
89 **drying phase [G]**, while flow declines, surface water contracts and lateral aquatic habitats become
90 disconnected. As drying progresses, riffles and other flowing surface habitats disappear, leaving the
91 riverbed as disconnected pools (**Figure 1c**). Eventually, the riverbed dries, although subsurface flow
92 can continue in saturated sediments beneath the dry channel (the hyporheic zone)^{20–22} (**Figure 1c**).
93 This loss of surface water is governed by the type of surface–groundwater interactions occurring at
94 the segment scale^{23–25}. In **losing segments [G]** surface water, the water table of the underlying
95 aquifer is generally deep and the hyporheic zone usually dries quickly^{21,25}, whereas in **gaining**
96 **segments [G]**, upwelling groundwater can maintain a saturated hyporheic zone throughout the dry
97 phase^{21,25}.

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

104 [H3] Perennial and non-perennial segment connections

105 Most NPRs are structurally connected to perennial segments by the spatial continuity of the river
106 corridor (the channel, hyporheic zone and floodplain³⁴) (**Figure 1a**), reflecting their ubiquitous co-

107 occurrence in river networks globally (**Figure 1b**). This connectivity is well captured by the meta-
108 ecosystem perspective that considers river networks as mutually dependent arrays of perennial river
109 segments and NPRs that are connected to nearby aquatic and terrestrial ecosystems³⁵. The connected
110 terrestrial ecosystems range from riparian zones and uplands in the headwaters to floodplains
111 downstream, and the connected aquatic ecosystems encompass nearby wetlands, lakes, subsurface
112 groundwaters, reservoirs, estuaries and coastal waters (**Figure 1a**).

113 The spatial arrangements of NPRs and perennial river segments and their connections are diverse,
114 complex and dynamic (**Figure 2 a&b**). Most river networks have naturally non-perennial
115 headwaters that span the interface between terrestrial and aquatic domains³⁶. Flow in headwater
116 segments is driven by a combination of surface runoff, groundwater inputs and/or meltwater and is
117 often seasonal^{18,37}. NPRs can also be in the downstream parts of river networks (**Figure 2b**).
118 Typically, river networks that flow out onto porous alluvial plains and recharge the underlying
119 groundwater have downstream NPRs, such as the Tagliamento River (Italy²⁶) and the Albarine
120 River (France³⁸). Other causes of downstream NPRs include excessive evaporation such as in the
121 Diamantina River (Australia³⁹) and human activities such as damming and water abstraction cause
122 artificial drying, for example in the Colorado River (USA) and Yellow River (China⁴⁰). In other
123 river networks, the upper and lower segments are perennial but the mid-segments are non-perennial,
124 such as in the Selwyn River (New Zealand⁴¹). In arid regions, whole river networks are often non-
125 perennial, such as many rivers in northern and southwestern Africa⁴² and the Nordeste region in
126 Brazil⁴³. Most braided sections of rivers comprise NPRs, which can also be prevalent across large,
127 alluvial floodplains^{26,44}. The varying physical settings (such as channel shape and size, streambed
128 permeability, groundwater influence and large wood deposits), flow regimes and catchment land-

129 uses of these different network configurations drive physical, chemical and ecological responses to
130 the connections between NPRs and perennial segments.

131 [H3] Functional connections among river segments

132 The different functional roles played by the varying connections between perennial and NPRs in
133 space and time can be classified by the general mechanisms by which stream segments influence
134 fluxes to downstream waters⁴⁵ (**Figure 2c, Supplementary 1**). Fluxes of water, sediments, material
135 and organisms from perennial to NPRs and *vice versa* are often altered, which can have contrasting
136 effects on downstream river segments (**Figure 2c**). These contrasting effects occur because the
137 fluxes can cease, increase, decrease or be stored when they pass through NPRs before entering
138 downstream waters⁴⁵.

139 Connections between perennial segments and NPRs can act as sources of material, notably when the
140 organic material accumulated during dry phases is leached during rewetting, causing high nutrient
141 fluxes to downstream waters⁴⁶ (**Figure 2c**). When NPRs dry, exchanges of water cease, both
142 vertically between surface and groundwaters and longitudinally from upstream to downstream
143 waters, transforming NPRs into sinks of material⁴⁷ (**Figure 2c**). As dry phases progress, terrestrial
144 leaf litter from riparian zones is retained in NPRs and gradually accumulates on the streambed³³
145 (**Figure 2c**). Upon rewetting, this organic material is flushed downstream, sometimes en masse²⁷,
146 with NPRs functioning to delay its release and processing (**Figure 2c**). Connections between NPRs
147 and perennial river segments can also transform spatial patterns in chemical parameters such as
148 dissolved oxygen when anoxic or hypoxic pulses of water from remnant pools or rewetting fronts
149 are carried downstream to connected aquatic ecosystems by rewetting flows^{19,48} (**Figure 2c**). The

150 types and direction of processes that are altered are likely to reflect flow regime characteristics such
151 as dry phase duration and the longitudinal sequence of perennial segments and NPRs.

