

1 **Reviews and Syntheses: Variable Inundation**

2 **Across Earth's Terrestrial Ecosystems**

3 James Stegen^{1,2}, Amy J Burgin³, Michelle H. Busch³, Joshua B. Fisher⁴, Joshua Ladau⁵, Jenna
4 Abrahamson⁶, Lauren Kinsman-Costello⁷, Li Li⁸, Xingyuan Chen¹, Thibault Datry⁹, Nate
5 McDowell¹, Corianne Tatariw¹⁰, Anna Braswell¹¹, Jillian M. Deines¹, Julia A. Guimond¹², Peter
6 Regier¹, Kenton Rod¹, Edward K. P. Bam¹³, Etienne Fluet-Chouinard¹, Inke Forbrich¹⁴, Kristin L.
7 Jaeger¹⁵, Teri O'Meara¹⁶, Tim Scheibe¹, Erin Seybold³, Jon N. Sweetman⁸, Jianqiu Zheng¹,
8 Daniel C Allen⁸, Elizabeth Herndon¹⁶, Beth A. Middleton¹⁷, Scott Painter¹⁶, Kevin Roche¹⁸,
9 Julianne Scamardo¹⁹, Ross Vander Vorste²⁰, Kristin Boye²¹, Ellen Wohl²², Margaret Zimmer²³,
10 Kelly Hondula²⁴, Maggi Laan¹, Anna Marshall²², and Kaizad F. Patel¹

11 ¹*Pacific Northwest National Laboratory, Richland, WA, USA*

12 ²*School of the Environment, Washington State University, Pullman, WA, USA*

13 ³*University of Kansas, Lawrence, KS, USA*

14 ⁴*Chapman University, Orange, CA, USA*

15 ⁵*University of California San Francisco, San Francisco, CA, USA*

16 ⁶*North Carolina State University, Raleigh, NC, USA*

17 ⁷*Kent State University, Kent, OH, USA*

18 ⁸*Penn State University, State College, PA, USA*

19 ⁹*National Institute for Agriculture, Food, and Environment (INRAE), Villeurbanne, France*

20 ¹⁰*Rowan University, Glassboro, NJ, USA*

21 ¹¹*University of Florida, Gainesville, FL, USA*

22 ¹²*Woods Hole Oceanographic Institution, Woods Hole, MA, USA*

23 ¹³*International Water Research Institute (IWRI), Mohamed VI Polytechnic University, Benguerir, Morocco*

24 ¹⁴*University of Toledo, Woods Hole, MA, USA*

25 ¹⁵*U.S. Geological Survey, Washington Water Science Center, Tacoma, WA, USA*

26 ¹⁶*Oak Ridge National Laboratory, Oak Ridge, TN, USA*

27 ¹⁷*U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA, USA*

28 ¹⁸*Boise State University, Boise, ID, USA*

29 ¹⁹*University of Vermont, Burlington, VT, USA*

30 ²⁰*University of Wisconsin, La Crosse, WI, USA*

31 ²¹*SLAC National Acceleratory Laboratory, Menlo Park, CA, USA*

32 ²²*Colorado State University, Fort Collins, CO, USA*

33 ²³*U.S. Geological Survey Upper Midwest Water Science Center, Madison, WI, USA*

34 ²⁴*Arizona State University, Tempe, AZ, USA*

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40 Correspondence: James C. Stegen, E-mail: james.stegen@pnnl.gov; james.stegen@pnnl.gov;
41 Phone: (509) 371-6763

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43 **Abstract**

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

68 **Introduction**

69 The chemical and biological processes within terrestrial ecosystems hinge on the presence,
70 residence time, volume, and chemistry of water. ~~(Schimel et al. 1991, Lohse et al. 2009, Arias-~~
71 ~~Real et al. 2024).~~ A variety of factors influence water retention, infiltration, ~~flow,~~ and ~~flow surface~~
72 ~~expression within an ecosystem~~, such as land surface relief, topographic slope, subsurface
73 permeability, evapotranspiration, and human-based modifications of the landscape. ~~(Horton~~
74 ~~1940, Ribolzi et al. 2011, Appels et al. 2016, McGrane 2016, Orozco-López et al. 2018,~~
75 ~~McDowell et al. 2023).~~ Water supply is most commonly 'top down' in the form of precipitation
76 and overland flow or 'bottom up' due to rising water tables and transient saturation in the
77 subsurface ~~(Smith et al. 2017).~~ ~~(Freeze 1974, Smith et al. 2017, Stewart et al. 2019).~~ Inundation,
78 however, may also occur from lateral inputs, as is common in tidal systems, or from upslope
79 inputs, as in floodplains. Regardless of where water comes from, ~~inundation's expression at the~~
80 ~~land-atmosphere interface~~ occurs when the rate of water supply is greater than the rate of
81 export via infiltration, evapotranspiration, and runoff. ~~(Tromp-van Meerveld and McDonnell~~
82 ~~2006).~~
83 ~~Here we define inundation as occurring when there is a near continuous aqueous barrier~~
84 ~~that limits gas phase transport between the atmosphere and the subsurface. This~~

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conceptualization is inclusive of diverse conditions, spanning from extreme events such as hurricane-driven flooding to shallow short-lived overland flow across hillslopes. We define variably inundated ecosystems (VIEs) as those that experience dynamic shifts between the presence and absence of inundated conditions, at any spatial and temporal scale. Variably inundated ecosystems cover at least 5-9 million km², or 4-7% of the Earth's land surface excluding Greenland and Antarctica. These estimates are according to monthly data over multiple decades (Zhang et al. 2017, 2021, Davidson et al. 2018), and are likely significant underestimates as many VIEs are not resolvable by commonly used remote sensing techniques.

Here, we define inundation as occurring when there is an uninterrupted aqueous barrier that limits diffusive gas exchange at the land-atmosphere interface (Elberling et al. 2011, Smith et al. 2018). This conceptualization includes diverse hydrological conditions ranging from free standing water to soil surface saturation. Hence, our broad definition spans from extreme events such as hurricane-driven inundation to shallow intermittent overland runoff across hillslopes. This definition does not attempt to separate 'inundation' from 'flooding' based on temporal frequency/duration, as has been proposed elsewhere (Flick et al. 2012). To avoid confusion from interchangeable use of these two words (as in USACE 2024), we exclusively use 'inundation' and avoid references to 'flooding' in this paper. We define variably inundated ecosystems (VIEs) as areas of any spatial and temporal scale that experience transitions between the presence and absence of inundated conditions. Variable inundation is natural in many systems and can be critical to system function (Shaeri Karimi et al. 2022, Tsoi et al. 2022), while in other systems it represents a disturbance (Sun et al. 2022a, Hopple et al. 2023). Variably inundated ecosystems cover at least 5-9 million km², or 4-7% of the Earth's land surface excluding Greenland and Antarctica. These estimates are according to monthly data over multiple decades (Zhang et al. 2017, 2021, Davidson et al. 2018). Current areal estimates of VIEs may, however, be underestimates as many VIEs are not detectable with current remote sensing techniques.

Variable inundation occurs across a wide range of terrestrial ecosystems, but the factors governing its influences are typically studied independently without cross-ecosystem comparisons. Some examples of VIEs are hillslopes with overland flow, non-perennial streams, floodplains and parafluvial zones, variably inundated wetlands, vernal ponds/pools/playas, tidal systems, coastal systems impacted by storm-driven flooding/inundation, and human-engineered systems intended to shift inundation dynamics (e.g., flood-irrigated agriculture, stormwater infrastructure, and constructed wetlands) (Fig. 1). While VIEs may be classified as wetlands under the broadest definition from the Ramsar Convention (Secretariat 2016), there is significant variation in how wetlands are defined (Finlayson and Van Der Valk 1995¹). A given system may not fit clearly into a single VIE category and/or may transition across categories through time. For example, when flow ceases and isolated pools form in a non-perennial stream network, the stream begins to behave more like a wetland or vernal pond as opposed to a flowing stream (Day et al. 2019). Further, while VIEs may be classified as wetlands under the broadest definition from the Ramsar Convention (Secretariat 2016), there is significant variation in how wetlands are defined (Finlayson and Van Der Valk 1995), and we do not attempt to rectify or clarify variation in those definitions. Here, when using the term 'wetland' we simply align with the perspective that wetlands are similar to marshes, swamps, and bogs.

