



1 **Reviews and Syntheses: Variable Inundation**

2 **Across Earth's Terrestrial Ecosystems**

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42 **Abstract**

43 The structure, function, and dynamics of Earth's terrestrial ecosystems are profoundly
44 influenced by the frequency and duration that they are inundated with water. A diverse array of
45 natural and human engineered systems experience temporally variable inundation whereby they
46 fluctuate between inundated and non-inundated states. Variable inundation spans from extreme
47 flooding and droughts to predictable sub-daily cycles. Variably inundated ecosystems (VIEs)
48 include hillslopes, non-perennial streams, wetlands, floodplains, temporary ponds, tidal
49 systems, storm-impacted coastal zones, and human engineered systems. VIEs are diverse in
50 terms of inundation regimes, water chemistry and flow velocity, soil and sediment properties,
51 vegetation, and many other properties. The spatial and temporal scales of variable inundation
52 are vast, ranging from sub-meter to whole landscapes and from sub-hourly to multi-decadal.
53 The broad range of system types and scales makes it challenging to predict the hydrology,
54 biogeochemistry, ecology, and physical evolution of VIEs. Despite all experiencing the loss and
55 gain of an overlying water column, VIEs are rarely considered together in conceptual,
56 theoretical, modeling, or measurement frameworks/approaches. Studying VIEs together has the
57 potential to generate mechanistic understanding that is transferable across a much broader
58 range of environmental conditions, relative to knowledge generated by studying any one VIE
59 type. We postulate that enhanced transferability will be important for predicting VIE function
60 under future, potentially non-analog, environmental conditions. Here we aim to catalyze cross-
61 VIE science that studies drivers and impacts of variable inundation across Earth's VIEs. To this
62 end, we complement expert mini-reviews of eight major VIE systems with overviews of VIE-
63 relevant methods and challenges associated with scale. We conclude with perspectives on how
64 cross-VIE science can derive transferable understanding via a 'continuum approach' in which
65 the impacts of variable inundation are studied across multi-dimensional environmental space.

66 **Introduction**

67 The chemical and biological processes within terrestrial ecosystems hinge on the presence,
68 residence time, volume, and chemistry of water. A variety of factors influence water retention,
69 infiltration and flow, such as land surface relief, topographic slope, subsurface permeability,
70 evapotranspiration, and human-based modifications of the landscape. Water supply is most
71 commonly 'top down' in the form of precipitation and overland flow or 'bottom up' due to rising
72 water tables and transient saturation in the subsurface (Smith et al. 2017). Inundation, however,
73 may also occur from lateral inputs, as is common in tidal systems, or from upslope inputs, as in
74 floodplains. Regardless of where water comes from, inundation occurs when the rate of water
75 supply is greater than the rate of export via infiltration, evapotranspiration, and runoff.

76 Here we define inundation as occurring when there is a near continuous aqueous barrier
77 that limits gas phase transport between the atmosphere and the subsurface. This
78 conceptualization is inclusive of diverse conditions, spanning from extreme events such as
79 hurricane-driven flooding to shallow short-lived overland flow across hillslopes. We define
80 variably inundated ecosystems (VIEs) as those that experience dynamic shifts between the
81 presence and absence of inundated conditions, at any spatial and temporal scale. Variably
82 inundated ecosystems cover at least 5-9 million km², or 4-7% of the Earth's land surface
83 excluding Greenland and Antarctica. These estimates are according to monthly data over



84 multiple decades (Zhang et al. 2017, 2021, Davidson et al. 2018), and are likely significant
85 underestimates as many VIEs are not resolvable by commonly used remote sensing
86 techniques.

87 Variable inundation occurs across a wide range of terrestrial ecosystems, but the factors
88 governing its influences are typically studied independently without cross-ecosystem
89 comparisons. Some examples of VIEs are hillslopes with overland flow, non-perennial streams,
90 floodplains and parafluvial zones, variably inundated wetlands, vernal ponds/pools/playas, tidal
91 systems, coastal systems impacted by storm-driven flooding, and human-engineered systems
92 intended to shift inundation dynamics (e.g., flood-irrigated agriculture, stormwater infrastructure,
93 and constructed wetlands) (**Fig. 1**). While VIEs may be classified as wetlands under the
94 broadest definition from the Ramsar Convention (Secretariat 2016), there is significant variation
95 in how wetlands are defined (Finlayson and Van Der Valk 1995) and we do not attempt to rectify
96 or clarify variation in those definitions. Here, when using the term ‘wetland’ we simply align with
97 the perspective that wetlands are similar to marshes, swamps, and bogs.

98 Inundation dynamics are changing due to increased variability and magnitudes of
99 precipitation and evapotranspiration, accelerated sea level rise, and human modifications to the
100 Earth’s land surface, including an increase in extreme events (Konapala et al. 2020, Li et al.
101 2022a). Extreme events such as coastal flooding are increasingly frequent, and while seasonal
102 drying of streams is now more common (Sweet et al. 2014, Zipper et al. 2021), some streams
103 are shifting from non-perennial to perennial (Döll and Schmied 2012, Datry et al. 2018a) while
104 others have fewer no-flow days than they did historically (Zipper et al. 2021). Wetland
105 inundation extent, duration, and seasonal timing are also projected to be altered by climate
106 change (Londe et al. 2022a). Thus, the dynamics of inundation are changing in different ways
107 across different VIEs (Zipper et al. 2021) such that we cannot rely exclusively on historical
108 dynamics to predict future impacts (e.g., on species diversity) of changing inundation dynamics
109 (Culley et al. 2016, Quinn et al. 2018, Rameshwaran et al. 2021, Li et al. 2022b).



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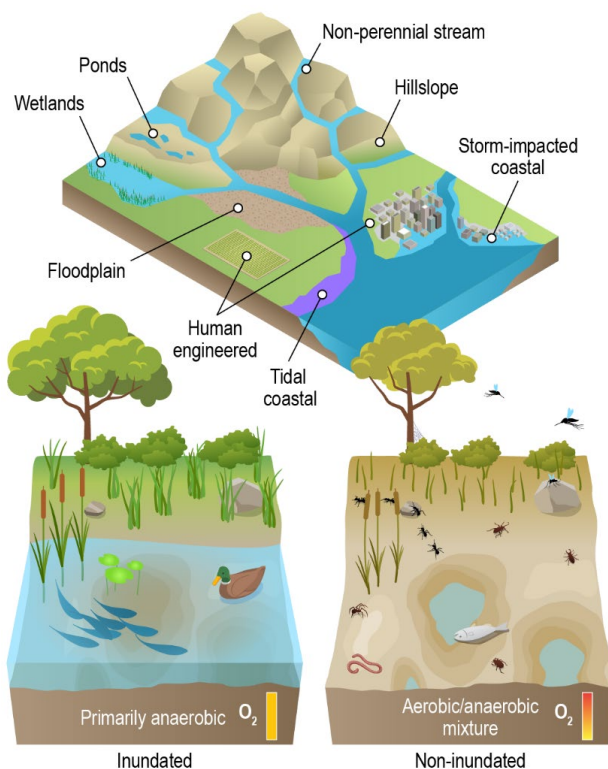
Figure 1. Variably inundated ecosystems (VIEs) span numerous ecosystem types and are globally distributed across the Earth's land surface. There are few places across Earth's land surfaces that do not experience variable inundation, which is defined here as the loss/gain of an aqueous barrier between the atmosphere and porous media (e.g., soil) that inhibits gas phase transport. Due to global changes in the dynamics of variable inundation, there is a need to integrate knowledge into models that are predictive across VIEs. This will require intentionally studying VIEs together to understand how the details of any given VIE modulate the impacts of variable inundation. Credit: Nathan Johnson. There are several photos from different sources and permissions granted as follows: (a) Sullivan et al 2019; (b) Jon Sweetman, co-author; (c) Shutterstock; (d) @WeirdBristol [Twitter] 2018; (e, f, g, h) Shutterstock; (i) Mikac et al 2018.



123 Mechanistic knowledge that is transferable across inundation regimes (i.e., from extreme
124 events to predictable cycling) and across VIEs is required to develop models that are predictive
125 across contemporary and future conditions. We envision the impacts of variable inundation as
126 dependent on the location of any given VIE in multi-dimensional environmental space. This
127 space can be defined with a variety of environmental variables such as inundation return
128 interval and duration, topographic slope, vegetation composition, precipitation, and temperature.
129 Many other variables could be used, but regardless, environmental change will cause VIEs to
130 move to different areas within multi-dimensional environmental space. Predicting future impacts
131 of variable inundation requires mechanistic understanding of how the location of a VIE in this
132 space influences those impacts. We propose that our best chance to achieve such
133 understanding is to generate knowledge of variable inundation impacts that is transferable
134 across VIEs.

135 Here we aim to catalyze cross-VIE science for the pursuit of transferable knowledge and
136 ultimately models that are predictive across and aid in conserving contemporary and future
137 VIEs. We briefly summarize high-level divergences in drivers of variable inundation,
138 commonalities in the impacts of variable inundation, and then present expert mini-reviews of
139 eight major VIE systems. Variable inundation occurs across vast ranges in spatial and temporal
140 scales, which presents challenges to cross-VIE science. As such, we overview these challenges
141 and offer suggested solutions along with a summary of methods that are most relevant to VIE
142 science. We conclude with perspectives on how cross-VIE science can derive transferable
143 understanding to better protect these systems and their biodiversity.

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148 **Figure 2. Conceptual overview of where different types of VIEs are commonly found**

149 **within watersheds and some common shifts in system states across inundated and non-**

150 **inundated conditions. VIEs are found from headwaters to coastal environments (Top) and the**

151 **impacts of variable inundation have some consistencies across these diverse landscapes**

152 **(Bottom). Organismal ecology, physiology, and demographics are altered by variable**

153 **inundation, leading to shifts in community composition. Biogeochemical processes also shift,**

154 **such as greater gas-phase transport of oxygen into soil/sediment when surface water is lost,**

155 **with associated shifts in redox processes. The details of these responses to variable inundation**

156 **are, however, likely to vary across VIEs due to variation in system properties such as dominant**

157 **vegetation types, rhizosphere development, soil/sediment texture, water salinity, flow velocity,**

158 **etc. A key goal for cross-VIE science is to mechanistically link variation in these system**

159 **properties to impacts of variable inundation across the multi-dimensional environmental space**

occupied by VIEs. Credit: Nathan Johnson.

160

Divergent Drivers, Common Responses, and VIE Mini-Reviews

161 The drivers of variable inundation differ markedly across VIEs and are linked to factors such as

162 long-term drought, heavy precipitation, evapotranspiration, changing groundwater storage,

163 soil/sediment properties, extreme climatic events, and dam operations. This leads to significant

164 variation across VIEs in inundation regimes, which includes inundation timing, return interval,



165 duration, spatial extent, depth, and flow rate. For example, sediments within the active channel
166 of tidal rivers can experience sub-daily losses and gains of surface water, while other coastal
167 zones may experience extreme inundation events on a 100 year return interval. Other systems,
168 such as non-perennial streams and vernal ponds, also experience a broad range of inundation
169 regimes, ranging from sporadic and extreme inundation following rain events to more regular
170 seasonal cycles. Variation in the spatial scale of inundation is also large, with floodplains and
171 storm-impacted coastal zones experiencing inundation over tens of kilometers, whereas non-
172 perennial streams and ponds can experience changes across a few meters. As discussed
173 below within the series of VIE mini-reviews, the temporal and spatial scales of inundation also
174 vary substantially within each type of VIE. Variation within a given type of VIE is large enough
175 that we suggest it cannot be used to clearly differentiate VIEs into named categories. As
176 discussed in the “Toward cross-VIE transferable understanding” section, this is one motivation
177 for pursuing a continuum approach to cross-VIE science.

178 Variable inundation impacts physical [e.g., sediment transport (Peruccacci et al. 2017, Siev
179 et al. 2019)], chemical [e.g. water quality (Whitworth et al. 2013)], and biological/ecological [e.g.,
180 invertebrate communities (Plum 2005)] attributes of both natural and anthropogenically modified
181 ecosystems, in addition to human society (Dube et al. 2021) (**Fig. 2**). Due to intense periods of
182 inundation and drought, these systems are often referred to as hotspots or ecosystem control
183 points (Bernhardt et al. 2017), with disproportionately high reaction rates or areas of high
184 diversity (Davidson et al. 2012, Palta et al. 2014). In a qualitative sense, some of these impacts
185 are common across VIEs even if the quantitative details vary.