152 *[H2] Global distribution and temporal trends*

153 NPRs are prevalent on all continents, representing more than half of the global river network⁴
154 (**Figure 1b**). For example, 94% of river lengths in the southwestern USA⁴⁹ and more than 70% of
155 river lengths in Australia are non-perennial⁵⁰. NPRs typically dominate in arid, semi-arid, and dry
156 sub-humid regions, which represent up to half of the Earth's land surfaces⁴⁰. These segments are
157 also common across alpine, boreal, continental, Mediterranean, oceanic, polar and tropical
158 regions^{16,51}. Every river network on Earth includes NPRs, especially in their headwaters.
159 Headwaters are estimated to represent more than 70% of the total river network length and are
160 typically prone to drying^{4,36}.

161

162 **[H1] The ecology of non-perennial segments**

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

168 *[H2] Non-perennial segment scale*

169 Biotic groups respond locally to recurrent shifts from flowing to non-flowing and dry conditions in
170 NPRs (**Figure 1c**). Aquatic biodiversity declines steadily in response to non-perenniality as taxa

171 lacking adaptations promoting resistance or resilience to drying are lost^{16,17}. The extent of these
172 declines is governed by hydrological parameters such as the duration of non-flowing and dry phases,
173 with longer dry phases resulting in greater declines^{38,52,53}. For example, a ten-day increase in the dry
174 phase in the Albarine River, France, led to an additional loss of six invertebrate taxa from the
175 benthic community and four invertebrate taxa from the hyporheic zone³⁸. An increase in the duration
176 of the non-flowing phase from 0 (perennial flow) to 78 days reduced the survival rate of Coho
177 salmon populations from 59 to 11% from tributaries of the Russian River in California (USA)⁵².

178 Concurrent increases in terrestrial species richness occur as colonizing species arrive from riparian
179 and wider terrestrial habitats⁵⁴. For example, 22 and 12 invertebrate taxa colonized the dry riverbeds
180 of the Albarine River (France) and Oaky Creek (Australia), respectively, within two months of the
181 onset of the dry phase⁵⁴. Although aquatic species richness during the flowing phase at the site-scale
182 can be considerably lower in NPRs than perennial segments⁵⁵, their contribution to regional
183 biodiversity can exceed those of perennial segments because of the inherently high beta diversity
184 [G] (regional variability in community composition) in space and time and the presence of
185 specialized species adapted to non-perennial conditions^{51,56}.

186 When flow resumes, aquatic organisms recolonize from various refuges, including upstream pools,
187 moist sediments and leaf litter⁵⁷⁻⁵⁹. Some aquatic macroinvertebrates and diatoms have desiccation-
188 tolerant forms that can survive in moist riverbed sediments^{60,61}. Recovery rates and trajectories vary
189 depending on connectivity to refuges and on species' dispersal abilities. Communities in NPRs
190 connected to upstream perennial waters are soon replenished by colonists⁶², whereas community
191 recovery in isolated NPRs can be slow and more stochastic^{58,63}. Recovery can be modified by
192 anthropogenic influences such as fragmentation by instream barriers that sever links between NPRs
193 and sources of colonists in perennial segments⁶⁴. Despite well-developed recovery mechanisms,

194 differences persist between communities in perennial and non-perennial segments^{38,55}. These
195 differences can be particularly pronounced and long-lasting when unprecedented dry phases occur
196 during drought events. In contrast, communities can recover rapidly, generally within a few weeks,
197 after ‘normal’ seasonal dry phases^{63,65}.

198 Aquatic species control fundamental ecosystem processes such as primary productivity and organic
199 matter decomposition, and changes in aquatic biodiversity related to non-perenniality therefore alter
200 ecosystem functioning. For example, desiccation-tolerant microorganisms in natural NPRs mediate
201 biogeochemical cycling. When flow decreases, hypoxic conditions that develop in disconnected
202 pools favor denitrification, reducing nitrate concentrations²⁵. During dry phases, the microorganisms
203 that make up biofilms coating the surfaces of sediment particles emit large quantities of CO₂⁶⁶ and
204 upon rewetting, large CO₂ pulses can occur from NPRs. Accounting for the global prevalence of
205 NPRs, a single rewetting event contribute up to 10% of the daily carbon dioxide emissions from all
206 perennial rivers and streams, particularly in temperate climates³³. When water returns, ecosystem
207 processes such as respiration⁶⁷, nitrification and denitrification⁶⁸ and decomposition of leaf litter⁶⁹
208 quickly resume to previous levels. Recognizing the active contribution of NPRs to carbon cycling –
209 during both wet and dry phases – could improve the accuracy of local-to-global-scale assessments⁷⁰.

210 Due to drying-driven decreases in the functional diversity of their aquatic communities, NPRs can
211 collectively perform fewer ecosystem functions than perennial ones during flowing phases⁷¹. These
212 declines could be mitigated by functional redundancy⁷² (multiple species sharing traits), making the
213 drying-induced loss of individual species functionally inconsequential⁷³. However, as losses
214 accumulate, the risk of losing functionally unique species increases, potentially representing a
215 tipping point that drives the ecosystem to an alternative state. For example, by eliminating pivotal
216 species, especially predators, drying can alter the structure and functioning of food webs, potentially

217 leading to partial food-web collapse⁷⁴. Similarly, the loss of desiccation-sensitive microorganisms
218 and invertebrate detritivores reduces decomposition rates of particulate organic matter that fuels
219 food webs⁷⁵, altering the quantity, quality and timing of energy sources transported downstream to
220 perennial segments after flow resumes^{46,76}.