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129 Inundation dynamics are changing due to increased variability and magnitudes of
130 precipitation and evapotranspiration, accelerated sea level rise, and human modifications to the
131 Earth's land surface, including an increase in extreme events (Konapala et al. 2020, Li et al.
132 2022a). Extreme events such as coastal flooding are increasingly frequent, and while seasonal
133 drying of streams is now more common (Sweet et al. 2014, Zipper et al. 2021), some streams
134 are shifting from non-perennial to perennial (Döll and Schmied 2012, Datry et al. 2018a) while
135 others have fewer no-flow days than they did historically (Zipper et al. 2021). Wetland
136 inundation extent, duration, and seasonal timing are also projected to be altered by climate
137 change (Londe et al. 2022a). Thus, the dynamics of inundation are changing in different ways
138 across different VIEs (Zipper et al. 2021) such that we cannot rely exclusively on historical
139 dynamics to predict future impacts (e.g., on species diversity) of changing inundation dynamics
140 (Culley et al. 2016, Quinn et al. 2018, Rameshwaran et al. 2021, Li et al. 2022b)(Konapala et al.
141 2020, Li et al. 2022a). For example, extreme events such as coastal inundation are increasingly
142 frequent (Vitousek et al. 2017). However, inundation patterns are changing in different ways
143 across different VIEs (Zipper et al. 2021, Londe et al. 2022). For example, in river systems
144 seasonal drying is becoming more common in multiple biomes (Sweet et al. 2014, Zipper et al.
145 2021). While some rivers are shifting from non-perennial to perennial (Döll and Schmied 2012,
146 Datry et al. 2018a) and others have fewer no-flow days than they did historically (Zipper et al.
147 2021). Divergence in the direction of change, with some systems inundating less and others
148 inundating more, is likely linked to diverse drivers of change associated with changing climates
149 and/or direct human impacts (Datry et al. 2023). Therefore, researchers and decision makers
150 cannot rely exclusively on historical trends to predict future impacts (e.g., on species diversity)
151 of changing inundation dynamics (Culley et al. 2016, Quinn et al. 2018, Rameshwaran et al.
152 2021, Li et al. 2022b).

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NON-PERENNIAL STREAMS



VERNAL PONDS, POOLS, PLAYAS, POTHOLES



HILLSLOPES



TIDAL COASTAL



HUMAN-MODIFIED SYSTEMS



STORM-IMPACTED COASTAL ZONES



WETLANDS



FLOOD PLAINS

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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; (global image, e, f, g-h) Shutterstock; (h) Mikac et al 2018.

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168 Mechanistic knowledge that is transferable (per Schuwirth et al. 2019) across inundation
169 regimes (i.e., from extreme events to predictable cycling) and across VIEs is required to develop
170 hydrologic, biogeochemical, and ecological models that are predictive across contemporary and
171 future conditions. We envision the impacts of variable inundation as dependent on the location
172 of any given VIE ~~in~~ within multi-dimensional environmental space. This space can be defined
173 with a variety of environmental variables such as inundation return interval and duration,
174 topographic slope, geology, vegetation composition, precipitation, salinity, and temperature.
175 ~~Many~~ Similar to multi-dimensional niche space (Hutchinson 1978), ~~many~~ other variables could
176 be used, but regardless, environmental change will ~~cause~~ alter the position of VIEs ~~to move to~~
177 ~~different areas~~ within continuous, multi-dimensional environmental space. Predicting future
178 impacts of variable inundation requires mechanistic understanding of how the location of a VIE
179 in this multi-dimensional space influences those potential impacts. We propose that our best
180 chance to achieve such understanding is to generate knowledge of variable inundation impacts
181 that is transferable across VIEs.

182 Here we aim to catalyze cross-VIE science for the pursuit of transferable knowledge and
183 ultimately models that are predictive across and aid in conserving contemporary and future
184 VIEs. We briefly summarize high-level divergences in drivers of variable inundation,
185 commonalities in the impacts of variable inundation, and then present expert mini-reviews of
186 eight major VIE systems. Variable inundation occurs across vast ranges in spatial and temporal
187 scales, which presents challenges to cross-VIE science. As such, we overview these challenges
188 and offer suggested solutions along with a summary of methods that are most relevant to VIE
189 science. We conclude with perspectives on how cross-VIE science can use conceptual models
190 based on environmental continuums to derive transferable understanding ~~to better protect~~ useful
191 ~~for protecting~~ these systems and their biodiversity.

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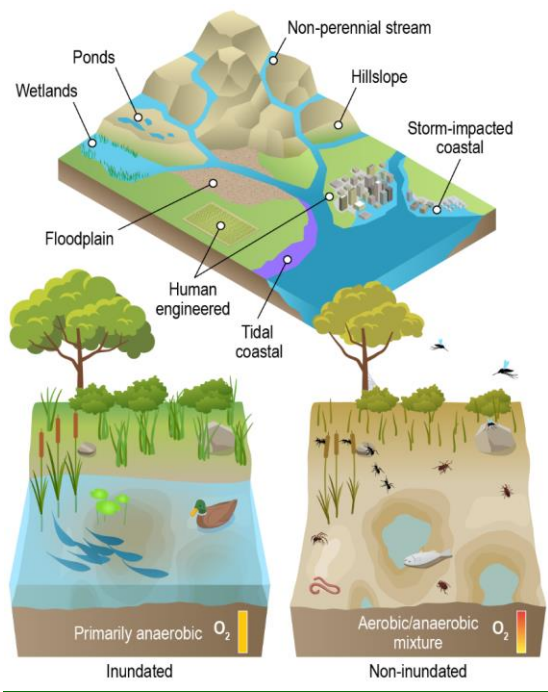
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Figure 2. Conceptual overview of where different types of VIEs are commonly often found within watersheds and some common shifts in system states across inundated and non-inundated conditions. VIEs are found from headwaters to coastal environments (Top) and the impacts of variable inundation have some consistencies across these diverse landscapes (Bottom). Organismal ecology, physiology, and demographics are altered by variable inundation, leading to shifts in community composition. Biogeochemical processes also shift, such as greater gas-phase transport of oxygen into soil/sediment when surface water is lost, with associated shifts in redox processes. The details of these responses to variable inundation are, however, likely to vary across VIEs due to variation in system properties such as dominant vegetation types, rhizosphere development, soil/sediment texture, water salinity, flow velocity, etc. A key goal for cross-VIE science is to mechanistically link understand variation in these system properties to the impacts of variable inundation across the multi-dimensional environmental space occupied by VIEs. Credit: Nathan Johnson.

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Divergent Drivers, Common Responses, and VIE Mini-Reviews

The drivers of variable inundation differ markedly across VIEs and are linked to factors such as long-term drought, heavy precipitation, evapotranspiration, changing groundwater storage, soil/sediment properties, extreme climatic events, and dam operations (Glaser et al. 2021, Shanafield et al. 2021, Arnold et al. 2023, Bourke et al. 2023, Swenson et al. 2024). This leads

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214 to significant variation across VIEs in inundation regimes, which includes inundation timing,
215 return interval, duration, spatial extent, depth, and flow rate- (Celi and Hamilton 2020, Dee and
216 Tank 2020, Van Appledorn et al. 2021). For example, sediments within the active channel of
217 tidal rivers can experience sub-daily losses and gains of surface water- (Tagestad et al. 2021),
218 while other coastal zones may experience extreme inundation events on a 100 year return
219 interval- (Slater et al. 2021, Clementson et al. 2021). Other systems, such as non-perennial
220 streams and vernal ponds, also experience a broad range of inundation regimes, ranging from
221 sporadic and extreme inundation following rain events to more regular seasonal cycles- (Allen et
222 al. 2020, Barczok et al. 2023). Variation in the spatial scale of inundation is also large, with
223 floodplains and storm-impacted coastal zones experiencing inundation over tens of kilometers,
224 whereas non-perennial streams and ponds can experience changes across a few meters-
225 (Hamilton et al. 2002, Vousdoukas et al. 2016, Allen et al. 2020). As discussed below within the
226 series of VIE mini-reviews, the temporal and spatial scales of inundation also vary substantially
227 within each type of VIE. Variation within a given type of VIE is large enough that we suggest it
228 cannot be used to clearly differentiate VIEs into named categories. As discussed in the "Toward
229 cross-VIE transferable understanding" section, this is one motivation for pursuing ~~a continuum~~
230 ~~approach to cross-VIE science~~ VIE conceptual models and investigations that span broad
231 continuums of environmental conditions.

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

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

256 Across VIEs, inundation impacts the structure, composition, and function of vegetation
257 communities. Growth and survival can either increase or decrease with inundation depending

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258 on local aridity and the impacts on soil hypoxia. Hypoxia kills roots, leading to reduced water
259 uptake, reduced photosynthesis, mortality (Pederson et al. 2021, McDowell et al. 2022, Cubley
260 et al. 2023), and shifts in vegetation composition. More broadly, inundation dynamics impact
261 organismal ecology (Datry et al. 2023) across all VIEs, such as herbivores responding to
262 inundation-induced shifts in vegetation (De Sassi et al. 2012). Inundation can also alter
263 arthropod communities leading to reductions in diversity, abundance, and biomass with flooding
264 (Plum 2005). Changes at the base of food webs can have further, cascading effects (Chen and
265 Wise 1999).

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298 2005). Changes at the base of food webs can have further, cascading effects (Chen and Wise
299 1999).