186 During inundated periods, biogeochemical processes in VIEs often shift from a dominance
187 of aerobic respiration during drier periods to a diverse suite of anaerobic processes, such as
188 methanogenesis (Datry et al. 2018b, Hondula et al. 2021b). Changes in the frequency of
189 inundation events change the dynamics of dry-wet, hot-cold, and aerobic-anaerobic transitions
190 (Valett et al. 2005). Such dynamics can challenge existing theories. For example, while rates of
191 soil respiration are expected to peak under aerobic conditions, periodic anaerobic conditions
192 can lead to unexpectedly high rates of soil carbon loss (Huang et al. 2021) and the anaerobic
193 process of methanogenesis can be fastest in well-oxygenated dry soils (Angle et al. 2017). More
194 broadly, variable inundation can alter fluxes of greenhouse gasses to the atmosphere such as
195 the common observation of soil rewetting leading to significant carbon loss arising from sudden
196 intensification of soil respiration (Schimel 2018, Shumilova et al. 2019). Variation in inundation
197 also has large impacts on the global CH₄ budget (Zhang et al. 2017, Peng et al. 2022) and
198 rewetting of dry sediment in intermittent streams can contribute considerably to the total CO₂
199 emissions from streams (von Schiller et al. 2019). More generally, top down and bottom up
200 hydrologic inundation events broadly influence biogeochemical cycles (Smith et al. 2017) and
201 can result in hysteretic responses to wetting and drying (Patel et al. 2022).

202 Across VIEs, inundation impacts the structure, composition, and function of vegetation
203 communities. Growth and survival can either increase or decrease with inundation depending
204 on local aridity and the impacts on soil hypoxia. Hypoxia kills roots, leading to reduced water
205 uptake, reduced photosynthesis, mortality (Pedersen et al. 2021, McDowell et al. 2022, Cubley
206 et al. 2023), and shifts in vegetation composition. More broadly, inundation dynamics impact
207 organismal ecology (Datry et al. 2023) across all VIEs, such as herbivores responding to
208 inundation-induced shifts in vegetation (De Sassi et al. 2012). Inundation can also alter



209 arthropod communities leading to reductions in diversity, abundance, and biomass with flooding
210 (Plum 2005). Changes at the base of food webs can have further, cascading effects (Chen and
211 Wise 1999).

212 To pursue cross-VIE science requires knowledge of the diverse array of ecosystems that
213 can be considered VIEs. Researchers that design and carry out cross-VIE studies may be
214 considered generalists in terms of the breadth of systems they study, even if their science
215 questions are highly specialized. To facilitate such researchers in the pursuit of cross-VIE
216 science, we go beyond the high-level summaries of divergences and commonalities (above)
217 and provide expert mini-reviews of eight primary VIE types. The following subsections present
218 these mini-reviews which summarize system characteristics, drivers, and impacts of variable
219 inundation with an emphasis on biogeochemistry and organismal ecology, and opportunities to
220 better understand spatiotemporal patterns and impacts of variable inundation. Each mini-review
221 is accompanied by a graphic that either provides a conceptual overview or imagery-based
222 examples, with the goal of collectively touching on key drivers, dynamics, impacts, and tangible
223 system examples. The collection is not meant to be a comprehensive classification of all
224 possible VIE types, but does cover a broad range of VIEs. The sequence of mini-reviews
225 roughly follows the flow of water moving from hillslopes to coastal environments (**Fig. 2**) and
226 includes variably inundated components of: (i) hillslopes, (ii) non-perennial streams, (iii) riverine
227 floodplains and parafluvial zones, (iv) wetlands, (v) temporary ponds, (vi) storm-impacted
228 coastal zones, and (vii) tidal systems. The final mini-review (viii) is focused on ecosystems that
229 have been engineered to modify inundation regimes, which occur throughout the continuum
230 from hillslopes to coasts.

231 We separate VIEs into categories as a heuristic simplification that allows for an appreciation
232 of variation and commonalities in drivers, impacts, and opportunities. We anticipate that the
233 disciplinary foci of individual researchers will align most closely with a subset of the summarized
234 VIE types. One goal of this manuscript is to facilitate researchers thinking about how their
235 science applies across VIEs. We emphasize that in many (and maybe all) cases there is not a
236 clear distinction among the types of VIEs we discuss below (e.g., non-perennial streams can be
237 flooded due to storm surge, resulting in floodplains or parafluvial zones). Ultimately, we
238 encourage a continuum perspective that does not rely on discrete system names or hard
239 boundaries, and instead views VIEs across multi-dimensional environmental space based on
240 inundation regimes and physical settings.

241 **Hillslopes with Surface Runoff**

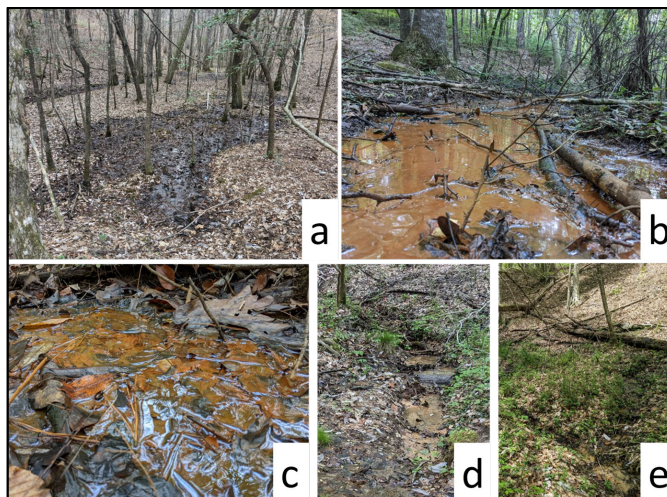
242 Hillslopes provide water to lower-lying areas, often concentrating the water in gullies and
243 depressions (**Fig. 3**). Hillslopes produce relatively transient VIE features and may often be seen
244 as extensions of other VIEs, such as hillslope seeps co-located with a wetland or the
245 unchanneled swales that contribute to a non-perennial network. In cold regions, snow, ice and
246 permafrost can create an impermeable layer resulting in near-surface soil being inundated for
247 days to weeks during spring thaw (Coles et al. 2017, Patel et al. 2020). In dry regions, intense
248 precipitation that exceeds the local infiltration capacity can result in water ponding on the
249 surface of hillslopes or overland flow generation down hillslopes, which can be exacerbated by
250 initial hydrophobicity of dry soil (Kirkby et al. 2002). Exceeding the infiltration capacity is more
251 likely on hillslopes with low-permeability, such as clay-rich soil or when near-surface soils are



252 frozen. This can be exacerbated by restrictive soil horizons located at shallow depths across
253 hillslopes that generate seasonal perched water tables and lead to inundation (McDaniel et al.
254 2008). Overland flow can be spatially heterogeneous due to variations in soil characteristics as
255 well as flow accumulation, leading to infiltration or exfiltration along the hillslope (Betson and
256 Marius 1969).

257 In forested hillslopes, soil infiltration often exceeds rainfall intensity (McDonnell 2009, Burt
258 and Swank 2010) and lateral flow towards topographic depressions can lead to saturation and
259 ponding (Anderson and Burt 1978) (**Fig. 3a**). Microtopography within hillslopes (**Fig. 3b**) can
260 also lead to temporary ponding, e.g., from rain in tropical environments and from spring
261 snowmelt in colder environments (Clark et al. 2014). Toe slopes can generate wedges of
262 saturation that grow upslope (Weyman 1973, Choularton and Perry 1986), although subsurface
263 saturation and ponding can also occur on upper slopes where the soil is thinner [e.g., (Tromp-
264 van Meerveld and McDonnell 2006)]. Finally, spatial variation in topographic characteristics
265 (e.g., aspect, slope, curvature) can result in differences in soil moisture, incoming energy, and
266 vegetation, affecting evapotranspiration and inundation patterns (McVicar et al. 2007).

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269 **Figure 3. Examples of variable inundation along hillslopes.** a) looking downslope at an
270 inundated slope; b) ponding due to microtopography; c) sheet wash across the surface of a
271 hillslope; d) rill formation with turbid water from erosion; e) vegetation community change on
272 slope due to differences in soil moisture. All photos taken by Corianne Tatariw at Tanglewood
273 Forest, Alabama.

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275 Surface runoff and inundation on hillslopes can result in the export of soil nutrients,
276 salinization of soil from groundwater seeps, erosion, and landslides. There is a balance between
277 the effects of variable inundation on hillslope vegetation and erosion. In water-limited systems,
278 inundation can increase plant productivity and diversity, as well as increased rooting strength of
279 soils (Zhao et al. 2022) (**Fig. 3e**). However, increased inundation can also lead to increased
280 chemical weathering and lower shear strength in hillslope soils during storms, leading to higher
281 erosion and landslide potential. Along with erosion, landslides and soil compaction are inherent



282 to many hillslopes, which also can create areas ripe for inundation (Bogaard and Greco 2016).
283 At shoulder and midslope positions, increased overland flow due to saturation- or infiltration-
284 excess increases sediment detachment, which is then deposited in foot and toe slopes (Huang
285 et al. 2002). The transport of particles also leads to the transport of nutrients that are sorbed to
286 the particles, such as phosphorus. Erosion can be concentrated in rills and gullies or can spread
287 out across a slope as 'sheet wash' that impacts large areas of hillslopes (**Fig. 3c,d**). Impacts of
288 erosion are dependent on interactions between the persistence of inundation and soil properties
289 (Thomas et al. 2020).

290 The aqueous chemistry of water that is transported over hillslope surfaces reflects the
291 chemistries of contributing water sources such as precipitation, shallow soil water, and
292 exfiltrating groundwater. Shallow soils in hillslopes have abundant organic materials and
293 nutrients (Herndon et al. 2015), whereas organic matter decreases with depth, solutes derived
294 from the parent rock material increase with depth (Brantley et al. 2017). These stratifications
295 collectively regulate source water chemistry in hillslopes. Dry to wet transitions shift flow paths
296 from groundwater to soil water dominance in streams, therefore shaping stream chemistry (Zhi
297 and Li 2020, Stewart et al. 2022). Dry to wet transitions also shift water content and pore space
298 oxygen concentrations (Jarecke et al. 2016, Smyth et al. 2019), often triggering the release of a
299 cascade of solutes produced under anaerobic conditions (Schlesinger and Bernhardt 2020).
300 These entangled, complex interactions among hydrological and biogeochemical processes
301 often challenge the differentiation of individual processes and mechanistic understanding on
302 how variable inundation regulates flow paths, reactions, stream chemistry, and solute and gas
303 export fluxes (Li et al. 2021).

304 Investigations of variably inundated hillslopes present significant and challenging research
305 opportunities due to their inherently dynamic nature. One key challenge is quantifying the
306 occurrence and spatial extent of hillslope VIEs across the globe. Remote sensing could be used
307 to identify and quantify these areas, spatially and temporally, based on sky-visible vegetation
308 (e.g., plant morphologies, leaf nutrient contents) and topographic signatures (e.g., erosional
309 patterns) caused by variable inundation. To fully understand the ecological and biogeochemical
310 impacts of variable inundation on hillslopes, research needs to focus on shallow subsurface
311 physical properties, hydrology, and their linkage to biogeochemical processes. This can be
312 pursued via environmental geophysics to map and characterize the influence of subsurface
313 restrictive layers (Fan et al. 2019 p. 201). Understanding the subsurface soil architecture is key
314 to predicting variable inundation from bottom-up and top-down water sources, along with the
315 follow-on impacts to ecology and biogeochemistry.

316 **Non-Perennial Streams**

317 Non-perennial streams, defined as rivers and streams that cease to flow at some point in either
318 space or time (Busch et al. 2020), are ubiquitous and comprise 50-60% of the global river length
319 (Messenger et al. 2021). These systems occur across all continents and biomes (Messenger et al.
320 2021). Streamflow in non-perennial streams ranges from nearly perennial (year-round) flow, to
321 seasonal flow, responding to drivers like snowmelt, to daily or sub-daily flow events responding
322 to rainfall/flood events or evapotranspiration (Price et al. 2021). At the reach scale, non-
323 perennial streams shift between three main states - flowing, ponded/pooled, or no-surface water
324 present (**Fig. 4**). As reaches become hydrologically connected (or disconnected), the spatial



325 footprint/extent of the connected stream network can grow or shrink over sub-daily to seasonal
326 to interannual timescales (Xiao et al. 2019). Spatial and temporal shifts among the three
327 hydrologic states strongly influence the network's capacity to process, transport, and export
328 material to downstream systems (Allen et al. 2020).

329 The high variability in the spatial and temporal scales of streamflow intermittency is
330 indicative of the complex set of interacting drivers that induce stream drying. At the global and
331 regional scales, the degree of aridity is a primary control on the abundance of non-perennial
332 streams (Hammond et al. 2021, Zipper et al. 2021). At smaller scales, catchment properties
333 exert strong control over both the capacity of water delivery to the channel and the subsequent
334 balance between the channel and near subsurface capacity to transport water (Hammond et al.
335 2021, Zipper et al. 2021, Price et al. 2021). Non-perennial flow can occur anywhere in the stream
336 network, from headwaters to higher order rivers. While some networks display longitudinal
337 transitions from non-perennial to perennial flow (or vice versa), other networks exhibit more
338 complex patterns in surface water flow and connectivity, which may be driven by topography,
339 geology, vegetation, or groundwater abstraction/use (Costigan et al. 2015, 2016).