221 *[H2] River-network scale*

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

228 Complex responses to drying also result from the propagation of biogeochemical and
229 ecological influences downstream by surface and subsurface flows. These transfers can slow, cease
230 or be amplified by functional connections across hydrological phases that are likely to lead to
231 ‘hotspots’ and ‘hot moments’ of material processing along a river network²⁵. For example, terrestrial
232 plant litter accumulates in dry and non-flowing segments and this litter decomposes very slowly³³
233 (**Figure 3**). When flow resumes in these segments, it can trigger rapid microbial decomposition of
234 the labile plant litter³³ and flush the decomposing litter downstream²⁷ to perennial segments,
235 providing a delayed subsidy of a resource that may be limiting to downstream consumers⁷⁹ (**Figure**
236 **3**). However, the network-scale effects of non-perenniality largely depend on the spatial
237 arrangement of NPRs within the river network (**Figure 3**). Where NPRs are concentrated in the
238 headwaters, particularly in deciduous forested areas³⁶, the downstream effects of non-perenniality
239 will be high seasonal inputs of unprocessed litter (**Figure 3**) that can reduce downstream water

240 quality⁸⁰ or cause technical problems for dam intakes⁸¹. In contrast, where NPRs are in downstream
241 segments of river networks, which are typically less dependent on terrestrial litter inputs from
242 riparian zones, lower fluxes of unprocessed litter are expected in downstream river network
243 segments. Meanwhile, periods of disconnectivity retain leaf litter in the headwaters, which can thus
244 become hotspots of carbon cycling (Figure 3).

245 **Synchrony [G]** can describe how local responses propagate at the river network scale and can be
246 enhanced by connectivity (upstream dispersal, advective transport) between segments or by a driver
247 such as drying that simultaneously affects multiple segments⁸². By reducing longitudinal
248 connectivity of flowing water, the effects of non-perenniality of river segments can reverberate
249 throughout a river network and desynchronize, for example, diel dissolved oxygen fluctuations¹⁹ or
250 the recovery of biological communities during flowing phases¹⁸. When flow resumes in NPRs,
251 hydrological connectivity is restored, promoting network-scale synchronization of such fluctuations
252 and processes¹⁹.

253 The dynamics of aggregate stream systems are typically less variable than their individual
254 contributing segments^{83,84} because combining asynchronous contributions from many segments has
255 a stabilizing effect (the ‘portfolio concept’⁸³). However, widespread non-perenniality in river
256 networks can synchronize dynamics across populations, increasing the risk of regional species
257 extinctions^{85,86}. Therefore, when aggregated in river networks, the variation in flow regimes between
258 perennial and NPRs contributes to persistence of regional biodiversity and, thus, stable ecosystem
259 functioning and associated availability of ecosystem services⁸⁴.

260 At the river-network scale, NPRs increase the beta diversity of aquatic communities because of the
261 simultaneous coexistence of different successional stages at the river network scale^{18,40,87} (**Figure 4**).
262 Depending on the spatial arrangement of NPRs and perennial segments within the river network,

263 communities in NPRs can comprise a subset of the taxa inhabiting perennial segments, notably
264 when NPRs are downstream of perennial segments acting as a source of colonizing organisms¹⁶
265 (**Figure 4**). Alternatively, when non-perenniality is concentrated upstream, their biological
266 communities can be more variable in space or time compared to their downstream perennial
267 counterparts^{87,88} (**Figure 4**). This variability is because recolonization from downstream perennial
268 segments is limited by the unidirectional flow along river networks and by topographic barriers,
269 particularly for weak aquatic dispersers, promoting alternative sources of colonists in the landscape
270 such as perennial waterbodies and the underlying hyporheic zone.

271 Including NPRs in the study of biodiversity dynamics within river networks demonstrates the
272 importance of dispersal, a regional process which can dominate over the local process of species-
273 sorting during rewetting phases^{18,89,90}. The spatial extent of drying influences the access to and from
274 refuges in the network during the dry periods and thus controls the dispersal of organisms and
275 overall metacommunity dynamics^{18,91,92}. However, the relative contribution of species dispersal in
276 shaping riverine biodiversity patterns is highly context-dependent, as well as being taxon-specific
277 and extends to nearby habitats such as riparian zones⁵⁶, hyporheic zones and groundwaters⁹³ and
278 downstream ecosystems⁹⁴.

279 **[H1] The future of river networks**

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

284 285 ***[H2] Widespread and increasing non-perennial flow***

286 The spatial extent of NPRs in global river networks has increased^{12,95,96} due to shifts in flow regimes
287 (**Figure 5a & b**). This increase is predicted to continue^{13,43,97}, driven in part by climatic trends such
288 as rising temperatures and associated increases in evaporation, changing precipitation patterns, and
289 the increasing occurrence of drought in many parts of the world^{98–100}. For example, previously
290 perennial rivers in Europe and China dried for the first time during the severe droughts that began in
291 2022^{101,102}. In addition, intensifying use of water resources, including surface and groundwater
292 abstraction, storage and diversion, are driving shifts from perennial to artificially non-perennial
293 flow^{40,101}. In Kansas (USA), for example, widespread irrigation from the High Plains aquifer since
294 the mid-1900s has lowered the regional water table, sometimes by more than 50 m, shifting rivers
295 and streams from naturally gaining and perennially flowing to artificially losing and non-perennial
296 flow^{103,104}.