300 To pursue cross-VIE science requires knowledge of the diverse array of ecosystems that
301 can be considered VIEs. Researchers that design and carry out cross-VIE studies may be

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302 considered generalists in terms of the breadth of systems they study, even if their science
303 questions are highly specialized. To facilitate such researchers in the pursuit of cross-VIE
304 science, we go beyond the high-level summaries of divergences and commonalities (above)
305 and provide expert mini-reviews of eight primary VIE types. The following subsections present
306 these mini-reviews which summarize system characteristics, drivers, and impacts of variable
307 inundation with an emphasis on biogeochemistry and organismal ecology, and opportunities to
308 better understand spatiotemporal patterns and impacts of variable inundation. Each mini-review
309 is accompanied by a graphic that either provides a conceptual overview or imagery-based
310 examples, with the goal of collectively touching on key drivers, dynamics, impacts, and tangible
311 system examples. The collection is not meant to be a comprehensive classification of all
312 possible VIE types, but it does cover a broad range of VIEs and is meant to serve as an
313 overview of individual VIEs to provide context for later sections of this manuscript. The
314 sequence of mini-reviews roughly follows the flow of water moving from hillslopes to coastal
315 environments (**Fig. 2**) and includes variably inundated components of: (i) hillslopes, (ii) non-
316 perennial streams, (iii) riverine floodplains and parafluvial zones, (iv) wetlands, (v) temporary
317 ponds, (vi) storm-impacted coastal zones, and (vii) tidal systems. The final mini-review (viii) is
318 focused on ecosystems that have been engineered to modify inundation regimes, which occur
319 throughout the continuum from hillslopes to coasts.

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

330 This continuum perspective is more fully developed as a conceptual model in the final
331 section of the paper, titled “Towards Cross-VIE Transferable Understanding.” However, we
332 briefly summarize here that it is based on two continuous environmental axes: inundation return
333 interval and topographic slope. These variables can be used to define a two-dimensional
334 environmental space that contains all VIE systems. With this model, impacts of variable
335 inundation can be studied across environment space instead of within discrete named types of
336 VIEs. When going through the following mini-reviews, we encourage the reader to conceptualize
337 each VIE type in context of return interval and slope (e.g., hillslopes may have a long return
338 interval and steep slopes relative to tidal systems, while coastal systems inundated by storms
339 may have similar slopes as tidal systems but much longer return intervals). When VIEs are
340 viewed through a unified lens of environmental continuums, larger interdisciplinary questions
341 may be answered.

342 **Hillslopes with Surface Runoff**

343 Hillslopes provide water to lower-lying areas, often concentrating the water in gullies and
344 depressions (**Fig. 3**). Hillslopes produce relatively transient VIE features and may often be seen

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345 as extensions of other VIEs, such as hillslope seeps co-located with a wetland or the
346 unchannelized swales that contribute to a non-perennial network. In cold regions, snow, ice and
347 permafrost can create an impermeable layer resulting in near-surface soil being inundated for
348 days to weeks during spring thaw (Coles et al. 2017, Patel et al. 2020). (Coles et al. 2017, Patel
349 et al. 2020). In dry regions, intense precipitation that exceeds the local infiltration capacity can
350 result in water ponding on the surface of hillslopes or overland flow generation down hillslopes,
351 which can be exacerbated by initial hydrophobicity of dry soil (Kirkby et al. 2002). (Kirkby et al.
352 2002). Exceeding the infiltration capacity is more likely on hillslopes with low-permeability, such
353 as clay-rich soil or when near-surface soils are frozen. This can be exacerbated by restrictive
354 soil horizons located at shallow depths across hillslopes that generate seasonal perched water
355 tables and lead to inundation (McDaniel et al. 2008). (McDaniel et al. 2008). Overland flow can
356 be spatially heterogeneous due to variations in soil characteristics as well as flow accumulation,
357 leading to infiltration or exfiltration along the hillslope (Betson and Marius 1969). (Betson and
358 Marius 1969).

359 In forested hillslopes, soil infiltration often exceeds rainfall intensity (McDonnell 2009, Burt
360 and Swank 2010) and lateral flow towards topographic depressions can lead to saturation and
361 ponding (Anderson and Burt 1978) (Fig. 3a). Microtopography within hillslopes (Fig. 3b) can
362 also lead to temporary ponding, e.g., from rain in tropical environments and from spring
363 snowmelt in colder environments (Clark et al. 2014). Toe slopes can generate wedges of
364 saturation that grow upslope (Weyman 1973, Choularton and Perry 1986), although subsurface
365 saturation and ponding can also occur on upper slopes where the soil is thinner [e.g., (Tromp-
366 van Meerveld and McDonnell 2006)]. Finally, spatial variation in topographic characteristics
367 (e.g., aspect, slope, curvature) can result in differences in soil moisture, incoming energy, and
368 vegetation, affecting evapotranspiration and inundation patterns (McVicar et al.
369 2007). (McDonnell 2009, Burt and Swank 2010) and lateral flow towards topographic depressions
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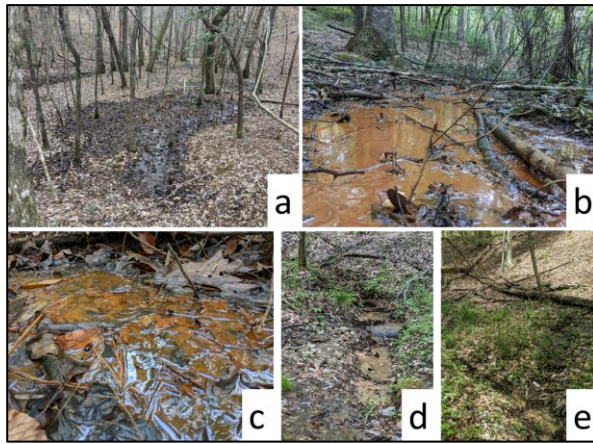


Figure 3. Examples of variable inundation along hillslopes. a) looking downslope at an inundated slope; b) ponding with no flow due to microtopography; c) sheet wash with directional flow across the surface of a hillslope; d) rill formation with turbid water from erosion; e) vegetation community change on slope due to differences in soil moisture. All photos taken by Corianne Tatariw at Tanglewood Forest, Alabama.

Surface runoff and inundation on hillslopes can result in the export of soil nutrients, salinization of soil from groundwater seeps, erosion, and landslides. There is a balance between the effects of variable inundation on hillslope vegetation and erosion. In water-limited systems, inundation can increase plant productivity and diversity, as well as increased rooting strength of soils (Zhao et al. 2022)(Zhao et al. 2022) (Fig. 3e). However, increased inundation can also lead to increased chemical weathering and lower shear strength in hillslope soils during storms, leading to higher erosion and landslide potential. Along with erosion, landslides and soil compaction are inherent to many hillslopes, which also can create areas ripe for inundation (Bogaard and Greco 2016),(Bogaard and Greco 2016). At shoulder and midslope positions, increased overland flow due to saturation- or infiltration-excess increases sediment detachment, which is then deposited in foot and toe slopes (Huang et al. 2002)(Huang et al. 2002). The transport of particles also leads to the transport of nutrients that are sorbed to the particles, such as phosphorus. Erosion can be concentrated in rills and gullies or can spread out across a slope as 'sheet wash' that impacts large areas of hillslopes (Fig. 3c,d). Impacts of erosion are dependent on interactions between the persistence of inundation and soil properties (Thomas et al. 2020)(Thomas et al. 2020).

The aqueous chemistry of water that is transported over hillslope surfaces reflects the chemistries of contributing water sources such as precipitation, shallow soil water, and exfiltrating groundwater. ~~Shallow soils in hillslopes have abundant organic materials and nutrients (Horndon et al. 2015), whereas organic matter decreases with depth, solutes derived from the parent rock material increase with depth (Brantley et al. 2017). These stratifications collectively regulate source water chemistry in hillslopes. Dry to wet transitions shift flow paths from groundwater to soil water dominance in streams, therefore shaping stream chemistry (Zhi~~

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411 and Li 2020, Stewart et al. 2022). Dry to wet transitions also shift water content and pore space
412 oxygen concentrations (Jarecke et al. 2016, Smyth et al. 2019), often triggering the release of a
413 cascade of solutes produced under anaerobic conditions (Schlesinger and Bernhardt 2020).
414 These entangled, complex interactions among hydrological and biogeochemical processes
415 often challenge the differentiation of individual processes and mechanistic understanding on
416 how variable inundation regulates flow paths, reactions, stream chemistry, and solute and gas
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427 how variable inundation regulates flow paths, reactions, stream chemistry, and solute and gas
428 export fluxes (Li et al. 2021).

429 Investigations of variably inundated hillslopes present significant and challenging research
430 opportunities due to their inherently dynamic nature. One key challenge is quantifying the
431 occurrence and spatial extent of hillslope VIEs across the globe. Remote sensing could be used
432 to identify and quantify these areas, spatially and temporally, based on sky-visible vegetation
433 (e.g., plant morphologies, leaf nutrient contents) (Hwang et al. 2012, Tai et al. 2020) and
434 topographic signatures (e.g., erosional patterns) (Trochim et al. 2016) caused by variable
435 inundation. To fully understand the ecological and biogeochemical impacts of variable
436 inundation on hillslopes, research needs to focus on shallow subsurface physical properties,
437 hydrology, and their linkage to biogeochemical processes. This can be pursued via
438 environmental geophysics to map and characterize the influence of subsurface restrictive layers
439 (Fan et al. 2019 p. 201) (Fan et al. 2019 p. 201). Understanding the subsurface soil architecture
440 is key to predicting variable inundation from bottom-up and top-down water sources, along with
441 the follow-on impacts to ecology and biogeochemistry.