340 The variable inundation dynamics in non-perennial streams have cascading implications for
341 biogeochemical cycling, water quality, ecosystem function, and community ecology. Under non-
342 flowing conditions, riverbeds are characterized by dry conditions or discontinuous and stagnant
343 water pools, often with high temperatures, low dissolved oxygen levels, and long residence
344 times, functioning more like soils (Arce et al. 2019), as described also in the hillslope section.
345 Pooled, non-flowing conditions can lead to steep redox gradients in the shallow subsurface that
346 drive nutrient processing (Datry and Larned 2008, Gómez-Gener et al. 2021, DelVecchia et al.
347 2022). During dry/non-flowing states, terrestrial organic matter accumulates in the channel and
348 is subjected to varying degrees of breakdown (Datry et al. 2018c, Del Campo et al. 2021).
349 Rewetting of accumulated substrates can stimulate microbial activity, nutrient attenuation
350 (Saltarelli et al. 2022), and generate pulses of greenhouse gasses such as CO₂ and N₂O (Datry
351 et al. 2018a, Song et al. 2018). During re-wetting and resumption of flow, non-perennial streams
352 can contain large amounts of terrestrial and aquatic organisms that can be flushed downstream
353 (Corti and Datry 2012, Rosado et al. 2015), with high sediment, dissolved organic carbon, and
354 solutes (Laronne and Reid 1993, Hladyz et al. 2011, Herndon et al. 2018, Wen et al. 2020,
355 Fortesa et al. 2021, Blaurock et al. 2021).

356 Biological responses to rewetting depend on the distribution of habitats and biota at the
357 watershed scale and the duration of the preceding dry phase. In highly dynamic river systems,
358 such as braided rivers, drying and wetting cycles can be spatially patchy and short-lived but
359 frequent, and thus ecological recovery following wetting can be very rapid due to the very active
360 hyporheic zones characterizing these systems (Arscott et al. 2002, Vorste et al. 2016). In other
361 systems recovery can be slow, depending on the proximity of refuges, such as springs, isolated
362 pools, and perennial reaches (Sarremejane et al. 2021, Fournier et al. 2023). Systems with
363 frequent and severe drying events are more likely to be colonized by aerial or other overland
364 dispersers than by aquatic dispersers (Bonada et al. 2007, Bogan et al. 2017a, Sarremejane et
365 al. 2021). Life-history events of some species coincide with predictable rewetting events, such
366 as post-snowmelt fish spawning (Hooley-Underwood et al. 2019) and amphibian and insect life
367 histories (Bogan et al. 2017a). Rewetting also partly determines the germination success and
368 establishment of riparian vegetation (Merritt and Wohl 2002).

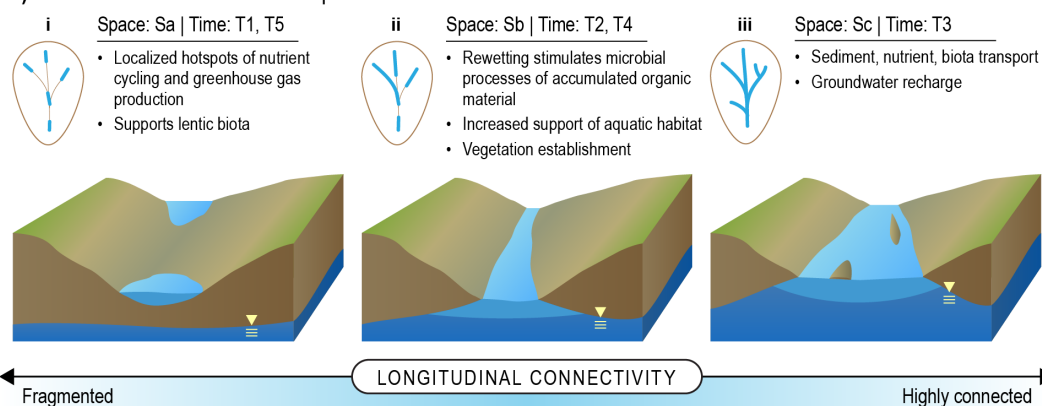


369 Compared to their perennial counterparts, non-perennial streams have received less
370 research and monitoring attention and tend to be undervalued relative to ecological/functional
371 performance of perennial streams (Palmer and Hondula 2014). As such, many of the pressing
372 research needs in non-perennial streams are limited by data availability (Van Meerveld et al.
373 2020, Zimmer et al. 2022). Non-perennial streams are systematically under-represented in
374 global gaging networks (Messenger et al. 2021, Krabbenhoft et al. 2022), leading to major gaps
375 in our understanding of the timing, magnitude, and duration of flow in diverse non-perennial
376 streams. In addition, our ability to predict the onset or cessation of flowing periods is limited by a
377 lack of gaging. Infrequent grab sampling for water chemistry tends to undersample non-
378 perennial streams specifically, leading to an even greater paucity of biogeochemical data from
379 these systems, particularly during rapid re-wetting events. Spatially explicit data on streamflow
380 intermittency and subsurface conditions at fine spatial scales (10s of meters) remain limited to a
381 few intensively studied catchments [e.g., (Zimmer and McGlynn 2017)]. While some global scale
382 datasets on streamflow intermittency have been developed (Messenger et al. 2021), the
383 resolution of these products necessarily omit smaller, headwater reaches, hindering our ability
384 to quantify hydrologic and biogeochemical processes in non-perennial streams broadly
385 (Benstead and Leigh 2012).

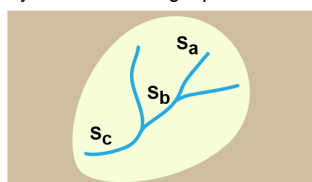
386 Major challenges and opportunities include accurate mapping of non-perennial streams and
387 accurate predictions of flow timing at annual, seasonal, and shorter time scales across scales.
388 With limited time series data, predictions of flow in terms of duration, frequency, and spatial
389 extent can be challenging. How the timing and frequency of flow will change under climate
390 change remains an open question. It is expected that an increased frequency and duration of
391 droughts will shift streams toward more non-perennial flow states (Döll and Schmied 2012). In
392 contrast, flow permanence may increase in select areas where streams are fed by melting
393 glaciers or snowpack, or where anthropogenic intervention occurs (Datry et al. 2023). The
394 changing frequency of extreme flow events and rapid no-flow/high-flow oscillations also have
395 the potential to further alter streamflow, biogeochemical processes, and organismal ecology in
396 non-perennial streams, necessitating further integrated hydro-biogeochemical studies in these
397 dynamic systems.
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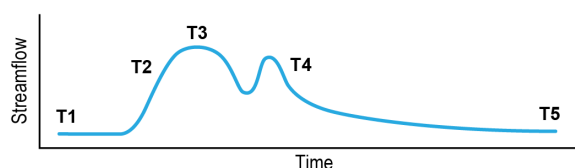
a) Inundation mechanisms in non-perennial streams



b) Spatial variation in inundation dynamics at a single point in time



c) Temporal variation in inundation dynamics at the watershed outlet



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Figure 4. Conceptual model of variable inundation in non-perennial streams. a) Water connections between groundwater, near surface, and surface regions at locations within a given network result in varying degrees of longitudinal connectivity with associated biogeochemical processes. b) At a single snapshot in time, water connections result in spatial variation in surface water inundation. c) Under time varying flow states, extent of surface inundation will also vary at a given location. Inundation mechanisms depicted in a) represent a losing system that is transitioning to a flowing state. We acknowledge that in some systems, a low flow fragmented state also occurs in gaining streams with locally connected groundwater. Spatial variation is signified by $S_a - S_c$ and temporal variation is signified by $T_1 - T_5$. Credit: Nathan Johnson.

410 Floodplains and Parafluvial Zones

411 Rivers, both perennial and non-perennial, create two types of VIEs, floodplains and parafluvial
412 zones (Fig. 5). Floodplains are alluvial landforms generated by river erosion and deposition and
413 hydrologically connected to the contemporary active channel but outside the active river channel
414 (Nanson and Croke 1992). Parafluvial zones are areas in the active channel without surface
415 water at low flow, i.e., at higher-elevation areas within an active channel that contains perennial
416 flow (Goldman et al. 2017). Nearly all rivers have parafluvial zones and adjacent floodplains,
417 although these may be longitudinally discontinuous (e.g., absent where the river flows through a
418 narrow bedrock gorge or descends into the subsurface). Consequently, the global distribution of
419 these environments is extensive, as few terrestrial surfaces do not include a river network.



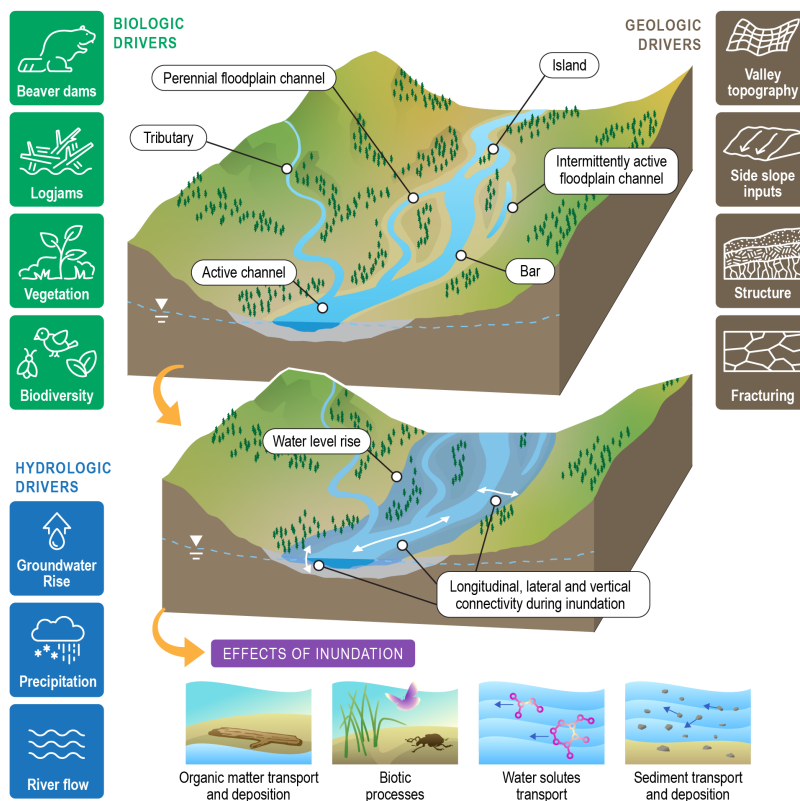
420 Spatial scales of inundation in floodplains and parafluvial zones are variable between rivers
421 and through time along a river. Fundamentally, spatial scales are governed by the interaction
422 between the magnitude of flow and available space as defined by topography. Floodplains of
423 the world's largest rivers such as the Amazon, Congo, or Mississippi can extend laterally for
424 kilometers on both sides of the active channel. In contrast, the floodplain of a headwater
425 channel may be only 1-2 m wide on each side of the channel.

426 Temporal scales of inundation (e.g., frequency, periodicity, intensity) vary substantially
427 across climates, topographic regions, and river network position. A snowmelt-dominated or
428 monsoon-fed river will have a regular annual flood that lasts for weeks, whereas a small stream
429 dominated by convective rainfall or tropical depressions may have irregular floods that only last
430 for hours. Although precipitation-driven over bank flow from the main and tributary channels is
431 the primary driver of inundation on floodplains and parafluvial zones, inundation also results
432 from direct precipitation, rising water tables, and overland flow from adjacent uplands (Mertes
433 2011). Thus, inundation of floodplains may be directly related to their proximity to variably
434 inundated hillslopes and streams.

435 The nature of floodplain/parafluvial inundation affects the dynamics of surface and
436 subsurface water, solutes, particulate organic matter, sediment, and biota (Junk et al. 1989).
437 Dynamics include volume and duration of storage; rate of movement; direction of movement
438 between surface, hyporheic, and groundwater; and biogeochemical alterations that in turn
439 impact river water quality, greenhouse gas emissions, plant function, and organismal ecology.
440 The duration, frequency, and areal extent of floodplain/parafluvial inundation control ecosystem
441 function, and the types and abundances of organismal communities, including both aquatic and
442 terrestrial species (Ward et al. 1999). Species distribution, movement, and biological
443 interactions, such as predator-prey, are intricately tied to these inundation patterns (Robinson et
444 al. 2002, Stanford et al. 2005). Fish species, for example, can migrate from dry season refugia
445 into floodplains during inundation, influencing food web structure and ecosystem productivity
446 (Crook et al. 2020).

447 Among the primary challenges to answering questions regarding the variation in
448 floodplain/parafluvial inundation are limited monitoring data and a lack of numerical models that
449 integrate knowledge across disciplines and processes. Measurements and models of hydrology
450 commonly treat floodplains as flat, impermeable surfaces, which ignores surface-subsurface
451 water exchanges that influence hydrology and ecosystem function (Wohl 2021). Models also
452 often ignore the micro-heterogeneities that influence spatially and temporally variable patterns
453 of inundation, biogeochemical cycling, and ecology in both floodplains and parafluvial zones.
454 The degree of physical detail represented in models often involves tradeoffs in spatiotemporal
455 extent; a one-dimensional model might ignore microtopography that influences important
456 inundation details, whereas a more representative two-dimensional or three-dimensional model
457 becomes computationally intensive for larger spatial extents. This problem gives rise to the
458 challenges and opportunities for (i) designing measurement campaigns across disciplines that
459 can create integrative data for diverse floodplains and parafluvial zones to adequately represent
460 the physical complexity of variable inundation processes at broad scales, and (ii) developing
461 floodplain/parafluvial functional groups [e.g., (Fryirs and Brierley 2022)] that can facilitate
462 understanding of scaling and transferability of data.