297 The predicted increase in the spatial extent of NPRs represents a network-scale decline in aquatic
298 habitat availability and hydrological connectivity which will alter riverine biodiversity, with
299 consequences for ecosystem functioning and services. For example, a decrease in the availability
300 and quality of wet refuges that support aquatic organisms during dry phases will synchronize
301 biological responses to drying, reducing metacommunity resilience and local community recovery
302 after flow resumes⁸⁶.

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

304 Flow regime characteristics such as the frequency, duration, severity and timing of flowing, non-
305 flowing and dry phases are changing, as is the rate of change during transitional drying and
306 rewetting phases. Despite considerable regional variability in the evidence for such changes^{12,96}
307 (**Figure 5a & b**), there is high confidence that changes will intensify in the near future. These

308 predicted changes include increases in dry-phase duration and in dry-phase frequency, severity⁹⁹ and
309 rates of onset of both dry phases and flow resumption¹⁰⁵. Inherent within the predicted increase in
310 dry-phase duration is the earlier onset and/or later cessation of dry phases in NPRs with seasonal
311 flow regimes, as well as an increased co-occurrence of dry phases and extreme climatic events,
312 particularly heatwaves^{106–108}.

313 In the context of megadroughts [G]^{109,110}, dry phases could continue uninterrupted for years in
314 NPRs that currently have seasonal flow regimes. Deglaciation and snow loss are expected to reduce
315 summer flows, resulting in shifts to non-perennial flow^{111,112}. Conversely, warmer winters with
316 greater snowmelt and glacial melting could cause NPRs to become perennial at higher elevations
317 and northern latitudes⁴³.

318

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

320 Biological communities in NPRs are expected to respond to future changes in flow regime
321 characteristics. An increase in dry-phase duration and severity (caused by a lack of precipitation,
322 water abstraction, and/or high temperatures and manifesting as reduced in-channel water
323 availability) is likely to reduce the survival of desiccation-tolerant life stages of aquatic organisms
324 within the riverbed sediments⁶⁰. Similarly, an increase in dry-phase duration and frequency in NPRs
325 could eliminate desiccation-sensitive species without enabling colonization by tolerant equivalents⁷²
326 (**Figure 5c**). Faster wet-to-dry transitions could shorten the time between environmental cues that
327 trigger insect metamorphosis and its completion, reducing the emergence of adults¹¹³. Rapid-onset
328 rewetting phases that wash insects, crustaceans, amphibians or fish straight from refuges to

329 downstream segments could reduce local community recovery rates^{114–116}. Both earlier dry-phase
330 onset and later dry-phase termination could reduce successful completion of aquatic stages of life
331 cycles by riverine animals. For example, earlier onset of drying could reduce the proportion of
332 aquatic juvenile insects that emerge as terrestrial adults in time to avoid desiccation¹¹³. Prolonging
333 the dry phase could prevent egg-laying behaviors by species that oviposit on water¹¹⁷. Distances and
334 connectivity to perennial refuges in the landscape may determine post-drying community
335 composition^{86,118}. In cases of shifts from perennial to non-perennial flow regimes, biological
336 responses might be particularly dramatic where species lack adaptations to drying. However, if
337 NPRs are abundant in a river network, they could provide colonists adapted to the newly non-
338 perennial conditions^{86,101}.

339 In terms of ecosystem processes, biofilms generally recover within a few days upon flow
340 resumption, from dormant forms and through drift¹¹⁹. Some ecosystem processes, such as primary
341 production and ecosystem respiration, are therefore highly resilient to drying. As such, natural NPRs
342 experiencing longer or more frequent dry periods might not be severely affected in the near future,
343 although shifts towards greater reliance on external energy sources could occur^{120,121}. Other
344 processes could be more dramatically affected by increasing drying, such as the decomposition of
345 terrestrial leaf litter, because they are more dependent on macroorganisms¹⁰¹. Where once-perennial
346 segments become non-perennial, biodiversity is predicted to respond strongly, with multiple
347 cascading effects on ecosystem processes, although these effects will depend on the functional
348 redundancy of a community and the types of organisms involved^{101,120,122}. Finally, increasing non-
349 perenniality is likely to occur in streams affected by other anthropogenic stressors, such as pollution
350 and water abstraction, that interact to cause complex changes to ecosystem processes. For example,
351 mesocosm experiments suggest that flow reductions and fine sediment pollution have synergistic

352 effects on both algal biomass and thus primary production, and on invertebrate abundance and thus
353 leaf litter decomposition¹²³.

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

368 **[H1] Managing NPRs in river networks**

369 The effects of alternating flowing, non-flowing and dry phases on water quality, ecosystem
370 processes, biodiversity and ecosystem services at the river network scale mean that management
371 expectations of natural NPRs must differ from those of perennial segments^{93,130,131}. In particular, to
372 be effective, management, conservation and restoration of river networks must explicitly recognize
373 perennial and NPRs and their multifaceted connections. This section discusses the management

374 implications of the presence of NPRs in river networks and of the connections between perennial
375 and NPRs.