442 Non-Perennial Streams

443 Non-perennial streams, defined as rivers and streams that cease to flow at some point in either
444 space or time (Busch et al. 2020), are ubiquitous and comprise 50-60% of the global river length
445 (Messenger et al. 2021). These systems occur across all continents and biomes (Messenger et al.
446 2021). Streamflow in non-perennial streams ranges from nearly perennial (year-round) flow, to
447 seasonal flow, responding to drivers like snowmelt, to daily or sub-daily flow events responding
448 to rainfall/flood events or evapotranspiration (Price et al. 2021). At the reach scale, non-
449 perennial streams shift between three main states – flowing, ponded/pooled, or no surface water
450 present (Fig. 4). As reaches become hydrologically connected (or disconnected), the spatial
451 footprint/extent of the connected stream network can grow or shrink over sub-daily to seasonal
452 to interannual timescales (Xiao et al. 2019). Spatial and temporal shifts among the three
453 hydrologic states strongly influence the network's capacity to process, transport, and export

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454 material to downstream systems (Allen et al. 2020)(Busch et al. 2020), are ubiquitous and
455 comprise 50-60% of the global river length (Messenger et al. 2021). These systems occur across
456 all continents and biomes (Messenger et al. 2021). Streamflow in non-perennial streams ranges
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463 and temporal shifts among the three hydrologic states strongly influence the network's capacity
464 to process, transport, and export material to downstream systems (Allen et al. 2020).

465 The high variability in the spatial and temporal scales of streamflow intermittency is
466 indicative of the complex set of interacting drivers that induce stream drying. At the global and
467 regional scales, the degree of aridity is a primary control on the abundance of non-perennial
468 streams (Hammond et al. 2021, Zipper et al. 2021). At smaller scales, catchment properties
469 exert strong control over both the capacity of water delivery to the channel and the subsequent
470 balance between the channel and near subsurface capacity to transport water (Hammond et al.
471 2021, Zipper et al. 2021, Price et al. 2021). Non-perennial flow can occur anywhere in the stream
472 network, from headwaters to higher-order rivers. While some networks display longitudinal
473 transitions from non-perennial to perennial flow (or vice-versa), other networks exhibit more
474 complex patterns in surface water flow and connectivity, which may be driven by topography,
475 geology, vegetation, or groundwater abstraction/use (Costigan et al. 2015, 2016).

476 The variable inundation dynamics in non-perennial streams have cascading implications for
477 biogeochemical cycling, water quality, ecosystem function, and community ecology. Under non-
478 flowing conditions, riverbeds are characterized by dry conditions or discontinuous and stagnant
479 water pools, often with high temperatures, low dissolved oxygen levels, and long residence
480 times, functioning more like soils (Arce et al. 2019), as described also in the hillslope section.
481 Pooled, non-flowing conditions can lead to steep redox gradients in the shallow subsurface that
482 drive nutrient processing (Datry and Larned 2008, Gómez-Gener et al. 2021, DelVecchia et al.
483 2022). During dry/non-flowing states, terrestrial organic matter accumulates in the channel and
484 is subjected to varying degrees of breakdown (Datry et al. 2018c, Del Campo et al. 2021).
485 Rewetting of accumulated substrates can stimulate microbial activity, nutrient attenuation
486 (Saltarelli et al. 2022), and generate pulses of greenhouse gasses such as CO₂ and N₂O (Datry
487 et al. 2018a, Song et al. 2018). During re-wetting and resumption of flow, non-perennial streams
488 can contain large amounts of terrestrial and aquatic organisms that can be flushed downstream
489 (Corti and Datry 2012, Rosado et al. 2015), with high sediment, dissolved organic carbon, and
490 solutes (Laronne and Reid 1993, Hladyz et al. 2011, Herndon et al. 2018, Wen et al. 2020,
491 Fortesa et al. 2021, Blaurock et al. 2021).

492 Biological responses to rewetting depend on the distribution of habitats and biota at the
493 watershed scale and the duration of the preceding dry phase. In highly dynamic river systems,
494 such as braided rivers, drying and wetting cycles can be spatially patchy and short-lived but
495 frequent, and thus ecological recovery following wetting can be very rapid due to the very active
496 hyperheic zones characterizing these systems (Arscott et al. 2002, Vorste et al. 2016). In other
497 systems recovery can be slow, depending on the proximity of refuges, such as springs, isolated

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498 pools, and perennial reaches (Sarremejane et al. 2021, Fournier et al. 2023). Systems with
499 frequent and severe drying events are more likely to be colonized by aerial or other overland
500 dispersers than by aquatic dispersers (Bonada et al. 2007, Bogan et al. 2017a, Sarremejane et
501 al. 2021). Life-history events of some species coincide with predictable rewetting events, such
502 as post-snowmelt fish spawning (Hoohey Underwood et al. 2019) and amphibian and insect life
503 histories (Bogan et al. 2017a). Rewetting also partly determines the germination success and
504 establishment of riparian vegetation (Merritt and Wohl 2002).

505 Compared to their perennial counterparts, non-perennial streams have received less
506 research and monitoring attention and tend to be undervalued relative to ecological/functional
507 performance of perennial streams (Palmer and Hondula 2014). As such, many of the pressing
508 research needs in non-perennial streams are limited by data availability (Van Meerveld et al.
509 2020, Zimmer et al. 2022). Non-perennial streams are systematically under-represented in
510 global gaging networks (Messenger et al. 2021, Krabbenhoft et al. 2022), leading to major gaps
511 in our understanding of the timing, magnitude, and duration of flow in diverse non-perennial
512 streams. In addition, our ability to predict the onset or cessation of flowing periods is limited by a
513 lack of gaging. Infrequent grab sampling for water chemistry tends to undersample non-
514 perennial streams specifically, leading to an even greater paucity of biogeochemical data from
515 these systems, particularly during rapid re-wetting events. Spatially explicit data on streamflow
516 intermittency and subsurface conditions at fine spatial scales (10s of meters) remain limited to a
517 few intensively studied catchments [e.g., (Zimmer and McClynn 2017)]. While some global scale
518 datasets on streamflow intermittency have been developed (Messenger et al. 2021), the
519 resolution of these products necessarily omit smaller, headwater reaches, hindering our ability
520 to quantify hydrologic and biogeochemical processes in non-perennial streams broadly
521 (Benstead and Leigh 2012).

522 Major challenges and opportunities include accurate mapping of non-perennial streams and
523 accurate predictions of flow timing at annual, seasonal, and shorter time scales across scales.
524 With limited time series data, predictions of flow in terms of duration, frequency, and spatial
525 extent can be challenging. How the timing and frequency of flow will change under climate
526 change remains an open question. It is expected that an increased frequency and duration of
527 droughts will shift streams toward more non-perennial flow states (Döll and Schmied 2012). In
528 contrast, flow permanence may increase in select areas where streams are fed by melting
529 glaciers or snowpack, or where anthropogenic intervention occurs (Datry et al. 2023). The
530 changing frequency of extreme flow events and rapid no-flow/high-flow oscillations also have
531 the potential to further alter streamflow, biogeochemical processes, and organismal ecology in
532 non-perennial streams, necessitating further integrated hydro-biogeochemical studies in these
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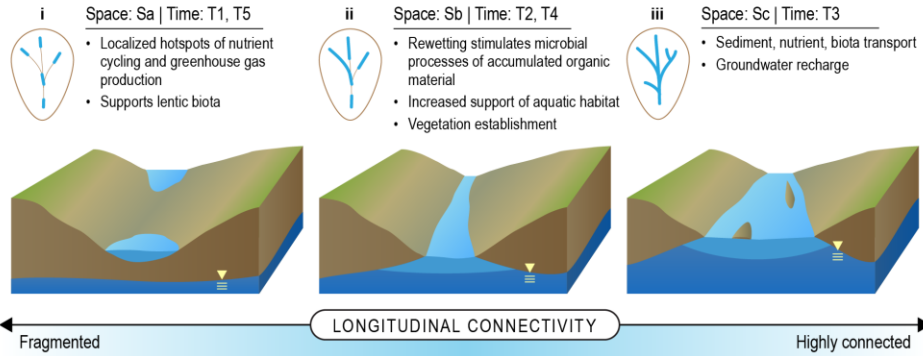
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592 (Benstead and Leigh 2012).