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466 **Figure 5. Conceptual model of variable inundation in floodplain and parafluvial systems.**
467 *Across floodplains and parafluvial zones a suite of biological, hydrologic, and geologic factors*
468 *drive inundation regimes in terms of spatiotemporal duration, timing, depth, flow rate, etc. These*
469 *systems include diverse subsystems as summarized in the top panel. Rising water levels, due*
470 *to one or more drivers, can inundate these subsystems as shown in the middle panel, resulting*
471 *in a variety of biogeochemical, ecological, and physical effects (bottom sub-panels). Credit:*
472 *Nathan Johnson.*

473 **Variably Inundated Wetlands**

474 While not all wetlands are variably inundated, variable inundation is a common feature of many
475 wetland ecosystems [e.g. (“Convention on wetlands of international importance especially as
476 waterfowl habitat” 1994), US 33 CFR § 328.3]. Here we focus primarily on wetlands that are
477 similar to swamps, marshes, and bogs (**Fig. 6**). Wetlands cover about 10% of the global land
478 area, and nearly half of global wetland area (46%) is temporarily inundated (Davidson et al.
479 2018). Generally, wetland inundation regimes are shaped by the wetland’s connectivity to
480 surface and subsurface hydrologic sources and landscape position (Åhlén et al. 2022). The
481 landscape position of wetlands is a first order indicator of the water source and chemistry,
482 ranging from headwater depressional locally-fed wetlands, to flow-through and fringing wetlands



483 to groundwater-fed low-lying wetlands (Fan and Miguez-Macho 2011, Tiner 2013). Wetland
484 typologies applied in several national inventories generally rely on a combination of three
485 criteria: soil type, hydrophytic vegetation and hydrology (Cowardin and Golet 1995).
486 Alternatively, hydrogeomorphic classification systems propose to exclusively draw on physical
487 drivers, such as geomorphology, hydrology and substrate to allow for cross-site comparisons of
488 biota and serve functional assessments (Brinson 1993, Semeniuk and Semeniuk 1995, 2011,
489 Davis et al. 2013).

490 While changes to inundation extent and depth can occur at time scales ranging from days to
491 decades, the most conspicuous inundation patterns occur on event (e.g., flooding due to rain
492 events), seasonal (e.g. snow melt or wet/dry seasons), and interannual time scales. Primary
493 drivers of inundation in unmanaged wetlands come from subsurface groundwater discharge and
494 surface flows including rainfall or snowmelt runoff that occur when antecedent soil moisture
495 conditions are high, preventing quick infiltration of water (Rasmussen et al. 2016). Many
496 wetlands are actively managed, such as to provide bird habitat, so that inundation can vary
497 based on management decisions [see below and (Fredrickson and Taylor 1982)].

498 The spatial scales of variable inundation are shaped both by wetland size and
499 geomorphology. Wetlands can be shallow over large spatial scales, and thus the size of variably
500 inundated wetland area can range from microtopographic (i.e., hummock/hollow, ~m² scales) to
501 larger ecosystem scales. Large wetland areas, especially in the tropics, experience strong
502 seasonal inundation cycles which depend on changes in water balance and local topography
503 (Zhang et al. 2021). While the largest variably inundated wetlands are connected to floodplains,
504 like the 130,000 km² Pantanal (Ivory et al. 2019), non-floodplain wetlands surrounded by upland
505 (also known as geographically isolated wetlands) as large as ~6 ha may also experience whole-
506 system drying and rewetting (Lane and D'Amico 2016).

507 Embedded within wetland ecosystems, microtopographic structures can create within-
508 system mosaics of inundation regimes. Microtopography in peaty wetlands is particularly
509 pronounced, ranging from several tens of meters [e.g., ridges and sloughs (Larsen et al. 2011)]
510 to meters [e.g. hummock-hollows (Shi et al. 2015)]. These spatial patterns result from dynamic
511 feedbacks between ecological processes (e.g. peat accumulation) and hydrology that reinforce
512 these patterns (Belyea and Baird 2006, Eppinga et al. 2008, Larsen et al. 2011).

513 Wetlands are widely acknowledged to be biogeochemical hot spots and ecosystem control
514 points (McClain et al. 2003, Bernhardt et al. 2017) because of the confluence in space and time
515 of allochthonous substrates into reactive environments (e.g., nitrate produced under oxic
516 conditions entering anaerobic environments where denitrification can occur). In addition,
517 variable inundation is associated with nutrient influx into wetlands that replenishes nutrient pools
518 and can drive productivity and organic matter decomposition (Venterink et al. 2002). The depth
519 and duration of flooding shapes the wetland vegetation community by controlling germination
520 success, modifying oxygen availability and changing concentrations of toxins and nutrients, by
521 desiccating aquatic plants or inundating terrestrial plants, and by changing the light availability
522 (Casanova and Brock 2000). Wetland vegetation is structurally adapted to low oxygen
523 environments, for example, some vegetation has developed air channels in leaves, stems, and
524 roots to transport oxygen belowground (Tiner 2017). Alternatively, wetland vegetation can also
525 respond to shifts in oxygen levels physiologically on shorter time scales (Colmer 2003).

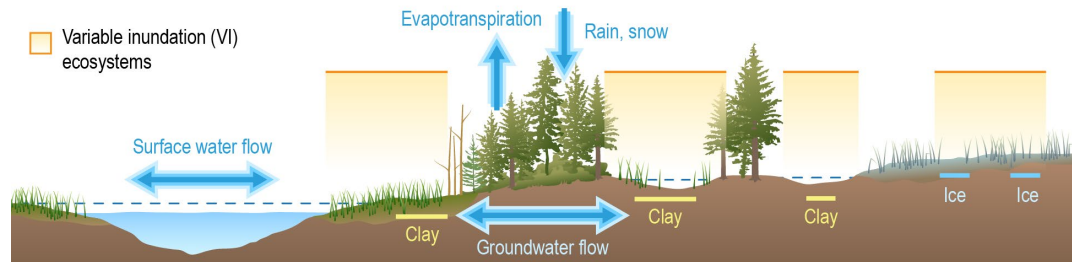
526 Variable inundation provides an environmental filter for biota adapted to live either under dry
527 or inundated conditions, resulting in distinct communities including wetland obligate and



528 facultative species (Gleason and Rooney 2018). The temporal duration of inundation (i.e.,
529 hydroperiod) indirectly controls the bird community composition through absence and presence
530 of wetland vegetation and availability of aquatic macroinvertebrate prey (Daniel and Rooney
531 2021). Amphibian communities are particularly impacted by hydroperiod: It needs to be long
532 enough for eggs to hatch and tadpoles to reach metamorphosis, but should not allow the
533 establishment of many predator species (Resetarits 1996).

534 Predicting how complex inundation patterns in wetlands will change under changing climate
535 is a major research challenge. Predictions span the range from a decrease in inundation in
536 some regions (Londe et al. 2022b) to an increase in others (Watts et al. 2014), with uncertain
537 consequences for wetland persistence overall. To improve regional or global predictions,
538 accurate maps of wetland extent on different scales that can be incorporated into mechanistic
539 models will be necessary (Melton et al. 2013). This is particularly challenging for non-permanent
540 wetlands, which are hard to reliably map and are generally understudied (Gallant 2015, Calhoun
541 et al. 2017), but which are, by definition, VIEs. As climate change alters wetland inundation
542 regimes, the net impacts to carbon storage and greenhouse gas fluxes are of particular concern
543 (Moomaw et al. 2018), because together they will determine the net climatic impact of changes
544 in wetland area and dynamics (Neubauer and Megonigal 2015).

545



546

547 **Figure 6. Conceptual model of variable inundation in wetland systems.** Different wetland
548 types are influenced and shaped by variable inundation. Absence and presence of surface
549 water is driven by (e.g., seasonally) changing water supply and the hydrologic function of the
550 wetland in the landscape. Sediment characteristics (e.g., clay or ice) and topographic positions
551 of wetlands in the landscape influence water loss to infiltration or gain from groundwater. Credit:
552 Nathan Johnson.

553 Freshwater Ponds

554 Freshwater ponds are among the most abundant and common freshwater ecosystems
555 worldwide, with estimates between 500 million and 3.2 billion ponds globally (Davidson et al.
556 2018, Hill et al. 2021). Ponds are generally small (less than 5 ha) and shallow (less than 5 m),
557 and consequently, are highly sensitive to changes in water levels that can result in highly
558 variable inundation regimes (Gendreau et al. 2021, Richardson et al. 2022a). Pond ecosystems
559 are extremely diverse, and include arctic thermokarst ponds, prairie potholes, vernal pools,
560 playas, rock pools and agricultural dugouts. The numbers of ponds globally are likely
561 underestimated, as their size and ephemeral/temporary nature has meant they are often



562 excluded from physical inventories and they are below the resolution of many remote sensing
563 techniques (Hayashi et al. 2016, Calhoun et al. 2017, Hill et al. 2021).

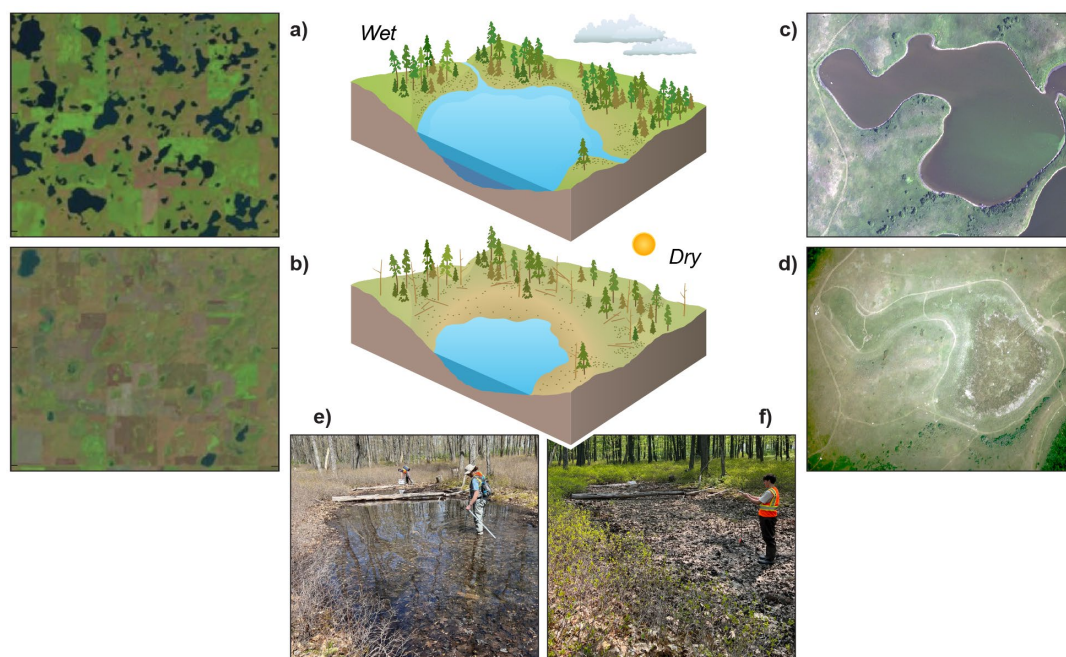
564 As in many other VIEs, inundation of freshwater ponds can be highly variable, and the
565 timing, duration and frequency of inundation can vary considerably (Williams 2006). Many
566 temporary or ephemeral ponds can become intermittently or seasonally flooded (**Fig. 7**). For
567 some ponds, particularly vernal pools, seasonal inundation is relatively predictable, as these
568 systems become inundated following snowmelt or spring runoff, and are subsequently drawn
569 down with increasing summer evapotranspiration (Zedler 2003, Brooks 2004). Variation in the
570 hydroperiod can alter the composition of biotic communities (Brooks 2004, Gleason and Rooney
571 2018), as well as impact biogeochemical and hydrological processes (Bam et al. 2020, Hondula
572 et al. 2021b). In more temperate regions, the timing of inundation is often driven by heavy
573 rainfall, and periods of inundation can be highly variable, with inundation durations lasting from
574 days to months, and sometimes occurring intermittently as ephemeral systems dry and rewet
575 multiple times in a year (Ripley and Simovich 2009, Kneitel 2014, Florencio et al. 2020). For
576 nearly permanent ponds, the pattern of wet and dry periods are more predictable, but the
577 initiation and length of the hydroperiod can vary spatially as water levels fluctuate, inundating
578 and exposing shallower areas (Brendonck et al. 2017). Freshwater ponds often demonstrate
579 both high inter- and intra-annual variability, and diurnal, annual and multidecadal periods of
580 inundation can occur due to changes in evapotranspiration, drought, drainage, flooding, and / or
581 hydrologic function of the pond on the landscape (Brooks 2004, Gendreau et al. 2021).
582 Modifications to ponds by humans (e.g. irrigation ponds, urban stormwater ponds; see section
583 on human-engineered systems) or other organisms, such as beavers, can also impact
584 hydroperiod and inundation regimes (Renwick et al. 2006, Brazier et al. 2021).