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

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

382 Dry-phase refuges located in NPRs are crucial to maintaining freshwater biodiversity at the river
383 network scale^{52,132}. For example, disconnected pools maintained in intermittent streams in coastal
384 Oregon¹³³ and in tributaries to the Russian River in California⁵² during dry phases provide refuges
385 that promote the survival of juvenile Coho salmon (*Oncorhynchus kisutch*) (**Figure 6a**). In the
386 Russian River tributaries, the mean cumulative survival of salmon in these pools reached 50%⁵².
387 The deterioration or loss of these habitats, together with the lack of access to them due to
388 fragmentation by anthropogenic barriers¹³⁴, reduces fish populations which, in turn, affects
389 subsistence fishers⁵². Therefore, management strategies for biodiversity conservation of entire river
390 networks should prioritize the identification and protection of these refuges^{135,136}.

391 NPRs can attenuate floods and act as flood protection zones in the catchment (**Figure 6b**). For
392 example, the dry channel of the ephemeral river Rambla de Nogalte, SE Spain, efficiently absorbs
393 flash flood waters and sediments except where walls and embankments have been built¹³⁷.
394 Infiltration potential (the extent to which water can enter the sediments) in NPRs should be
395 integrated in flood risk management at the river network scale by identifying priority zones where

396 this function is maximized. The high infiltration capacity of dry riverbeds in NPRs can also limit
397 evaporative losses and facilitate groundwater recharge (**Figure 6c**). For example, flooding after a
398 rain event in the ephemeral Sand River, Kenya, recharged the groundwater level in only 1.5
399 hours¹³⁸. Similarly, 49% of the monsoon flood volume from the ephemeral Río Puerco basin in New
400 Mexico, USA, recharged the aquifer and the rest entered a downstream reservoir⁴⁷. The resultant
401 availability of water resources can be a major benefit for people living and depending on these water
402 resources in arid and semi-arid regions.

403 Nutrients released from NPRs during flowing phases can subsidize downstream connected waters
404 and support biodiversity and ecosystem functioning downstream, enhancing services provided by
405 freshwater and marine fisheries (**Figure 6d**). For example, the timing of a nutrient pulse from the
406 ephemeral Santa Clara River (California, USA) to at least 20 km offshore during the 1998 floods
407 was key to supporting marine productivity at a time when nutrient inputs from oceanic upwelling
408 were less available¹³⁹.

409 Non-perenniality has major consequences for provisioning, regulating and cultural ecosystem
410 services made available by river networks. River drying prevents surface water abstraction for uses
411 such as crop irrigation and public water supply¹⁴⁰. However, in many regions, a substantial fraction
412 of public water supply comes from sources that include NPRs¹⁴¹ or their underlying groundwater
413 sources¹⁴². Surface water loss is also likely to reduce fish populations that support subsistence
414 fishers⁵². Regulating services such as water purification, flood mitigation and climate regulation are
415 all compromised by drying¹⁴³. For example, drying eliminates desiccation-sensitive microorganisms
416 from biofilms and slows assimilation of inorganic nutrients (including anthropogenic pollutants)
417 after flow resumes¹⁴⁴. Drying also affects cultural services of river networks by limiting water-
418 associated activities such as boating while creating opportunities for new activities such as

419 rambling^{140,145,146}. These impacts on cultural services depend on people's perceptions of
420 drying^{147,148}, which greatly affects how river networks with extensive NPRs are likely to be
421 managed.

422 ***[H2] Improving river network management***

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

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

441 Major obstacles need to be overcome to extend legislative protection for NPRs^{149,151}. In Europe, the
442 Water Framework Directive (WFD)¹⁵² largely omits NPRs from conservation, restoration and
443 biomonitoring¹⁵³. For example, the WFD only recognizes NPRs in one 'river type' in some countries
444 in the Mediterranean region. Elsewhere, where NPRs are less prevalent but nonetheless diverse and
445 extensive, such as in France¹⁵⁴, the UK⁵¹ and the Czech Republic¹⁵⁵, river typologies used to
446 implement the WFD do not distinguish between perennial and NPRs. In some cases, such as France,
447 there are attempts to remove NPRs from national legislation and regulations (**Figure 7h**). In the US,
448 under implementation of the Clean Water Act, some NPRs are not included as Waters of the United
449 States, potentially exposing them to impacts from activities such as dredging and waste dumping.

450 Another obstacle is the public perception of NPRs in river networks as less valuable than perennially
451 flowing waters^{147,148,156}. Consequently, NPRs are often overlooked in restoration and conservation
452 plans¹⁴⁸ and there is little appreciation of their ecosystem services^{143,146}. Even in Australia, where
453 the need for separate water quality guidelines for NPRs is accepted¹⁵⁷, there is limited appreciation
454 of the importance of connectivity between perennial and NPRs in influencing water quality.

455 Scientists need to communicate the importance of ecosystem services provided by NPRs to the
456 general public, river managers, politicians, policy makers and other stakeholders. Such evidence-
457 informed actions could include producing fact sheets and policy briefs, using social media and
458 conducting collaborative research projects with citizen scientists, river managers and stakeholders.
459 For example, the open-source smartphone application DryRivers enables both citizen and
460 professional scientists to map NPRs throughout Europe¹⁵⁸ and has substantially increased public
461 appreciation of the nature and extent of NPRs.