593 Major challenges and opportunities include accurate mapping of non-perennial streams and
594 accurate predictions of flow timing at annual, seasonal, and shorter time scales across scales.
595 Headwaters, which are small, numerous, and often non-perennial (Kampf et al. 2021), are
596 difficult to map and understand hydrologically, leading to knowledge gaps in the hydrological
597 integrity of ecosystems at regional scales (Benstead and Leigh 2012, Dugdale et al. 2022).
598 While challenges remain, the use of drones and thermal infrared remote sensing could connect
599 field observations with modeling to better understand the hydrology of these valuable systems
600 (Dugdale et al. 2022). In addition to mapping issues, limited time series data makes predictions
601 of flow in terms of duration, frequency, and spatial extent challenging. How the timing and
602 frequency of flow will change under climate change remains an open question. It is expected
603 that an increased frequency and duration of droughts will shift streams toward more non-
604 perennial flow states (Döll and Schmied 2012). In contrast, flow permanence may increase in
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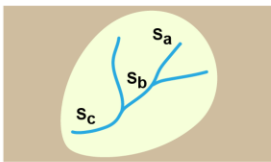
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a) Inundation mechanisms in non-perennial streams



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



c) Temporal variation in inundation dynamics at the watershed outlet

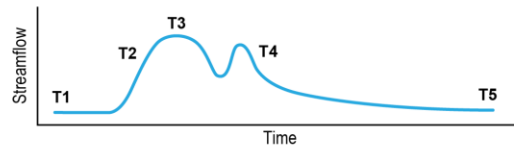


Figure 4. Conceptual model of variable inundation in non-perennial streams. a) Water connections between groundwater, near surface, and surface regions at locations within a given network result in varying degrees of longitudinal connectivity with associated biogeochemical processes. b) At a single snapshot 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 Sa - Sc and temporal variation is signified by T1 - T5. Credit: Nathan Johnson.

Floodplains and Parafluvial Zones

Rivers, both perennial and non-perennial, create two types of VIEs, floodplains and parafluvial zones (Fig. 5). Floodplains are alluvial landforms generated by river erosion and deposition and hydrologically connected to the contemporary active channel but outside the active river channel (Nanson and Croke 1992). Parafluvial zones are areas in the active channel without surface water at low flow, i.e., at higher elevation areas within an active channel that contains perennial flow (Goldman et al. 2017) at higher-elevation areas within an active channel that contains perennial flow (Goldman et al. 2017). Nearly all rivers have parafluvial zones and adjacent floodplains, although these may be longitudinally discontinuous (e.g., absent where the river flows through a narrow bedrock gorge or descends into the subsurface).

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632 Consequently, the global distribution of these environments is extensive, as few terrestrial
633 surfaces do not include a river network.

634 Spatial scales of inundation in floodplains and parafluvial zones are variable between rivers
635 and through time along a river. Fundamentally, spatial scales are governed by the interaction
636 between the magnitude of flow and available space as defined by topography- (Nardi et al.,
637 2006), Floodplains of the world's largest rivers such as the Amazon, Congo, or Mississippi can
638 extend laterally for kilometers on both sides of the active channel- (Arnesen et al. 2013), In
639 contrast, the floodplain of a headwater channel, in high-relief terrain, may be only 1-2 m wide on
640 each side of the channel- (Adams and Spotila 2005),

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

650 The nature of floodplain/parafluvial inundation affects the dynamics of surface and
651 subsurface water, solutes, particulate organic matter, sediment, and biota (Junk et al.
652 1989)(Junk et al. 1989), Dynamics include volume and duration of storage; rate of movement;
653 direction of movement between surface, hyporheic, and groundwater; and biogeochemical
654 alterations that in turn impact river water quality, greenhouse gas emissions, plant function, and
655 organismal ecology. The duration, frequency, and areal extent of floodplain/parafluvial
656 inundation control ecosystem function, and the types and abundances of organismal
657 communities, including both aquatic and terrestrial species (Ward et al. 1999)-(Ward et al.
658 1999), Species distribution, movement, and biological interactions, such as predator-prey, are
659 intricately tied to these inundation patterns (Robinson et al. 2002, Stanford et al.
660 2005)-(Robinson et al. 2002, Stanford et al. 2005), Fish species, for example, can migrate from
661 dry season refugia into floodplains during inundation, influencing food web structure and
662 ecosystem productivity (Crook et al. 2020)(Crook et al. 2020),

663 Among the primary challenges to answering questions regarding the variation in
664 floodplain/parafluvial inundation are limited monitoring data and a lack of numerical models that
665 integrate knowledge across disciplines and processes. Measurements and models of hydrology
666 commonly treat floodplains as flat, impermeable surfaces, which ignores surface-subsurface
667 water exchanges that influence hydrology and ecosystem function (Wohl 2021)-(Wohl 2021),
668 Models also often ignore the micro-heterogeneities that influence spatially and temporally
669 variable patterns of inundation, biogeochemical cycling, and ecology in both floodplains and
670 parafluvial zones. The degree of physical detail represented in models often involves tradeoffs
671 in spatiotemporal extent; a one-dimensional model might ignore microtopography that
672 influences important inundation details, whereas a more representative two-dimensional or
673 three-dimensional model becomes computationally intensive for larger spatial extents. This
674 problem gives rise to the challenges and opportunities for (i) designing measurement
675 campaigns across disciplines that can create integrative data for diverse floodplains and

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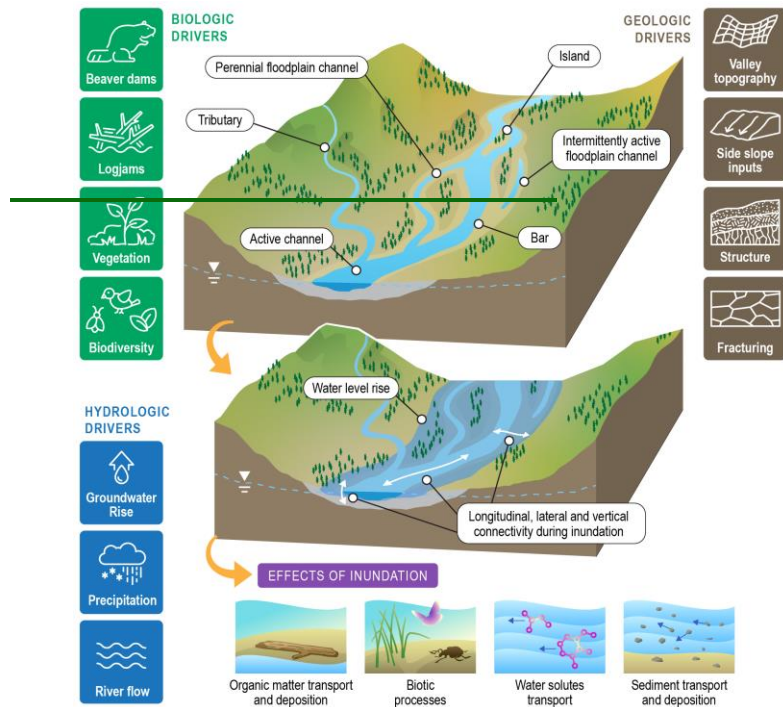
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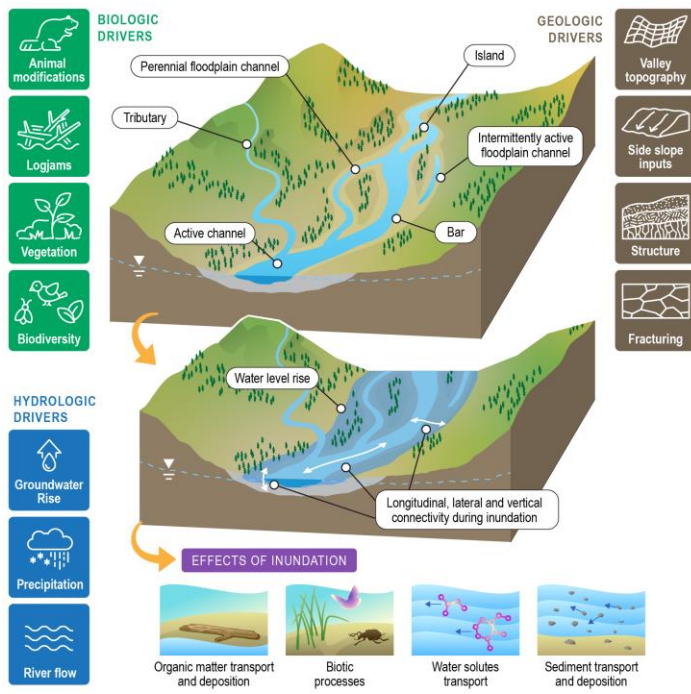
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676 parafluvial zones to adequately represent the physical complexity of variable inundation
 677 processes at broad scales, and (ii) developing floodplain/parafluvial functional groups [e.g.,
 678 (Fryirs and Brierley 2022)(Fryirs and Brierley 2022)] that can facilitate understanding of scaling
 679 and transferability of data.



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684
685 **Figure 5. Conceptual model of variable inundation in floodplain and parafluvial systems.**
686 Across floodplains and parafluvial zones a suite of biological, hydrologic, and geologic factors
687 drive inundation regimes in terms of spatiotemporal duration, timing, depth, flow rate, etc. These
688 systems include diverse subsystems as summarized in the top panel. Rising water levels, due
689 to one or more drivers, can inundate these subsystems as shown in the middle panel, resulting
690 in a variety of biogeochemical, ecological, and physical effects (bottom sub-panels). Credit:
691 Nathan Johnson.