585 Like many of the other ecosystems that experience variable inundation, freshwater ponds
586 are also considered biodiversity and biogeochemical hotspots, providing many critical
587 ecosystem services (Capps et al. 2014, Marton et al. 2015). Despite their relatively small size,
588 ponds can have considerable variability in both community composition and in biogeochemical
589 processes, in part due to differences in inundation regimes, where pond margins are more likely
590 to be more frequently desiccated for longer periods than central regions (Reverey et al. 2018).
591 Models that explicitly incorporate remotely sensed variable inundation predict that ephemeral
592 systems with shorter hydroperiods retain nitrogen at greater rates than larger systems with less
593 variable inundation and longer hydroperiods, particularly in semi-arid regions like the Prairie
594 Potholes of the North American northern Great Plains and playas in the south-central United
595 States (Cheng et al. 2023). In addition, research suggests reproduction is largely impacted by
596 inundation. Salamanders, for example, tend to lay more eggs during years with greater rainfall
597 while hatching success decreases with desiccation (Della Rocca et al. 2005). Variable
598 inundation across ponds can result in ecosystem heterogeneity at the landscape scale,
599 increasing local abiotic and biotic variation (Jeffries 2008), but the number and distribution of
600 inundated ponds can also impact regional biodiversity through processes like dispersal
601 (Brendonck et al. 2017).

602 Climate change will likely alter the inundation regimes in freshwater ponds in terms of timing,
603 frequency, duration, and extent. Decreases in precipitation and increases in extreme drought
604 can result in shortened hydroperiods, and increasing temperatures can alter water temperatures
605 and evaporation rates (Matthews 2010). The persistence of freshwater ponds may, therefore, be



606 reduced with climate change (Londe et al. 2022b). Understanding how future changes in
607 inundation regimes impact freshwater ponds will be critical. Similar to wetland ecosystems,
608 improved remote sensing methods, including incorporating multispectral imagery and radar
609 along with finer spatial resolution mapping approaches may improve the mapping, counting and
610 inclusion of small ponds in freshwater inventories (Bie et al. 2020, Rosentreter et al. 2021,
611 Hofmeister et al. 2022). As inundation regimes may become more variable, increasing
612 conservation and protection efforts for ephemeral and temporary ponds may become more
613 essential to maintain these critical VIEs.
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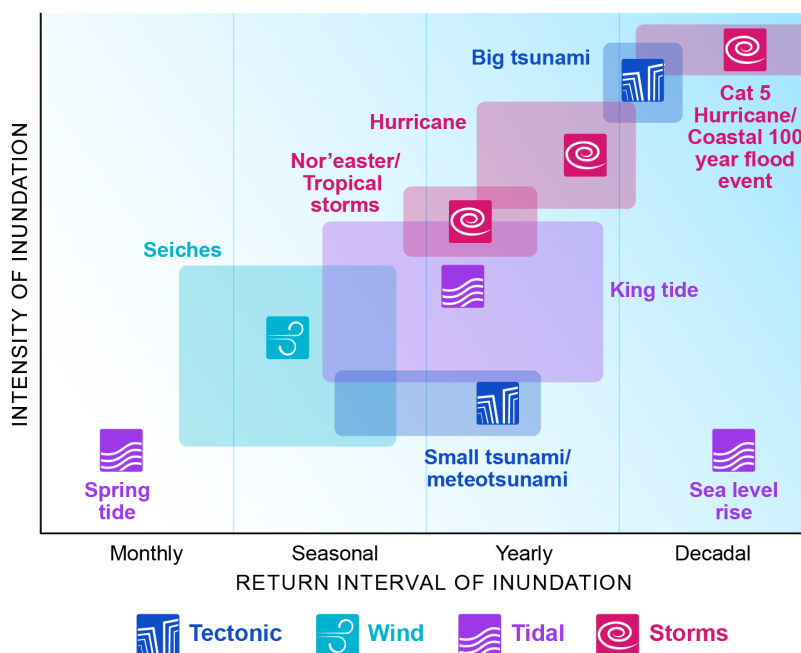
617 **Figure 7. Examples of variable inundation across scales in pond systems.** Satellite
618 imagery of the Prairie Pothole Region, North Dakota, USA illustrating decadal variable
619 inundation at a landscape scale a) September 2, 1992; b) May 23, 2013 [modified from
620 (Scientific Investigations Report 2015)] and at the pond scale; Aerial Imagery of Pond P1,
621 Cottonwood Lake Study Area, North Dakota c) September, 2002 d) September, 1992 (Images
622 from (U.S. Geological Survey 2017)). Seasonal changes in a vernal pond in Moshannon State
623 Forest, Pennsylvania, USA) inundated (May 11, 2023) non-inundated (May 23, 2023) (J.N.
624 Sweetman). Conceptual drawings by Nathan Johnson.

625 Storm-Impacted Coastal Zones

626 The coastal zone includes ecosystems and communities (cities/towns) that are adjacent and
627 hydrologically connected to a large water body (e.g., ocean, Great Lakes). These systems
628 influence, are impacted by, and are dependent on coastal zone hydrologic processes, such as
629 flooding, that occur at the interface between terrestrial and aquatic domains. Unlike tidal



630 environments, inundation that affects the coastal zone is driven by temporary, often stochastic
 631 events including storms, seiches, and king tides. Depending on the topography of the area,
 632 infrastructure of the community, and size of the event, the size of coastal inundation varies from
 633 event to event (both geographic impact and aerial extent of inundation; **Fig. 8**). The frequency of
 634 these events ranges from multiple times a season to decadal (**Fig. 8**). Tropical storms and
 635 cyclones develop in tropical regions during seasonal periods of warm water each year. Due to
 636 their high energy and movement, they influence more temperate regions as well (Colbert and
 637 Soden 2012). In temperate or cold regions, storms develop in the winter time due to large
 638 temperature differences between land and ocean (Liberato et al. 2013). Natural systems will
 639 display some form of resilience and recovery to storm impacts (Lugo 2008, Wang et al. 2016),
 640 but human settlements and infrastructure are vulnerable to both intense winds and flooding
 641 (Lane et al. 2013, Hinkel et al. 2014, Braswell et al. 2022). Land use development also alters
 642 the natural resilience of coastal environments through the proliferation of gray infrastructure
 643 such as jetties and seawalls (Gittman et al. 2015). Systems in low-lying regions are particularly
 644 vulnerable to inundation as opposed to rocky shores with steep slopes. While regional or global
 645 data sets based on elevation data exist, the extent at any given time of storm surges, king tides,
 646 and other high water episodes depend locally/regionally on where the event hits, flooding
 647 infrastructure, and topography of the area.
 648



649 **Figure 8. Coastal VIEs experience inundation events with different frequencies and**
 650 **intensities.** Some events occur rarely, but are very high intensity events (category 5 hurricanes;
 651 large tsunamis), increasing the area of inundation and affecting areas that seldom experience
 652 flooding. The impacted systems are often less adapted to inundation, increasing the extent of
 653 destruction or reorganization of the system. Other events occur more regularly and/or are lower
 654



655 *in intensity (spring tide, seiches), leading to less extensive inundation and impacting coastal*
656 *systems that are more adapted to inundation. Credit: Nathan Johnson.*

657

658 Inundation in the coastal zone impacts sediment transport, solute and nutrient mobilization,
659 vegetation distribution, biological diversity, and biogeochemical processes. Erosion and
660 sediment deposition alter ecosystem geomorphology (e.g., dune shape, marsh accretion)
661 (Houser and Hamilton 2009, Dissanayake et al. 2015) and ecosystem nutrient pools [e.g.,
662 (O'Mara et al. 2019, Castañeda-Moya et al. 2020)]. In coastal zones adjacent to marine and
663 estuarine waters, saltwater intrusion changes surface (Schaffer-Smith et al. 2020) and
664 groundwater (Cantelon et al. 2022) quality and mobilizes nutrients through porewater ionic
665 exchange processes (Herbert et al. 2018). Coastal zone inundation as a natural process alters
666 dune systems, which generates a mosaic of habitats that increase biodiversity (Smith et al.
667 2021) and alter distributions of vegetation and animals. For example, the frequency of overwash
668 events affects plant composition and diversity on sand dunes (Stallins and Parker 2003) and
669 regular inundation is thought to provide necessary habitats for some insects and birds (Smith et
670 al. 2021). Increased salinity and associated geochemical changes alter microbial community
671 diversity and population heterogeneity (Nelson et al. 2015), shifting to more specialized
672 communities as an adaptation to anaerobic conditions, redox fluctuation, and salt stress.
673 Previous studies found high variability in relationships between salinity and ecosystem carbon
674 dioxide fluxes (Morrisey and Franklin 2015, van Dijk et al. 2015, Dang et al. 2019, Hopple et al.
675 2022).

676 Human communities within the coastal zone are impacted by inundation events as well.
677 Inundation of coastal agricultural lands from storm surge and sea level rise reduces agricultural
678 productivity (Lei et al. 2016). In particular, risk is high to coastal zone communities in developing
679 nations, where inundation events can lead to food insecurity, loss of livelihood, and increased
680 transmission of waterborne diseases. As climate change alters the magnitude and frequency of
681 inundation in the coastal zone, it will be necessary to integrate both natural and human
682 adaptations, such as enabling salt marsh transgression (marsh migration upland) to mitigate
683 storm surge impacts on crop yield (Guimond and Michael 2021).

684 While we understand many of the linkages between the ecology, biogeochemistry,
685 hydrology, and geomorphology that regulate ecosystem structure and function in coastal
686 systems (Fagherazzi et al. 2012, Hinshaw et al. 2017, Braswell and Heffernan 2019, Cantelon
687 et al. 2022), we know little of how to predict the future effects of the interacting stressors
688 associated with climate change (O'Meara et al. 2017, Ward et al. 2020, Arrigo et al. 2020). Our
689 ability to predict is reliant on our understanding of shifting inundation regimes in the context of
690 elevated CO₂, nutrient pollution, and coastal development which can generate antagonistic,
691 synergistic, or additive effects. These knowledge gaps stem from the dynamic and
692 unpredictable nature of events that drive coastal inundation. Observational data to inform
693 mechanistic models is limited and governed by where and when events happen (not necessarily
694 within monitored sites), funding periods, and accessible coastlines. This difficulty is exacerbated
695 by the fact that 40% of the world's population lives within 100 km of the coast (Maul and Duedall
696 2019), which heightens social impacts of variable inundation while also adding logistical
697 difficulty to coastal monitoring. When events do overlap with instrumented sites, the extreme
698 nature of inundation events threaten instrumentation arrays, risking washout or flooding of



699 monitoring infrastructure. Lastly, high-latitude coastlines are also susceptible to coastal
700 inundation, yet few models incorporate physical, biogeochemical, and ecological implications of
701 inundation on permafrost bound coastlines and environments (Ekici et al. 2019, Bevacqua et al.
702 2020). Opportunities of critical knowledge advancement exist in 1) monitoring events through *in-*
703 *situ* or remotely sensed monitoring data, 2) model development that integrates more robust
704 process-based understanding, and 3) expansion into urban and permafrost-bound coastlines.

705 Tidally Driven Coastal Zones

706 Tidally-influenced coastal zones exist at the intersection of terrestrial and marine environments
707 and encompass diverse intertidal ecosystems including tidal wetlands, flats, and beaches (**Fig.**
708 **9**). Globally, tidal wetlands exist on 6 of 7 continents, and are spread across tropical, temperate,
709 and polar latitudes (Murray et al. 2022a). Tidal flats are predominantly found along low sloping
710 coastlines with approximately 70% of global tidal flat area existing in Asia, North America, and
711 South America (Murray et al. 2022b), while beaches encompass 31% of ice-free shorelines
712 (Luijendijk et al. 2018).