462 Logistically, there are serious limitations in fundamental hydrological data and hydrographic
463 mapping for NPRs in river networks. Stream gauges that quantify flow and describe flow regime

464 components of a stream segment are typically placed along larger perennial streams and fail to
465 capture NPR flow regimes¹⁵⁹. Most available maps are based on static, low-resolution surveys and
466 cartography that omit many headwater NPRs^{36,160}. Despite increasing efforts at various scales to
467 statistically^{4,161–163} and mechanistically model^{164,165} the distribution and flow regimes of NPRs, such
468 efforts are hampered by the scant stream gauge and groundwater-level data, which amplifies
469 uncertainty over large areas^{4,163}.

470 Further development and refinement of multi-platform remote-sensing technology could be
471 combined with modeling approaches that target stream gauging or field observations to reduce bias
472 and fill gaps. The approach would enable the production of hydrographic maps that better reflect the
473 dynamic connections between all segments in river networks. Remote-sensing platforms with
474 synthetic aperture radar (SAR) are better able to capture surface water blocked by clouds, vegetation
475 or shadows than multi-spectral platforms such as LandSat or CubeSat^{166,167}. Future use of high
476 spatial and temporal resolution SAR datasets (for example, from NASA-ISRO SAR) to map NPRs,
477 in tandem with advances in data interpretation¹⁶⁸, could support better integration of NPRs in
478 distributed hydrological models¹⁶⁹.

479 Another major obstacle to more effective management of connected perennial and NPRs in river
480 networks is the limited availability of monitoring tools and approaches that perform equally well in
481 both segment types. Most river management tools have been developed primarily or exclusively for
482 perennial segments^{131,170,171} and typically perform poorly in NPRs. For example, biomonitoring
483 indices used to indicate river health can rarely disentangle the effects of drying from those of
484 stressors associated with human activities^{131,170,172,173}. Functional traits¹⁷³, metacommunity approaches¹⁷⁴,
485 molecular tools¹⁷⁵ and data on composition of terrestrial and semi-aquatic assemblages^{176,177} all have
486 the potential to enhance assessment of NPR health. Developing common tools and approaches that

487 are applicable in both perennial and NPRs could encourage river managers to include both types of
488 segments in river network biomonitoring.

489

490 *[H2] Restoration and conservation of NPRs*

491 Many NPRs are severely degraded by human activities, and thus require restoration to recover lost
492 biodiversity and ecological integrity. NPRs that are not degraded are seldom adequately protected
493 yet many urgently need conservation to preserve their current values. However, ignorance of these
494 values, especially in ephemeral NPRs¹⁷⁸, and of the importance of NPRs to connected perennial
495 segments has meant that efforts to restore or conserve NPRs are rare. It is likely that the same tools
496 and approaches used for conserving and restoring perennial segments are equally applicable to
497 NPRs. However, expectations of the outcomes, especially rates and trajectories of responses to
498 restoration, need to consider these systems' inherent intermittence and their resilience to different
499 types of impacts (such as altered flow regimes versus altered water quality).

500

501 The few attempts at targeted restoration of NPRs have focused on riparian revegetation¹⁷⁹. Of these
502 attempts, even fewer have sought to evaluate restoration success or investigate pathways and
503 mechanisms of ecological recovery. An experiment assessing ecosystem responses to reach-scale
504 riparian replanting and livestock exclusion in three degraded NPRs in southeastern Australia found
505 no differences in water quality, organic matter or aquatic invertebrate community composition
506 between paired treatment and control sites after 6–8 years, ascribing the lack of response to a
507 drought and pervasive effects of catchment-scale degradation¹⁸⁰. The effectiveness of NPR
508 restoration activities could also be enhanced by recovering natural flow regimes, reducing pollutant
509 inputs, remediating degraded catchments, controlling invasive species and repairing damaged

510 channels and streambeds. These multiple restoration activities must be implemented at appropriately
511 broad spatial scales, and prioritize recovery of lost functional connections between NPRs and
512 perennial segments (such as through removal of instream barriers like weirs or dams). As responses
513 to restoration in NPRs are likely to be slower than in equivalent-sized perennial segments because of
514 their inherent intermittence and often-arid or semi-arid climatic setting, expectations must be
515 modified to reflect these key differences.

516
517 Like restoration, targeted conservation of NPRs at the river-network scale has been rare, with most
518 protected NPRs occurring in areas conserved for other reasons. For example, conservation actions
519 targeting the endangered Coho salmon (*Oncorhynchus kisutch*) in the Russian River, California
520 consisted of fish rescues during the non-flowing phase¹⁸¹. In NPRs in Texas, local habitat restoration
521 increased populations of the endangered desert pupfish (*Cyprinodon bovinus*)¹⁸². In Australia,
522 standard methods have been developed to classify disconnected pools (riverine waterholes)^{183,184},
523 informing actions taken to protect refuges that act as drought refuges for biodiversity during
524 drought^{58,184}. However, connectivity is required among individual refuges to maintain
525 metapopulation and metacommunity dynamics⁵, thus achieving effective network-scale
526 conservation. In addition, effective network-scale conservation should seek to identify and protect
527 key NPRs and their riparian zones. Systematic conservation planning tools such as Marxan¹⁸⁵ are
528 powerful approaches for identifying priority sites acting as refuges for fish across entire river
529 networks^{135,136}, and for evaluating the conservation value of NPRs considering both their aquatic
530 and terrestrial species¹⁸⁶.