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692 **Variably Inundated Wetlands**

693 While not all wetlands are variably inundated, variable inundation is a common feature of many
694 wetland ecosystems [e.g. ("Convention on wetlands of international importance especially as
695 waterfowl habitat" 1994), US 33 CFR § 328.3]. Here we focus primarily on wetlands that are
696 similar to swamps, marshes, and bogs (Fig. 6). Wetlands cover about 10% of the global land
697 area, and nearly half of global wetland area (46%) is temporarily inundated (Davidson et al.
698 2018). Generally, wetland inundation regimes are shaped by the wetland's connectivity to
699 surface and subsurface hydrologic sources and landscape position (Åhlén et al. 2022). The
700 landscape position of wetlands is a first order indicator of the water source and chemistry,
701 ranging from headwater depressional locally fed wetlands, to flow through and fringing wetlands
702 to groundwater fed low lying wetlands (Fan and Miguez Macho 2011, Tiner 2013). Wetland
703 typologies applied in several national inventories generally rely on a combination of three

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704 ~~criteria: soil type, hydrophytic vegetation and hydrology (Cowardin and Golet 1995).~~
705 ~~Alternatively, hydrogeomorphic classification systems propose to exclusively draw on physical~~
706 ~~drivers, such as geomorphology, hydrology and substrate to allow for cross-site comparisons of~~
707 ~~biota and serve functional assessments (Brinson 1993, Semeniuk and Semeniuk 1995, 2011,~~
708 ~~Davis et al. 2013)(Arias-Real et al. 2024). Here we focus primarily on wetlands that are similar~~
709 ~~to swamps, marshes, and bogs (Fig. 6). Wetlands cover about 10% of the global land area, and~~
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720 ~~biota and serve functional assessments (Brinson 1993, Semeniuk and Semeniuk 1995, 2011,~~
721 ~~Davis et al. 2013).~~

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

731 The spatial scales of variable inundation are shaped both by wetland size and
732 geomorphology. Wetlands can be shallow over large spatial scales, and thus the size of variably
733 inundated wetland area can range from microtopographic (i.e., hummock/hollow, ~m² scales) to
734 larger ecosystem scales. Large wetland areas, especially in the tropics, experience strong
735 seasonal inundation cycles which depend on changes in water balance and local topography
736 (~~Zhang et al. 2021). While the largest variably inundated wetlands are connected to floodplains,~~
737 ~~like the 130,000 km² Pantanal (Ivory et al. 2019), non-floodplain wetlands surrounded by upland~~
738 ~~(also known as geographically isolated wetlands) as large as ~6 ha may also experience whole-~~
739 ~~system drying and rewetting (Lane and D'Amico 2016)(Zhang et al. 2021). While the largest~~
740 ~~variably inundated wetlands are connected to floodplains, like the 130,000 km² Pantanal located~~
741 ~~in Brazil and extending into Bolivia and Paraguay (Ivory et al. 2019), non-floodplain wetlands~~
742 ~~surrounded by upland (also known as geographically isolated wetlands) as large as ~6 ha may~~
743 ~~also experience whole-system drying and rewetting (Lane and D'Amico 2016).~~

744 Embedded within wetland ecosystems, microtopographic structures can create within-
745 system mosaics of inundation regimes. Microtopography in peaty wetlands is particularly
746 pronounced, ranging from several tens of meters [e.g., ridges and sloughs (Larsen et al. 2014)]
747 to meters [e.g. hummock hollows (Shi et al. 2015)], These spatial patterns result from dynamic

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748 ~~feedbacks between ecological processes (e.g. peat accumulation) and hydrology that reinforce~~
749 ~~these patterns (Belyea and Baird 2006, Eppinga et al. 2008, Larsen et al. 2014).~~

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

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781 ~~respond to shifts in oxygen levels physiologically on shorter time scales (Colmer 2003).~~

782 ~~Variable inundation provides an environmental filter for biota adapted to live either under dry~~
783 ~~or inundated conditions, resulting in distinct communities including wetland obligate and~~
784 ~~facultative species (Gleason and Rooney 2018). (Gleason and Rooney 2018). The temporal~~
785 ~~duration of inundation (i.e., hydroperiod) indirectly controls the bird community composition~~
786 ~~through absence and presence of wetland vegetation and availability of aquatic~~
787 ~~macroinvertebrate prey (Daniel and Rooney 2021). (Daniel and Rooney 2021). Amphibian~~
788 ~~communities are particularly impacted by hydroperiod: It needs to be long enough for eggs to~~
789 ~~hatch and tadpoles to reach metamorphosis, but should not allow the establishment of many~~
790 ~~predator species (Resetarits 1996). (Resetarits 1996).~~

791 ~~Predicting how complex inundation patterns in wetlands will change under changing climate~~
792 ~~is a major research challenge. Predictions span the range from a decrease in inundation in~~
793 ~~some regions (Londe et al. 2022b) to an increase in others (Watts et al. 2014), with uncertain~~
794 ~~consequences for wetland persistence overall. To improve regional or global predictions,~~

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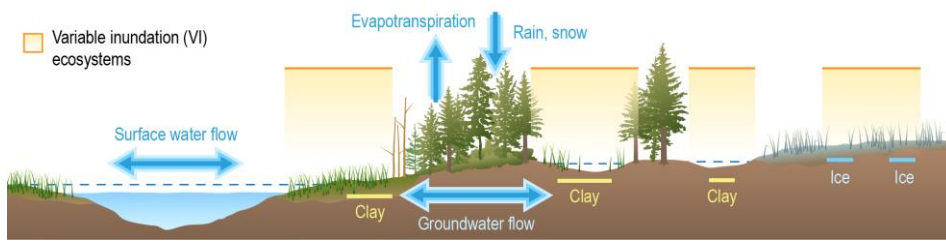
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795 accurate maps of wetland extent on different scales that can be incorporated into mechanistic
 796 models will be necessary (Melton et al. 2013). This is particularly challenging for non-permanent
 797 wetlands, which are hard to reliably map and are generally understudied (Gallant 2015, Calhoun
 798 et al. 2017), but which are, by definition, VIEs. As climate change alters wetland inundation
 799 regimes, the net impacts to carbon storage and greenhouse gas fluxes are of particular concern
 800 (Moomaw et al. 2018), because together they will determine the net climatic impact of changes
 801 in wetland area and dynamics (Neubauer and Megonigal 2015). Predictions span the range from
 802 a decrease in inundation in some regions (Londe et al. 2022) to an increase in others (Watts et
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814 **Figure 6. Conceptual model of variable inundation in wetland systems.** Different wetland
 815 types are influenced and shaped by variable inundation. Absence and presence of surface
 816 water is driven by (e.g., seasonally) changing water supply and the hydrologic function of
 817 the wetland in the landscape. Sediment characteristics (e.g., clay or ice) and topographic positions
 818 of wetlands in the landscape influence water loss to infiltration or gain from groundwater. Credit:
 819 Nathan Johnson.

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820 **Freshwater Ponds**

821 Freshwater ponds are among the most abundant and common freshwater ecosystems
 822 worldwide, with estimates between 500 million and 3.2 billion ponds globally (Davidson et al.
 823 2018, Hill et al. 2021). Ponds are generally small (less than 5 ha) and shallow (less than 5 m),
 824 and consequently, are highly sensitive to changes in water levels that can result in highly
 825 variable inundation regimes (Gondreau et al. 2021, Richardson et al. 2022a). Pond ecosystems
 826 are extremely diverse, and include arctic thermokarst ponds, prairie potholes, vernal pools,
 827 playas, rock pools and agricultural dugouts. The numbers of ponds globally are likely
 828 underestimated, as their size and ephemeral/temporary nature has meant they are often
 829 excluded from physical inventories and they are below the resolution of many remote sensing

830 techniques (Hayashi et al. 2016, Calhoun et al. 2017, Hill et al. 2021)(Davidson et al. 2018, Hill
831 et al. 2021). Ponds are generally small (less than 5 ha) and shallow (less than 5 m), and
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836 as their size and ephemeral/temporary nature has meant they are often excluded from physical
837 inventories and they are below the resolution of many remote sensing techniques (Hayashi et
838 al. 2016, Calhoun et al. 2017, Hill et al. 2021).

839 As in many other VIEs, inundation of freshwater ponds can be highly variable, and the
840 timing, duration and frequency of inundation can vary considerably (Williams 2006). Many
841 temporary or ephemeral ponds can become intermittently or seasonally flooded (Fig. 7). For
842 some ponds, particularly vernal pools, seasonal inundation is relatively predictable, as these
843 systems become inundated following snowmelt or spring runoff, and are subsequently drawn
844 down with increasing summer evapotranspiration (Zedler 2003, Brooks 2004). Variation in the
845 hydroperiod can alter the composition of biotic communities (Brooks 2004, Gleason and Rooney
846 2018), as well as impact biogeochemical and hydrological processes (Bam et al. 2020, Hondula
847 et al. 2021b). In more temperate regions, the timing of inundation is often driven by heavy
848 rainfall, and periods of inundation can be highly variable, with inundation durations lasting from
849 days to months, and sometimes occurring intermittently as ephemeral systems dry and rewet
850 multiple times in a year (Ripley and Simovich 2009, Knoitel 2014, Florencio et al. 2020). For
851 nearly permanent ponds, the pattern of wet and dry periods are more predictable, but the
852 initiation and length of the hydroperiod can vary spatially as water levels fluctuate, inundating
853 and exposing shallower areas (Brendonck et al. 2017). Freshwater ponds often demonstrate
854 both high inter- and intra-annual variability, and diurnal, annual and multidecadal periods of
855 inundation can occur due to changes in evapotranspiration, drought, drainage, flooding, and/or
856 hydrologic function of the pond on the landscape (Brooks 2004, Gendreau et al. 2021).
857 Modifications to ponds by humans (e.g. irrigation ponds, urban stormwater ponds; see section
858 on human engineered systems) or other organisms, such as beavers, can also impact
859 hydroperiod and inundation regimes (Renwick et al. 2006, Brazier et al. 2021).