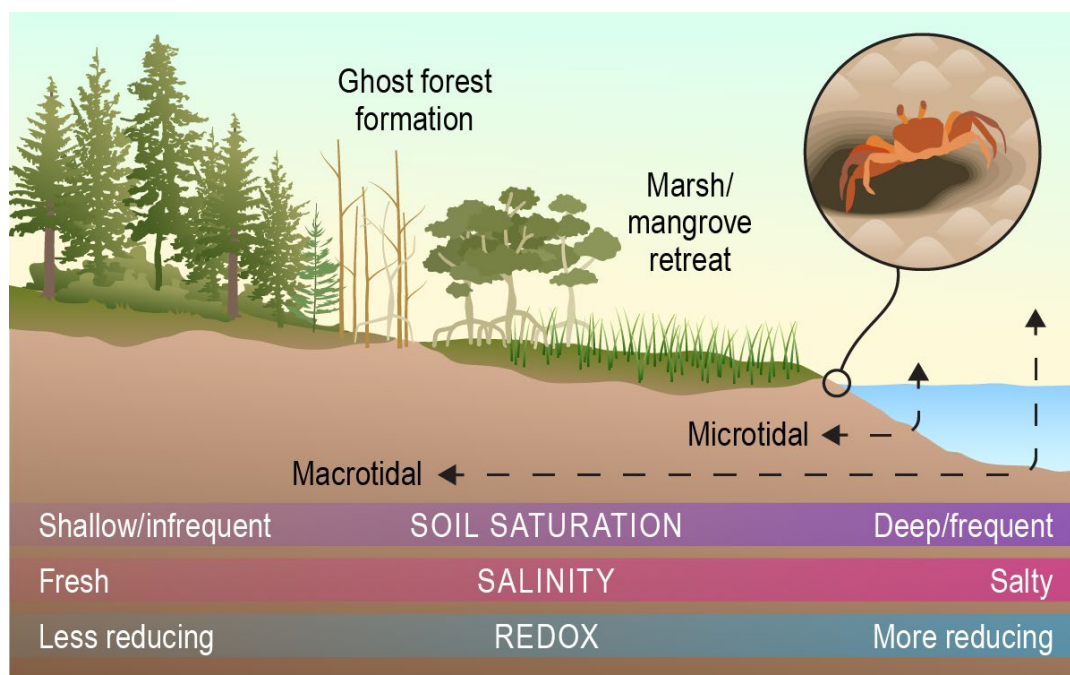
713 Tidally-driven coastal zones are inundated semi-diurnally (i.e., twice a day) or diurnally (i.e.,
714 once a day). Unlike VIE systems summarized above, where inundation events may be difficult
715 to predict, inundation in tidally-driven coastal zones varies primarily based on predictable
716 drivers. For example, high tide and low tide water levels dictate the spatial extent and duration
717 of inundation. In addition, intra-annual tidal dynamics are largely controlled by lunar cycles
718 which drive approximately monthly highest (spring) and lowest (neap) tides, as well as annual
719 high (king) and low tides. Inter-annual tidal dynamics are linked to sea level rise, which is
720 shifting the zone of variable inundation inland (Ensign and Noe 2018, Tagestad et al. 2021). We
721 note that while the timing of king tides is predictable (perigean spring tide), their impacts can be
722 difficult to predict, as mentioned in the storm-impacted coastal zones section. In addition,
723 topography (e.g., slope) and other natural physical factors, including wind speed and direction,
724 waves, and even localized high and low pressure events mediate the lateral extent of surface
725 water inundation in tidal ecosystems. Human modifications further alter both vertical and
726 longitudinal extent of tidal flooding via control structures which may exclude tides (gates, weirs,
727 etc.) and channels that transport tidal waters well inland of the natural intertidal zone.

728 The extent of tidal influence, which spans microtidal (< 2 meter tidal range) to macrotidal (>
729 10 meter tidal range in some locations), controls water quality, terrestrial-aquatic interactions
730 and resulting biogeochemical and ecological responses [e.g., (Tweedley 2016)]. Estuaries,
731 where tides mix saltwater and freshwater, are dynamic biogeochemical mixing zones
732 characterized by sharp chemical gradients that regulate biological activity [e.g., (Crump et al.
733 2017)]. Shifts in tidal zones associated with sea-level rise are predicted to alter the extent of key
734 intertidal habitats, with potential disruptions to coastal food webs (Rullens et al. 2022). Changes
735 in duration and extent of inundation associated with tides control soil saturation and salinity,
736 which influence redox dynamics, and hydrologically driven exchange of carbon, nutrients, and
737 pollutants (Pezeshki and DeLaune 2012, Bogard et al. 2020, Regier et al. 2021). Biological
738 activity, including crab burrows that alter hydrologic flow paths (Crotty et al. 2020), also
739 influence tidal exchanges across the coastal terrestrial-aquatic interface (Crotty et al. 2020).
740 Increased saltwater exposure due to shifting tidal ranges can alter the stability of coastal soils
741 [e.g., (Chambers et al. 2019)], which represent a globally important carbon sink (McLeod et al.



742 2011). In addition, tidal regimes structure vegetation gradients, where salt-sensitive
743 communities including low-lying forests and freshwater marsh species are replaced by salt-
744 tolerant communities including mangroves and saltmarsh species (Kirwan and Gedan 2019,
745 Lovelock and Reef 2020). This shift in tidal range leads to the creation of ghost forests (Kirwan
746 and Gedan 2019), which can impact coastal biogeochemical cycles [e.g., (Cawley et al. 2014).
747 Similarly, sea level rise may lead to mangrove or marsh retreat as inundation patterns change
748 (Xie et al. 2020).

749 Due to the frequency of inundation, tidally inundated ecosystems are hydrologically,
750 biogeochemically, and geomorphologically dynamic, creating challenges for scientists and land
751 managers seeking accurate estimations of land surface area, elevation, and carbon storage.
752 These challenges are exacerbated by sea level rise, which exerts heterogeneous and non-linear
753 influences on tidal ranges (Du et al. 2018). Methodological approaches to assess tidal
754 ecosystem area and elevation that are based on satellite imagery will be critical for present and
755 future management and decision making. Similarly, complex feedbacks across three-
756 dimensional physical space exist among hydrology, biogeochemistry, ecology, and
757 geomorphology (Xin et al. 2022); these dynamics may need to be considered in future
758 ecosystem projections. Thus, a deeper understanding of feedbacks and their variability in space
759 and time in response to tidal activity is needed (Ward et al. 2020). Lastly, with sea-level rise,
760 tidal constituents may change, with nonlinear impacts on tidal range and inundation extent
761 (Pickering et al. 2017). Tidally inundated VIEs represent the interface between marine and
762 terrestrial ecosystems, and to predict their future will require understanding bi-directional
763 connections among physical, chemical, and biological system components.
764





766 **Figure 9. Conceptual model of variable inundation in tidal systems.** Tidally driven coastal
767 zones span sediments exposed at low tide to marshes and coastal forests inundated at high
768 tide. This lateral gradient of tidal exposure is characterized by gradients in vegetation and soil
769 characteristics, and modified by the physical, chemical, and biological factors discussed in the
770 tidal systems section. Credit: Nathan Johnson.

771 Human-Engineered Systems

772 Human-engineered systems are environments where inundation magnitude, frequency, timing,
773 and duration are either actively managed or have been dramatically altered by structural
774 modifications to the landscape (**Fig. 10**). Human-engineered VIEs rival natural systems in area
775 and extent (Clifford and Heffernan 2018), yet the significance of engineered VIEs in influencing
776 landscape processes is relatively unexplored compared to natural systems (Koschorreck et al.
777 2020) and they are historically excluded from water and nutrient budgets (Abbott et al. 2019).
778 The primary drivers of human-engineered VIE formation explored here are land use change and
779 restoration, though hydrologic modifications impact inundation regimes of the natural VIEs
780 explored earlier in the manuscript. Examples of land-use driven human-engineered VIEs
781 include, but are not limited to, croplands irrigated by flooding (e.g., rice paddies, cranberry
782 bogs); irrigation and drainage canals, stormwater control structures (e.g., roadside ditches,
783 retention ponds), as well as unintentional VIE formation following landscape modification such
784 as “accidental” urban wetlands (Palta et al. 2017) or ponding in agricultural fields (Saadat et al.
785 2020). Whereas the purpose of land-use driven engineered VIEs is to redistribute water for
786 human purposes, the goal of VIEs engineered for restoration is to either replace or enhance
787 ecosystems lost or damaged as a result of human activity. VIE restoration efforts vary in scope
788 and form, spanning local (e.g., residential living shorelines, individual stream reaches,
789 agricultural ditch wetlands) to ecosystem [e.g., adding sediment to degrading marshes
790 (VanZomeran et al. 2018)], to regional (e.g., dam removal) scales.

791 While the full extent of human-engineered VIEs is difficult to quantify, key examples highlight
792 their significance in the landscape. Agriculture covers nearly 40% of the earth’s land surface
793 (Siebert et al. 2010), and nearly a quarter of that is variably inundated by flood irrigation (Wu et
794 al. 2023). In urban systems, the extent of stormwater control networks rival those of natural
795 systems. For example, the total linear length of residential canals in North America nearly
796 equals that of the Mississippi River (Waltham and Connolly 2011). While restoration efforts are
797 not as widely distributed as land-use change, restoration still contributes to extensive VIE
798 creation. For example, restoration accounts for 14% of areal gain of tidal wetlands globally
799 (Murray et al. 2022b). Inundation regimes in human-engineered VIEs can be driven by natural
800 hydrologic processes, such as connectivity with the water table or tidal inputs. This is
801 particularly important in VIEs built for restoration, as establishing natural inundation regimes
802 enhances landscape connectivity and mediates ecosystem functions (Reis et al. 2017, Jones et
803 al. 2018). However, unlike the previously discussed natural systems, the drivers and duration of
804 inundation in human-engineered VIEs may be decoupled from natural hydrologic processes.
805 Controlling drainage, such as for stormwater management, land reclamation, or effluent
806 releases, is a key motivation for VIE construction and system design, resulting in inundation
807 periods largely driven by precipitation that persist at event to seasonal scales depending on
808 local hydrology and climate. Inundation duration may also occur on longer timescales, such as



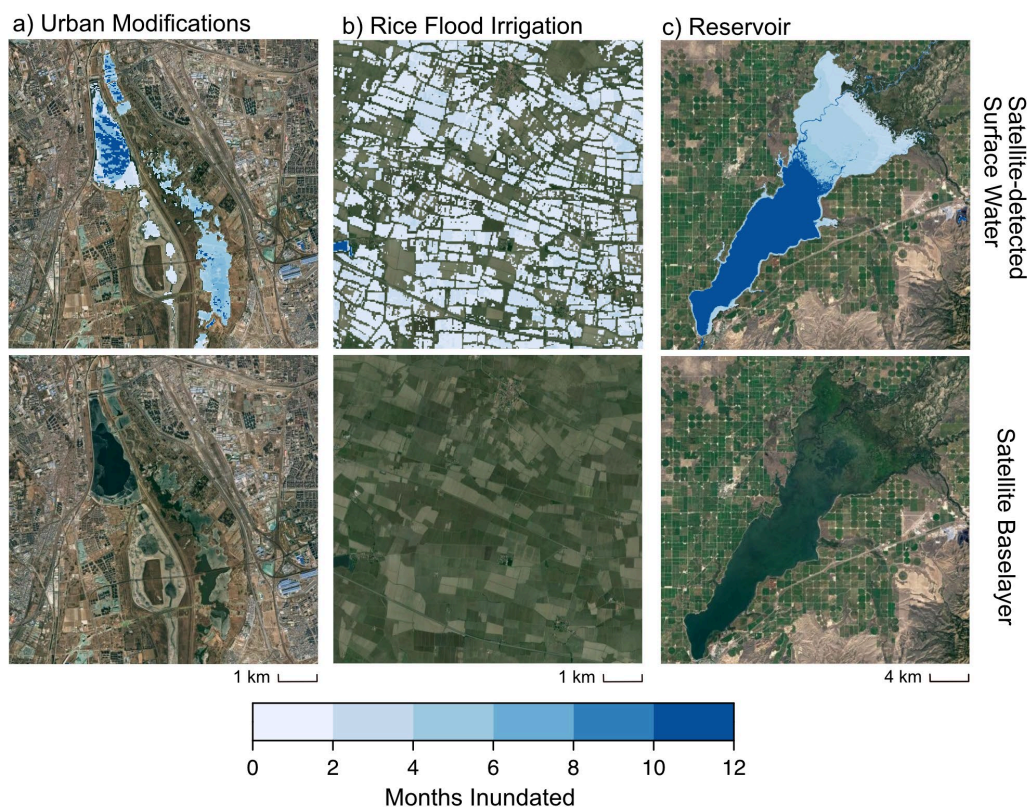
809 seasonal flooding in paddy systems (De Vries et al. 2010). Finally, direct human interventions,
810 such as floodgates, weirs, and dams, may affect water residence time at timescales that are
811 asynchronous from natural drivers, such as seasonality or tides.

812 Human-engineered VIEs fundamentally alter the landscape, changing the spatial and
813 temporal patterns of ecosystem processes. Agricultural inundation, such as flood irrigation or
814 ponding, alters redox conditions, greenhouse gas emissions, groundwater recharge,
815 evapotranspiration fluxes, plant growth, and pollutant export to natural water bodies (Hale et al.
816 2015, Pan et al. 2017, Pool et al. 2021, Buszka and Reeves 2021). For example, a recent study
817 showed that variably inundated depressions in agricultural fields can account for ~30% of
818 nitrous oxide emissions across cultivated areas despite comprising ~1% of the land surface
819 (Elberling et al. 2023). The creation of drainage canals increases waterborne carbon fluxes from
820 VIEs by producing a newly decomposed stock of labile soil carbon to be leached as well as by
821 increasing the hydrological runoff rate through the soil and receiving canals and ditches (Stanley
822 et al. 2012). Human-engineered VIEs can also provide ecosystem services that supplement or
823 replace those of natural VIEs in the landscape (Clifford and Heffernan 2018). For example, they
824 can enhance habitat (Connolly 2003, Herzon and Helenius 2008), nitrogen removal (Bettez and
825 Groffman 2012, Reisinger et al. 2016), and recreation (Beckingham et al. 2019). Further, the
826 services these systems provide can be improved through targeted management [e.g.,
827 vegetation composition; (Castaldelli et al. 2015)] or restoration practices [i.e., two-stage ditches;
828 (Speir et al. 2020)].