531
532 We suggest the most effective approach for river network management will be multifaceted,
533 integrating targeted conservation and restoration strategies in an appropriate legislative context and

534 explicitly acknowledging the importance of functional connections between NPRs and perennial
535 segments. Although some biomonitoring approaches developed for perennial segments are effective
536 in NPRs during flowing phases, biological indicators should include terrestrial communities to
537 encompass the dry phases and provide a more nuanced and comprehensive perspective of ecological
538 responses to the management strategies¹⁷⁶.

539

540 **[H1] Summary and future perspectives**

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

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

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

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

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

579

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1052 **Related links:**

1053 **EcoFlows Channel:** <https://www.youtube.com/@ecoflows6550>

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1056 **Key points**

1057 1. Non-perennial segments comprise over half the global river network. Ongoing climate change and
1058 human activities will further increase the occurrence of river drying.

1059 2. Recurrent cycles of flowing, non-flowing and dry phases influence exchanges of water, energy,
1060 nutrients and organisms between non-perennial segments and connected perennial waters.

1061 3. Physical, chemical and biological processes in non-perennial segments affect water quality and
1062 quantity, and ecological integrity in downstream receiving waters and entire river networks.

1063 4. Historically, river science and management have focused on perennial river segments, neglecting
1064 the ubiquity and importance of non-perennial segments. This imbalance has often led to
1065 environmental problems such as poor water quality, loss of biodiversity and alteration of natural
1066 flow regimes at the river network scale.

1067 5. Sustaining the water quality and ecological integrity of entire river networks and associated
1068 downstream waters requires integrated management strategies that explicitly consider non-perennial
1069 segments and their connections with perennial ones.

1070

1071

1072 **Figure 1. Non-perennial river segments: definition, abundance and flow regimes.**

1073 a| An idealized river network, indicating the different types of non-perennial (ephemeral and
1074 intermittent) river segments and their linkages with nearby waters. b| A typical hydrological
1075 sequence of a non-perennial segment, from flowing, non-flowing, dry and rewetting phases in the
1076 Calavon River, France. c| Global prevalence of non-perennial river networks. Panel b images
1077 courtesy of Bertrand Launay. Panel C reprinted from Ref⁴ Springer Nature Limited.

1078

1079 **Figure 2. The connections between non-perennial and perennial river segments.**

1080 a| Examples of connections between perennial and non-perennial segments. b| River-network
1081 patterns of co-occurring non-perennial (dashed lines) and perennial (solid lines) segments. c|
1082 Functions affecting fluxes of water, materials and organisms through non-perennial segments (blue
1083 triangle) before entering downstream waters (gray triangle), as in Ref⁴⁵. Changes in arrow thickness
1084 reflect changes in the fluxes through the functional connections. Changes in arrow color reflect
1085 conversion of material or energy form. Changes in arrow shape reflect delayed delivery of material
1086 or energy.

1087

1088 **Figure 3. Effects of non-perenniality on river-scale leaf litter decomposition and transport.**

1089 Two theoretical river networks with contrasting spatial arrangement of non-perennial segments,
1090 upstream (panel a) and downstream (panel b). Leaf litter is poorly decomposed during dry phases in
1091 non-perennial segments. Instead, it accumulates and is then transported downstream en masse when
1092 flow resumes. As such, fluxes of decomposed and undecomposed litter vary substantially between
1093 the two river networks.

1094

1095 **Figure 4. Non-perenniality impacts on biodiversity patterns at the river network scale.**

1096 Expected diversity patterns of two hypothetical river networks in which non-perennial sections are
1097 located upstream (panel a) and downstream (panel b). Circles represent communities hosting
1098 different species (symbols). For the two river networks, the magnitude of the effect of drying on
1099 biodiversity is the same (the same number of species disappears along a longitudinal gradient of
1100 drying). When non-perenniality is concentrated in the headwaters, the species-poor communities are
1101 composed of species not found in species-rich communities in downstream perennial segments.
1102 Conversely, when non-perenniality occurs downstream, the species-poor communities of these
1103 segments are subsets of species-rich communities from upstream perennial segments. These network
1104 patterns emerge because recolonization is faster from upstream to downstream, following the
1105 directionality of river flow. Adapted with permission from Ref¹⁰, Elsevier.

1106

1107 **Figure 5. The future hydrological and biological fate of non-perennial rivers.**

1108 a. Increasing (upward triangle) or decreasing (downward triangle) trends at the European scale
1109 (crosses indicate no trend) at the 10% significance level for the annual mean number of zero-flow
1110 days⁹⁶. b. Mann–Kendall trends in annual no-flow days across the USA; red indicates longer no-
1111 flow duration, blue indicates a shorter flow duration¹¹. Unfilled circles indicate there was not a
1112 significant tren. c. Relationships between annual no-flow duration (as a percentage) and the
1113 taxonomic richness (as the number of taxa) of lotic communities. The letter labels mark (1) benthic
1114 invertebrates in the Albarine River, France³⁸; (2) benthic invertebrates in the Selwyn River, New
1115 Zealand⁴¹; (3) hyporheic invertebrates in the Selwyn River¹⁸⁷; (4) riparian plants in the San Pedro
1116 River, Arizona¹⁸⁸; and (5) fish in the Selwyn River¹⁸⁹. The lines are based on regression models
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1119 Part c reprinted with permission from ref 16, Oxford University Press.