860 Like many of the other ecosystems that experience variable inundation, freshwater ponds
861 are also considered biodiversity and biogeochemical hotspots, providing many critical
862 ecosystem services (Capps et al. 2014, Marton et al. 2015). Despite their relatively small size,
863 ponds can have considerable variability in both community composition and in biogeochemical
864 processes, in part due to differences in inundation regimes, where pond margins are more likely
865 to be more frequently desiccated for longer periods than central regions (Reverey et al. 2018).
866 Models that explicitly incorporate remotely sensed variable inundation predict that ephemeral
867 systems with shorter hydroperiods retain nitrogen at greater rates than larger systems with less
868 variable inundation and longer hydroperiods, particularly in semi-arid regions like the Prairie
869 Potholes of the North American northern Great Plains and playas in the south-central United
870 States (Cheng et al. 2023). In addition, research suggests reproduction is largely impacted by
871 inundation. Salamanders, for example, tend to lay more eggs during years with greater rainfall
872 while hatching success decreases with desiccation (Della Rocca et al. 2005). Variable
873 inundation across ponds can result in ecosystem heterogeneity at the landscape scale,

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874 increasing local abiotic and biotic variation (Jeffries 2008), but the number and distribution of
875 inundated ponds can also impact regional biodiversity through processes like dispersal
876 (Brendonck et al. 2017).

877 Climate change will likely alter the inundation regimes in freshwater ponds in terms of timing,
878 frequency, duration, and extent. Decreases in precipitation and increases in extreme drought
879 can result in shortened hydroperiods, and increasing temperatures can alter water temperatures
880 and evaporation rates (Matthews 2010). The persistence of freshwater ponds may, therefore, be
881 reduced with climate change (Londe et al. 2022b). Understanding how future changes in
882 inundation regimes impact freshwater ponds will be critical. Similar to wetland ecosystems,
883 improved remote sensing methods, including incorporating multispectral imagery and radar
884 along with finer spatial resolution mapping approaches may improve the mapping, counting and
885 inclusion of small ponds in freshwater inventories (Bio et al. 2020, Rosentreter et al. 2021,
886 Hofmeister et al. 2022). As inundation regimes may become more variable, increasing
887 conservation and protection efforts for ephemeral and temporary ponds may become more
888 essential to maintain these critical VIEs.

890
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893 temporary or ephemeral ponds can become intermittently or seasonally inundated (Fig. 7). For
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915 ponds can have considerable variability in both community composition and in biogeochemical
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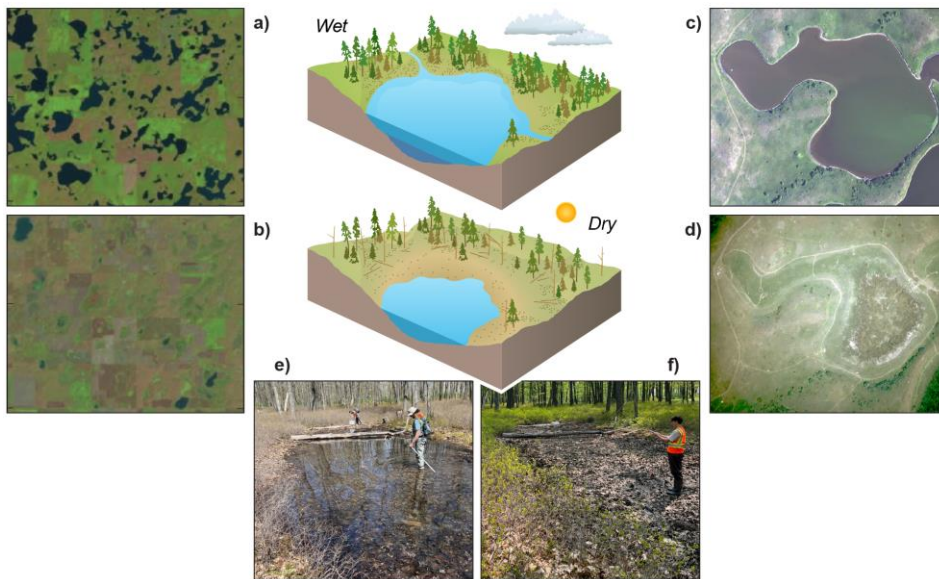
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918 Models that explicitly incorporate remotely sensed variable inundation predict that ephemeral
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943
944 **Figure 7. Examples of variable inundation across scales in pond systems.** Satellite
945 imagery of the Prairie Pothole Region, North Dakota, USA illustrating decadal variable
946 inundation at a landscape scale a) September 2, 1992; b) May 23, 2013 [modified from
947 ~~(Scientific Investigations Report 2015)~~(Scientific Investigations Report 2015)] and at the pond
948 scale; Aerial Imagery of Pond P1, Cottonwood Lake Study Area, North Dakota c) September,
949 2002 d) September, 1992 (Images from ~~(U.S. Geological Survey 2017)~~(U.S. Geological Survey
950 2017), Seasonal changes in a vernal pond in Moshannon State Forest, Pennsylvania, USA)
951 inundated (May 11, 2023) non-inundated (May 23, 2023) (J.N. Sweetman). Conceptual
952 drawings by Nathan Johnson.

953 Storm-Impacted Coastal Zones

954 The coastal zone includes ecosystems and communities (cities/towns) that are adjacent and
955 hydrologically connected to a large water body (e.g., ocean, Great Lakes). These systems
956 influence, are impacted by, and are dependent on coastal zone hydrologic processes, such as
957 ~~flooding, that occur at the interface between terrestrial and aquatic domains. Unlike tidal~~
958 ~~environments, inundation that affects the coastal zone is driven by temporary, often stochastic~~
959 ~~events including storms, seiches, and king tides. Depending on the topography of the area,~~
960 ~~infrastructure of the community, and size of the event, the size of coastal inundation varies from~~
961 ~~event to event (both geographic impact and aerial extent of inundation; Fig. 8). The frequency of~~
962 ~~these events ranges from multiple times a season to decadal (Fig. 8). Tropical storms and~~
963 ~~cyclones develop in tropical regions during seasonal periods of warm water each year. Due to~~
964 ~~their high energy and movement, they influence more temperate regions as well (Colbert and~~
965 ~~Soden 2012). In temperate or cold regions, storms develop in the winter time due to large~~
966 ~~temperature differences between land and ocean (Liberato et al. 2013). Natural systems will~~
967 ~~display some form of resilience and recovery to storm impacts (Lugo 2008, Wang et al. 2016),~~
968 ~~but human settlements and infrastructure are vulnerable to both intense winds and flooding~~
969 ~~(Lane et al. 2013, Hinkel et al. 2014, Braswell et al. 2022). Land use development also alters~~
970 ~~the natural resilience of coastal environments through the proliferation of gray infrastructure~~
971 ~~such as jetties and seawalls (Gittman et al. 2015). Systems in low-lying regions are particularly~~
972 ~~vulnerable to inundation as opposed to rocky shores with steep slopes. While regional or global~~
973 ~~data sets based on elevation data exist, the extent at any given time of storm surges, king tides,~~
974 ~~and other high water episodes depend locally/regionally on where the event hits,~~
975 ~~flooding~~inundation, that occur at the interface between terrestrial and aquatic domains. Unlike
976 tidal environments, inundation that affects the coastal zone is driven by temporary, often
977 stochastic events including storms, seiches, and king tides. The impact and areal extent of
978 coastal inundation varies across events, depending on topography, infrastructure, and event
979 size (Fig. 8). The frequency of these events ranges from multiple times a season to decadal
980 (Fig. 8). Tropical storms and cyclones develop in tropical regions during seasonal periods of
981 warm water each year. Due to their high energy and movement, they influence more temperate
982 regions as well (Colbert and Soden 2012). In temperate or cold regions, storms develop in the
983 winter time due to large temperature differences between land and ocean (Liberato et al. 2013).
984 Natural systems will display some form of resilience and recovery to storm impacts (Lugo 2008,
985 Wang et al. 2016), but human settlements and infrastructure are vulnerable to both intense

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winds and inundation (Lane et al. 2013, Hinkel et al. 2014, Braswell et al. 2022). Land use development also alters the natural resilience of coastal environments through the proliferation of gray infrastructure such as jetties and seawalls (Gittman et al. 2015). Systems in low-lying regions are particularly vulnerable to inundation as opposed to rocky shores with steep slopes. While regional or global data sets based on elevation data exist, the extent at any given time of storm surges, king tides, and other high water episodes depend locally/regionally on where the event hits, infrastructure, and topography of the area.