829 Including human-engineered systems in our conceptualization of VIEs emphasizes the
830 growing significance of these systems as human landscape modifications continue to alter and
831 eliminate natural VIEs. Recent efforts have synthesized the role and impacts of human-
832 engineered VIEs at large scales (Peacock et al. 2021, Li et al. 2022b) but, as with many natural
833 systems, the majority of studies on human-engineered VIEs are based in North America and
834 Europe (González et al. 2015, Zhang et al. 2018, Bertolini and da Mosto 2021). Thus, our
835 knowledge may not reflect the social, political, and economic challenges of developing areas
836 where the highest rates of VIE modification are occurring (Wantzen et al. 2019). The knowledge
837 gaps surrounding human-engineered VIEs will become increasingly important to address as
838 global change continues to alter the spatial and temporal patterns of inundation. Given that
839 human-engineered VIEs can enhance or disrupt hydrologic connectivity, they potentially
840 magnify the effects of human driven changes such as sea level rise and impacts of
841 contamination from anthropogenic “chemical cocktails” (Kaushal et al. 2022). We lack a
842 baseline standard for how human-engineered VIEs function in the landscape, even as global
843 change continues to shift existing baselines [e.g., (Palmer et al. 2014)]. Addressing these
844 knowledge gaps will require the incorporation of human-engineered VIEs into large-scale
845 synthesis and modeling efforts, particularly those that address hydrologic and biogeochemical
846 fluxes. Conclusive definitions and inventories of human-engineered VIEs is essential for
847 estimating their ecological and biogeochemical roles at the global scale. Finally, human-
848 engineered VIEs need to be conceptualized within an ecological, rather than managerial,
849 context for integration and comparison with natural systems. Human-engineered VIEs rival the
850 range of natural VIEs in structure, inundation regime, and global distribution. Understanding
851 their role in the Earth system is, therefore, critical for understanding both the impacts of and
852 potential solutions to global change.



853



854

855

856 **Figure 10. Examples of human-engineered Variably Inundated Ecosystems.** a) Yongding
857 River in Beijing, China; b) Paddy rice fields in northern Italy; c) American Falls Reservoir on the
858 Snake River in Idaho, United States. These three examples emphasize significant variation in
859 the degree of variable inundation across human-engineered VIEs, with some regions being
860 perennially inundated. Top row: Satellite-derived map data on months inundated is derived from
861 the “seasonality” product in the Global Surface Water Mapping Layers v1.4 (Pekel et al. 2016).
862 Credit: Jillian Deines.

863 Inundation Processes are Relevant at the Scale of the Beholder

864 VIEs span broad spatiotemporal scales of variable inundation, from microenvironments like
865 mosses and pore spaces that are periodically covered by droplets of water, to vast endorheic
866 lakes and rivers. Inundation volumes and surface areas of VIEs vary by at least sixteen orders
867 of magnitude, from under 10^{-3} L to over 10^{13} L (<https://www.k26.com/lake-eyre-papers-lake-eyre-basics>), and 10^{-6} m² to over 10^{10} m² (<https://www.guinnessworldrecords.com/world-records/92443-largest-ephemeral-lake>), respectively. The duration of inundation varies by up to
870 eight orders of magnitude, spanning a few seconds, in the case of droplets, to decades, in the
871 case of endorheic lakes, and centuries in the case of sea level rise. Non-inundated periods



872 likewise span seconds to centuries and longer. This variability in spatial and temporal extent has
873 profound consequences for the ecology and biogeochemistry of VIEs. This section highlights
874 the importance of considering scale and explores hypotheses regarding how scale drives
875 variability in drivers, processes, and impacts across VIEs and how we study them.

876 Spatial and temporal scales of VIEs can be categorized along two axes – extent and
877 granularity. Extent comprises the total size of the spatial domain or time duration of a defined
878 system, while granularity pertains to the spatial or temporal intervals of system transitions
879 (Ladau and Eloë-Fadrosh 2019). For example, the dynamics of water droplets across North
880 America would represent a large extent with fine granularity, relative to the inundation dynamics
881 of a several square meter desert playa (smaller extent but coarser grain). The impacts of
882 variable inundation are dependent ‘on the scale of the beholder’ relative to the extent and grain
883 of variable inundation, where a ‘beholder’ may be a molecule, organism, population, community,
884 land manager, or otherwise. The expressed metabolism of an individual microbe will be
885 influenced by inundation down to the spatial scale of water films and on hourly or shorter time
886 scales. An individual microbe may not, however, be influenced by whether variable inundation
887 occurs only within a square meter or across many square kilometers because it does not
888 perceive these larger scales. In contrast, macroinvertebrate behavior is influenced by variable
889 inundation down to scales of meters and days, and is likely further influenced by larger and
890 longer scales of stream network connectivity (Bogan et al. 2017b, Sarremejane et al. 2017).

891 VIEs can be viewed as habitat patches of different sizes that vary in how long they persist in
892 a given state and that have dynamic connectivity among patches. Terrestrial and aquatic biota
893 respond on ecological and evolutionary time scales to the expansion and contraction cycles of
894 inundation (Bornette et al. 1998, Ward et al. 2002). Biotic diversity is influenced by productivity,
895 connectivity, disturbance severity and disturbance frequency, all of which operate at hierarchical
896 scales (Ward et al. 1999). Biogeographical and ecological theories posit that patch size (e.g.,
897 species area scaling) and disturbance regimes (e.g., intermediate disturbance hypothesis) are
898 strong determinants of community composition (Adler et al. 2005, Svensson et al. 2012),
899 suggesting that VIE community composition may vary predictably with these factors. The
900 duration, predictability, and frequency of inundation likely have consistent community-level
901 consequences that vary predictably with VIE extent and grain. Different extents and grains of
902 inundation have the potential to change habitat connectivity in addition to directly selecting for
903 different groups of organisms. Isolated marshes may, for example, become merged during a
904 flood, thereby enhancing dispersal of aquatic organisms. The scale of variable inundation has
905 numerous influences over ecological processes and dynamics that need to be understood.

906 From a biogeochemical perspective, variable inundation generates spatial and temporal
907 variation in rates and patterns of biogeochemical processes. This variability is important for
908 scaling biogeochemical rates because of process nonlinearity and Jensen’s inequality (Ruel and
909 Ayres 1999). That is, a rate based on average conditions differs systematically from the average
910 rate across variable conditions. This is important because the scales of processes (e.g.,
911 microbial activity occurring within pore channels) are typically not aligned with the scales of
912 measurements and models (e.g., core-scale or above). The lack of clear understanding for how
913 variable inundation influences variation in biogeochemical processes and how these
914 relationships change with extent and grain of inundation can, therefore, lead to unreliable
915 predictions for the scaling of biogeochemical processes.



916 Understanding the biogeochemical influences of variable inundation across a broad range of
917 scales is important for informing a diverse suite of needs across models, decision makers, and
918 other interested parties. Our ability to inform these needs depends on our ability to rigorously
919 understand and predict influences of variable inundation across scales. This is a challenge as
920 variable inundation likely has direct, but unknown, influences over the scaling of biogeochemical
921 function. For example, cumulative metabolism in streams is predicted to increase faster than
922 their upstream drainage area for perennial stream networks (Wollheim et al. 2022). The
923 influence of variable inundation on biogeochemical processes cannot yet be accounted for in
924 such scaling theory. More generally, perturbations like variable inundation can drive systems
925 away from steady-state assumptions from which scaling relationships are derived (McCarthy et
926 al. 2019), therefore, we expect significant changes in scaling behavior across inundation
927 regimes. A research frontier is to quantify the direction, magnitude, and duration of changes in
928 scaling patterns in response to variable inundation and to modified variable inundation regimes
929 wrought by climate, land-use, and other environmental changes.

930 **Summary of Primary Methods used to Study VIEs**

931 The multi-scale nature of VIE systems has led to experimental and observational studies that
932 span from point-scale lab-based characterization, to reach- or watershed-scale monitoring
933 networks, and to regional- and global-scale remote sensing. Point-scale measurements at the
934 smallest scales help reveal processes that underlie larger scale dynamics. For example, point
935 measures of water presence, water absence, and low flow detection within a watershed are
936 increasingly available with the development of small, inexpensive, and easily deployable
937 sensors, meters, and time-lapse cameras [e.g., (Soupir et al. 2009, Chapin et al. 2014, Costigan
938 et al. 2017, Zimmer et al. 2020)] (**Fig. 11**). While these measurements are easy to take and can
939 provide a long temporal dataset for little effort, they are not always detailed and require regular
940 calibrations.

941 A broad range of methods can be used to link the hydrologic dynamics to ecological and
942 biogeochemical responses. Standardized field surveys and biomolecular methods (e.g., isotopic
943 ratios, including compound specific analyses) are commonly used to study organismal,
944 population, and community ecology across multiple taxa [e.g., (Ode et al. 2016, Gates et al.
945 2020)] and can be standardized for both inundated and non-inundated states. There is
946 increasing use of crowdsourcing for biogeochemical characterization to consistently obtain
947 samples across diverse systems (von Schiller et al. 2019, Garayburu-Caruso et al. 2020).
948 Sample collection can be followed by a variety of laboratory measurements of properties (e.g.,
949 carbon content, redox potential and redox-active elements, microbial genetic potential, sediment
950 grain size) and processes, such as CO₂ production and methanogenesis related to variable
951 inundation. Point-scale measurements often operate at instantaneous to daily scales.
952 Conversely, larger scale measurements integrate across finer-scale processes to quantify
953 ecosystem dynamics and properties, but without necessarily revealing the governing the
954 processes. Spatially distributed monitoring networks using *in situ* sensors (e.g., the United
955 States Geological Survey, USGS, gage network) can connect event-scale responses across
956 hydrologically linked locations as well as reveal long-term trends [e.g., (Zipper et al. 2021)].
957 Long-term field manipulations are another complementary *in situ* technique that can reveal



958 mechanisms underlying system responses to changes in inundation state. There are numerous
959 configurations of such experiments that directly or indirectly impact inundation dynamics, such
960 as intentional inundation (Hopple et al. 2023), water exclusion (Kundel et al. 2018) and heating
961 (Hanson et al. 2017). Despite the plethora of data produced by such large scale projects, these
962 are expensive and require deep buy-in of researchers and landowners.

963 Remote sensing can complement *in situ* measurements to facilitate more spatially
964 continuous characterization of surface water dynamics and their impacts. There are different
965 types of remote sensing techniques that can capture different aspects of VIEs. For example, soil
966 surface saturation may be captured through passive microwave radiometer as well as C and L-
967 band radar backscatter, which can also penetrate through thin canopies, clouds, and through
968 the top few centimeters of the soil (Schumann and Moller 2015). Recent missions such as the
969 Surface Water and Ocean Topography (SWOT) mission provide increased capabilities for
970 monitoring changes in surface water over time with radar data (Biancamaria et al. 2016), while
971 NASA's forthcoming NISAR mission will allow for detection of inundation even under tree
972 canopy. Thermal infrared measurements can indirectly reveal saturation at very high
973 spatiotemporal resolutions, as well as evapotranspiration associated with water table depth, soil
974 moisture, and rooting depth (Fisher et al. 2020, Lalli et al. 2022). Long time series from
975 moderate resolution (~30 m) optical satellites can document multi-decadal open water trends
976 and seasonal regimes across the globe (Pekel et al. 2016), while some combinations of indices
977 have shown success in detecting mixed vegetation and inundation cover (Jones 2019).
978 Recently launched satellite constellations provide daily global imagery at < 4 m resolution,
979 enabling monitoring of more dynamic water bodies [e.g., Arctic lakes, (Cooley et al. 2017) and
980 forested wetlands (Hondula et al. 2021a)]. Finally, deep groundwater and changes in the total
981 water column storage are detectable through measurements of gravitational anomalies at very
982 high precision but low spatial resolution (Bloom et al. 2010, 2017, Richey et al. 2015, Pascolini-
983 Campbell et al. 2021).