1120
1121 **Figure 6 Examples of ecosystem processes and services occurring in non-perennial segments**
1122 **and management opportunities.**

1123 a| Residual and disconnected pools in a non-perennial river segment from Oregon (USA)¹³³ and
1124 Coho salmon juveniles in a non-perennial segment from the Russian River in California (USA). b|
1125 Rambla de Nogalte (SE Spain) during a flood in 2012, and an example risk inundation map. c| The
1126 Puerco River, a tributary of Río Grande (USA) during the flowing period, and the comparison of
1127 flood hydrographs and well response during floods in 2003⁴⁷. d| Satellite image of Santa Clara
1128 ephemeral river inputs to the Channel Islands in California (USA) during flooding in 1998.
1129 Nutrients and chlorophyll-a were carried out from the river to the coastal waters during these
1130 floods¹³⁹. Arrows show the river mouth. Panel a schematic is adapted from ref 190 CC BY 4.0

1131 (<https://creativecommons.org/licenses/by/4.0/>). Panel a image courtesy of the Russian River
1132 Monitoring Program. Part b image is reprinted from ref 190, CC BY 4.0
1133 (<https://creativecommons.org/licenses/by/4.0/>). Part c, d photo reprinted with permission from the
1134 USGS. Part d adapted with permission from Ref 139, Elsevier.

1135

1136 **Figure 7. Examples of threats on non-perennial river segments.**

1137 Garbage in the dry riverbed of the Hodgsons Creek, Victoria (panel a) and in Madura gully, West
1138 Australia (panel b). A non-perennial segment of the Chitterne Brook flows through an intensively
1139 grazed cow pasture in England, UK (panel c). Sheep in the non-flowing segments of the Barranc del
1140 Carraixet, Spain (panel d). Sewage effluent turning the non-perennial segment of the Sant Miquel
1141 River artificially perennial in Spain (panel e). Gravel extractions from dry riverbeds in France
1142 (Albarine River) (panel f) and Bolivia (Janq'u Qala) (panel g). An example of a map showing in red,
1143 the NPRs to be removed from protection by legislation in France, on the basis of their non-
1144 perennality (panel h). The perennial segment in blue is the only part of the river network under
1145 protection by law. Sewage effluent discharge generates a permanent pool in a non-perennial
1146 segment of the Albarine River, France (panel i). Example of an NPR that is no longer under
1147 protection in eastern France, le Ruisseau des Tendasses (panel j). Photos courtesy of T. Sykes (panel
1148 c, h), H. Pella (panel j).

1149

1150 **TOC Summary:**

1151 Non-perennial segments of rivers undergo cycles of flowing, non-flowing and dry phases,
1152 influencing ecosystem dynamics and services across the river network. This Review describes the
1153 occurrence, ecology, and future of these intermittent and ephemeral flows, and highlights the
1154 importance of protecting these segments.

1155 **Glossary**

1156 **Beta diversity.** Spatial and temporal variability in community composition.

1157 **Dry phase.** In a non-perennial river segment, a period of time with no spatially continuous flowing
1158 or non-flowing surface water, although disconnected surface-water pools and subsurface water can
1159 be present.

1160 **Drying phase.** In a non-perennial river segment, the transitional period between a flowing or non-
1161 flowing phase and a dry phase, during which most or all surface water is lost.

1162 **Ephemeral.** A non-perennial flow regime in which water only flows in response to rainfall events,
1163 and flowing phases are thus unpredictable and typically short (hours to weeks).

1164 **Flow cessation.** The point in time at which surface water ceases to flow from upstream to
1165 downstream in a non-perennial segment.

1166 **Flowing phase.** In a non-perennial river segment, a period of time in which water flows from
1167 upstream to downstream.

1168 **Flow regime.** The temporal variability in the quantity and timing of discharge

1169 **Gaining segment.** A stream segment in which flow increases due to the upwelling of groundwater
1170 into the surface channel.

1171 **Losing segment:** A stream segment in which flow decreases due to the 'loss' of surface water that
1172 infiltrates the streambed towards the groundwater. **Intermittent.** A non-perennial flow regime, often
1173 seasonal, that is typically characterized by long flowing phases (usually multiple months) and short
1174 dry phases.

1175 **Megadrought.** A drought that exceeds the duration of most droughts in the instrumental record.

1176 **Non-flowing phase.** In a non-perennial river segment, a period of time when spatially continuous
1177 non-flowing (still or lentic) surface water is present.

1178 **Non-perennial segments.** Those in which surface water recurrently stops flowing. These segments
1179 lose all or most of their surface water.

- 1180 **Perennial segments.** Those in which surface water never stops flowing.
- 1181 **Rewetting phase.** In a non-perennial river segment, the transitional period between a dry phase and
1182 a flowing or non-flowing phase.
- 1183 **Synchrony.** The degree of concurrent change across spatially distinct segments or populations.

1184