984



985 **Figure 11. Monitoring inundation regimes is increasingly possible via *in situ* sensors.**
986 *Stream Temperature, Intermittency, and Conductivity Sensors (STICs) (Chapin et al. 2014), one*
987 *of the types of increasingly available sensors to measure water presence/absence in an*
988 *inexpensive and easily deployable manner. These sensors can be used across all types of VIEs.*
989 *Credit: Amy Burgin.*

991



992 To advance predictive understanding requires integration of data with models. Process-
993 based models can be used to simulate hydrological and biogeochemical processes under dry
994 and wet conditions (Fatichi et al. 2016, Li et al. 2017). These models are often built upon mass
995 conservation principles, with ordinary or partial differential equations that describe coupled
996 hydrological, ecological, and biogeochemical processes. They rely on existing knowledge on
997 processes, including, for example, theories or empirical relationships between discharge and
998 water storage (Wittenberg 1999), biogeochemical reaction rate dependence on temperature and
999 water content (Davidson et al. 1998, Mahecha et al. 2010) and redox reactions (Borch et al.
1000 2010). Among process-based models, there are spatially distributed models that couple surface
1001 and subsurface flow dynamics explicitly (Kollet and Maxwell 2006, Coon et al. 2020). This class
1002 of models has recently been extended to include reactive transport (Wu et al. 2021), which may
1003 be considered as a set of tools to understand the biogeochemical effects of variable inundation
1004 (Molins et al. 2022). However, spatial resolution and data requirements for the integrated
1005 surface and subsurface models are high, which places practical limits on the spatial scales that
1006 can be addressed. Semi- or fully-distributed models with coarse spatial resolution are able to
1007 work at larger scales, but require theories or empirical relationships to represent processes and
1008 impacts at subgrid-scales. Data-driven machine learning methods present new opportunities to
1009 blend models with various levels of mechanistic representations into hybrid models (Reichstein
1010 et al. 2019). Increases in the volume of observational data sets combined with advances in high
1011 performance computing have triggered a shift towards machine learning applications for
1012 capturing inundation dynamics. More recently, integration of physics-based models with
1013 machine learning have improved the interpretability of machine learning methods and increased
1014 their ability to model complex ecosystem processes (Sun et al. 2022). These hybrid approaches
1015 have the potential to optimize the characterization and prediction of inundation dynamics by
1016 incorporating the strengths of multiple models to achieve predictions with minimized uncertainty
1017 and greater accuracy than either model alone.

1018 Coordinated integration (Patel et al. 2023) between model development and data generation
1019 is key to deepening our understanding of VIEs and increasing our ability to predict their future
1020 ecosystem function and ecological integrity. More specifically, we promote iterating between
1021 model-guided data generation and observation-informed model development. This iterative
1022 cycle between models and ‘experiments’ (i.e., real-world data generation) has previously been
1023 termed ‘ModEx’ (Atchley et al. 2015) and is similar to approaches used in ‘ecological
1024 forecasting’ (Dietze et al. 2017, 2018). It also aligns generally with the scientific method based
1025 on continuous iteration between conjectures (hypotheses / models) and refutation (falsification
1026 of hypothesis using observations and data) to drive scientific discovery and knowledge growth
1027 (Popper 2014). The ModEx approach often starts by using experimental or field data to
1028 parameterize and calibrate models and/or generate new data based on known model input
1029 needs. This can be expanded whereby models generate hypotheses via *in silico* experiments,
1030 and field or lab studies can be designed to test those hypotheses. Models can also be used to
1031 optimize the design of real-world experiments by indicating when, where, and what to measure
1032 to provide the strongest hypothesis evaluation. In the context of VIEs, we expect ModEx to
1033 touch scales ranging from molecular microbiology to landscape ecology to regional ecosystem
1034 function to Earth system elemental cycles. Key to enabling this is the further development of
1035 models and measurement techniques that can capture system states in both inundated and



1036 non-inundated conditions. Techniques/models designed for specific kinds of ecosystems (e.g.,
1037 perennial rivers) may be difficult to adapt. This emphasizes a need to do ModEx using models
1038 and measurements intentionally designed to span inundated and non-inundated system states.

1039 Across the continuum of ModEx, it is important to consider the scales at which models and
1040 measurements operate, as discussed above. The issues around scale could, in part, be
1041 addressed by Integrated Coordinated Open Networked (ICON) science principles (Goldman et
1042 al. 2022). ICON is based on intentional design of research efforts to be Integrated across
1043 disciplines and scales, Coordinated across research efforts via consistent methods, Open
1044 throughout the research lifecycle, and Networked across stakeholders to understand collective
1045 needs. We propose using ICON principles for *in situ* data generation and remote sensing, jointly
1046 guided by model-generated predictions (i.e., ModEx). Embedding ICON throughout the research
1047 life cycle can help to ensure that new data are at the right scale and can be used to link
1048 disciplines (e.g., hydrology, biogeochemistry, and community ecology). This can also ensure
1049 that data are interoperable across VIEs, are available to everyone and connected to deep
1050 metadata, and are useful to a broad range of stakeholders with interests spanning different
1051 types and locations of VIEs. The use of ICON in cross-VIE science could bridge existing data
1052 across multiple spatial and temporal scales, and potentially bridge gaps among VIEs.

1053 **Towards Cross-VIE Transferable Understanding**

1054 We propose that a key goal for VIE science is the development and open sharing of knowledge,
1055 models, algorithms, and data that transcend individual system types. This can enhance our
1056 capacity to predict and protect the future of VIE function and integrity. Knowledge that crosses
1057 VIE systems will inherently span scales and levels of certainty from predictable, sub-daily
1058 inundation regimes to rare extreme events; integrating perspectives of these dynamic systems
1059 can aid in understanding and anticipating tipping points of physical, chemical, and biological
1060 components across VIEs. Development of such knowledge should be done via ModEx
1061 approaches coupled with ICON principles, which can generate models that can be used across
1062 VIEs with different physical settings and hydrologic dynamics. We suggest this can be achieved
1063 by taking a continuum approach based on key physical characteristics of VIEs (**Fig. 12**). While
1064 the categorical approach in the above mini-review sections was used to emphasize the breadth
1065 of VIE systems, we encourage research efforts to move beyond those artificial bins by invoking
1066 this continuum approach. For example, a dynamic, unified classification model has been
1067 proposed in wetlands, including a suite of temporally variable ecological and geomorphological
1068 characteristics (Lisenby et al. 2019). This framework has improved the understanding of human
1069 impacts on wetlands and led to more effective management (Wierzbicki et al. 2020, Mandishona
1070 and Knight 2022).

1071 The impacts of variable inundation depend on multiple characteristics of the inundation
1072 regimes (e.g., return interval and duration) and factors that influence those regimes (e.g.,
1073 subsurface permeability, topography, climate, and vegetation). Furthermore, there are dynamic
1074 attributes that influence process rates (e.g., water residence time and hydrologic connectivity),
1075 which can create additional feedback to the impacts of inundation variation. We hypothesize
1076 that despite this complexity, cross-VIE science can make progress towards transferable
1077 understanding by studying impacts of variable inundation across relatively simple physical



1078 variables that can be easily measured. Two such variables are inundation return interval and
1079 topographic slope (**Fig. 12**).

1080 Inundation return interval represents a key component of the continuum of inundation
1081 regimes and may be considered as a forcing factor. Topographic slope represents a key
1082 component of the continuum of VIE characteristics that influence how VIE systems respond to
1083 inundation-based forcing. In turn, these two variables can jointly influence nearly every physical,
1084 chemical, and biological aspect of VIEs. We do not, however, imply that these two variables
1085 capture all relevant processes. Other variables such as sediment/soil mineralogy and climate
1086 also have influences over biogeochemistry and community ecology. Nonetheless, we propose
1087 that significant progress can be made towards cross-VIE understanding of the controls over
1088 biogeochemistry and community ecology by pursuing the continuum approach via inundation
1089 return interval and topographic slope.

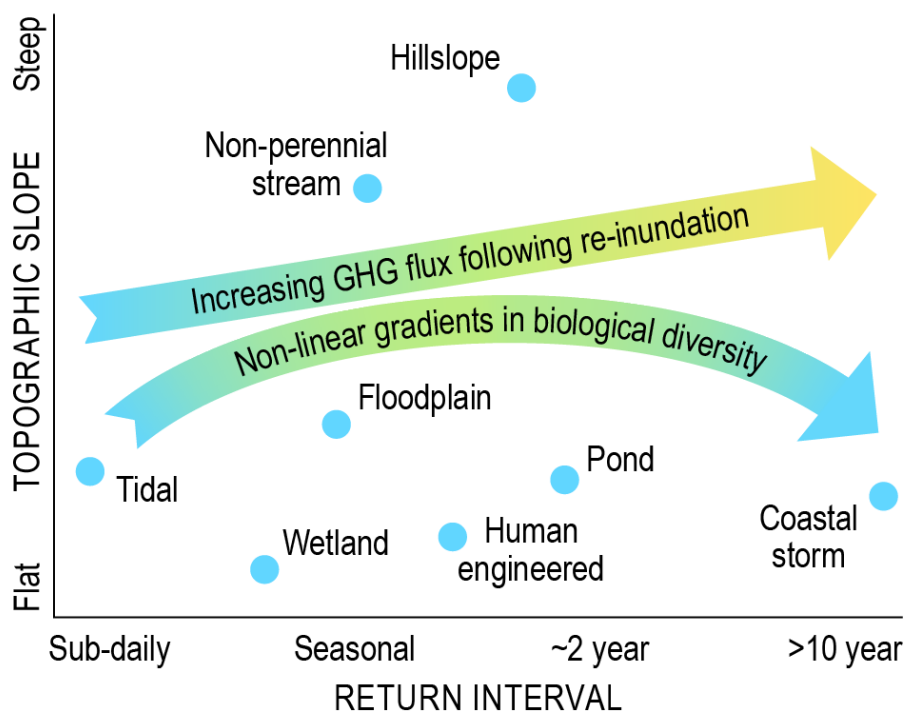
1090 The continuum approach can be applied to questions representing science challenges that
1091 span all VIEs, such as how greenhouse gas fluxes and biological diversity respond to variable
1092 inundation (**Fig. 12**). Similarly, metabolism research has suggested using a continuum of flow
1093 predictability and light availability to better unify river metabolism research (Bernhardt et al.
1094 2022). In this approach there is no need to bin VIEs into discrete categories, many of which
1095 have varying definitions and levels of overlap. Rather, we can observe and study continuous
1096 response surfaces across multiple physical axes and identify patterns within this quantitative
1097 space. In addition to generating transferable understanding, bringing all VIEs together via the
1098 continuum approach could help raise awareness of VIE diversity, importance, vulnerabilities,
1099 and how they may change in the future. This may, in turn, help address the fact that VIEs are
1100 often overlooked in terms of conservation and monitoring efforts (Calhoun et al. 2017, Hill et al.
1101 2018, Krabbenhoft et al. 2022, Zimmer et al. 2022). The continuum approach can also be used
1102 to learn where, along environmental continuums, functional thresholds exist that could help with
1103 categorizations important for policy and management (Richardson et al. 2022b).

1104 Cross-VIE understanding of the drivers, patterns, and processes linking inundation to
1105 system responses can greatly improve with increased collaboration and communication across
1106 scientific fields and systems. Communities working in VIEs are scattered across different
1107 societies and funding programs. Studying VIEs together via the continuum approach can bring
1108 these science communities together. To this end, we encourage training and collaborations
1109 focused on consistent data generation methods that may be adopted across the VIE community
1110 and in pursuit of the continuum approach. In addition, disciplinary conferences could also
1111 recognize VIE commonalities with special sessions to bring people together from across the VIE
1112 continuum to discuss research needs.

1113 Cross-VIE knowledge and models are needed to address human impacts to environments
1114 across the globe. Humans both directly (i.e., dams, weirs, surface water and groundwater
1115 abstraction, channelization, draining, invasive species introduction and spread, etc.) and
1116 indirectly (i.e., climate change) alter VIEs. As climate change and other anthropogenic impacts
1117 increasingly alter these already dynamic systems, it is imperative that knowledge and models
1118 transcend VIEs. Future environmental change can alter the position of a given VIE within
1119 environmental space, including what is depicted in **Fig. 12** (e.g., by changing the inundation
1120 return interval). The ability to predict impacts of such environmental change can be facilitated by
1121 mechanistic knowledge that is transferable across the environmental space occupied by VIEs.



1122 We hypothesize that use of the continuum approach proposed here can be an effective
1123 approach to achieving this mechanistic, transferable knowledge.
1124



1125 **Figure 12.** We encourage a continuum perspective for VIE science whereby these
1126 systems are studied across broad ranges of key controlling variables without regard for
1127 what names may be attached to a given studied place and time. Two potential axes are
1128 topographic slope and inundation return interval. Points represent approximate locations of
1129 where each VIE type may lie. Each VIE type spans a range of slopes and inundation return
1130 intervals, but we do not define these ranges as the continuum perspective is based on how
1131 study systems fall across the environmental space represented here, rather than within specific
1132 nomenclature. Two priority research directions are greenhouse gas (GHG) fluxes and biological
1133 diversity, and the arrows represent possible hypotheses that could be evaluated with cross-VIE
1134 studies. We propose that knowledge and models that are transferable across VIEs can be
1135 achieved through evaluation of such hypotheses across broad environmental extents tied to key
1136 environmental variables, such as slope and return interval. Credit: Nathan Johnson.

1138
1139

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1149

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1151

1152 **References**

1153

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