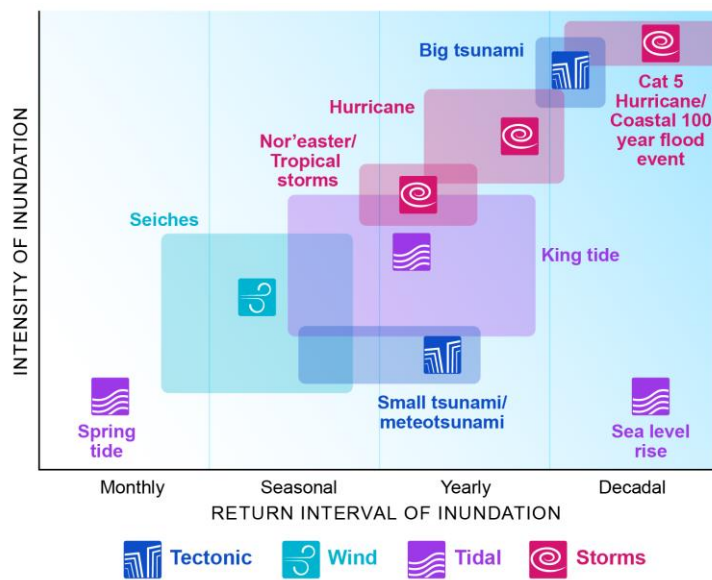


Figure 8. Coastal VIEs experience inundation events with different frequencies and intensities. Some events occur rarely, but are very high intensity events (category 5 hurricanes; large tsunamis), increasing the area of inundation and affecting areas that seldom experience flooding/inundation. The impacted systems are often less adapted to inundation, increasing the extent of destruction or reorganization of the system. Other events occur more regularly and/or are lower in intensity (spring tide, seiches), leading to less extensive inundation and impacting coastal systems that are more adapted to inundation. Credit: Nathan Johnson.

Inundation in the coastal zone impacts sediment transport, solute and nutrient mobilization, vegetation distribution, biological diversity, and biogeochemical processes. Erosion and sediment deposition alter ecosystem geomorphology (e.g., dune shape, marsh accretion) (Houser and Hamilton 2009, Dissanayake et al. 2015) and ecosystem nutrient pools [e.g., (O'Mara et al. 2019, Castañeda Moya et al. 2020)]. In coastal zones adjacent to marine and estuarine waters, saltwater intrusion changes surface (Schaffer-Smith et al. 2020) and groundwater (Cantolon et al. 2022) quality and mobilizes nutrients through porewater ionic

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1011 ~~exchange processes (Herbert et al. 2018). Coastal zone inundation as a natural process alters~~
1012 ~~dune systems, which generates a mosaic of habitats that increase biodiversity (Smith et al.~~
1013 ~~2021) and alter distributions of vegetation and animals. For example, the frequency of overwash~~
1014 ~~events affects plant composition and diversity on sand dunes (Stallins and Parker 2003) and~~
1015 ~~regular inundation is thought to provide necessary habitats for some insects and birds (Smith et~~
1016 ~~al. 2021). Increased salinity and associated geochemical changes alter microbial community~~
1017 ~~diversity and population heterogeneity (Nelson et al. 2015), shifting to more specialized~~
1018 ~~communities as an adaptation to anaerobic conditions, redox fluctuation, and salt stress.~~
1019 ~~Previous studies found high variability in relationships between salinity and ecosystem carbon~~
1020 ~~dioxide fluxes (Morrissey and Franklin 2015, van Dijk et al. 2015, Dang et al. 2019, Hopple et al.~~
1021 ~~2022)Erosion and sediment deposition alter ecosystem geomorphology (e.g., dune shape,~~
1022 ~~marsh accretion) (Houser and Hamilton 2009, Dissanayake et al. 2015) and ecosystem nutrient~~
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1024 ~~marine and estuarine waters, saltwater intrusion changes surface (Schaffer-Smith et al. 2020)~~
1025 ~~and groundwater (Cantelon et al. 2022) quality and mobilizes nutrients through porewater ionic~~
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1027 ~~dune systems, which generates a mosaic of habitats that increase biodiversity (Smith et al.~~
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1029 ~~events affects plant composition and diversity on sand dunes (Stallins and Parker 2003) and~~
1030 ~~regular inundation is thought to provide necessary habitats for some insects and birds (Smith et~~
1031 ~~al. 2021). Increased salinity and associated geochemical changes alter microbial community~~
1032 ~~diversity and population heterogeneity (Nelson et al. 2015), shifting to more specialized~~
1033 ~~communities as an adaptation to anaerobic conditions, redox fluctuation, and salt stress.~~
1034 ~~Previous studies found high variability in relationships between salinity and ecosystem carbon~~
1035 ~~dioxide fluxes (Morrissey and Franklin 2015, van Dijk et al. 2015, Dang et al. 2019, Hopple et al.~~
1036 ~~2022).~~

1037 Human communities within the coastal zone are impacted by inundation events as well.
1038 Inundation of coastal agricultural lands from storm surge and sea level rise reduces agricultural
1039 productivity (Lei et al. 2016)(Lei et al. 2016). In particular, risk is high to coastal zone
1040 communities in developing nations, where inundation events can lead to food insecurity, loss of
1041 livelihood, and increased transmission of waterborne diseases. As climate change alters the
1042 magnitude and frequency of inundation in the coastal zone, it will be necessary to integrate both
1043 natural and human adaptations, such as enabling salt marsh transgression (marsh migration
1044 upland) to mitigate storm surge impacts on crop yield (Guimond and Michael 2021)(Guimond
1045 and Michael 2021).

1046 While we understand many of the linkages between the ecology, biogeochemistry,
1047 hydrology, and geomorphology that regulate ecosystem structure and function in coastal
1048 systems (Fagherazzi et al. 2012, Hinshaw et al. 2017, Braswell and Hoffman 2019, Cantelon
1049 et al. 2022), we know little of how to predict the future effects of the interacting stressors
1050 associated with climate change (O'Meara et al. 2017, Ward et al. 2020, Arrigo et al. 2020). Our
1051 ability to predict is reliant on our understanding of shifting inundation regimes in the context of
1052 elevated CO₂, nutrient pollution, and coastal development which can generate antagonistic,
1053 synergistic, or additive effects. These knowledge gaps stem from the dynamic and
1054 unpredictable nature of events that drive coastal inundation. Observational data to inform

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1055 mechanistic models is limited and governed by where and when events happen (not necessarily
1056 within monitored sites), funding periods, and accessible coastlines. This difficulty is exacerbated
1057 by the fact that 40% of the world's population lives within 100 km of the coast (Maul and Duedall
1058 2019), which heightens social impacts of variable inundation while also adding logistical
1059 difficulty to coastal monitoring. When events do overlap with instrumented sites, the extreme
1060 nature of inundation events threaten instrumentation arrays, risking washout or flooding of
1061 monitoring infrastructure. Lastly, high-latitude coastlines are also susceptible to coastal
1062 inundation, yet few models incorporate physical, biogeochemical, and ecological implications of
1063 inundation on permafrost bound coastlines and environments (Ekici et al. 2019, Bevacqua et al.
1064 2020). Opportunities of critical knowledge advancement exist in 1) monitoring events through *in-*
1065 *situ* or remotely sensed monitoring data, 2) model development that integrates more robust
1066 process-based understanding, and 3) expansion into urban and permafrost-bound coastlines.

1067 **Tidally Driven Coastal Zones**

1068 Tidally influenced coastal zones exist at the intersection of terrestrial and marine environments
1069 and encompass diverse intertidal ecosystems including tidal wetlands, flats, and beaches (Fig.
1070 9). Globally, tidal wetlands exist on 6 of 7 continents, and are spread across tropical, temperate,
1071 and polar latitudes (Murray et al. 2022a). Tidal flats are predominantly found along low-sloping
1072 coastlines with approximately 70% of global tidal flat area existing in Asia, North America, and
1073 South America (Murray et al. 2022b), while beaches encompass 34% of ice-free shorelines
1074 (Luijendijk et al. 2018).

1075 Tidally driven coastal zones are inundated semi-diurnally (i.e., twice a day) or diurnally (i.e.,
1076 once a day). Unlike VIE systems summarized above, where inundation events may be difficult
1077 to predict, inundation in tidally driven coastal zones varies primarily based on predictable
1078 drivers. For example, high tide and low tide water levels dictate the spatial extent and duration
1079 of inundation. In addition, intra-annual tidal dynamics are largely controlled by lunar cycles
1080 which drive approximately monthly highest (spring) and lowest (neap) tides, as well as annual
1081 high (king) and low tides. Inter-annual tidal dynamics are linked to sea level rise, which is
1082 shifting the zone of variable inundation inland (Ensign and Nee 2018, Tagestad et al.
1083 2024) While we understand many of the linkages between the ecology, biogeochemistry,
1084 hydrology, and geomorphology that regulate ecosystem structure and function in coastal
1085 systems (Fagherazzi et al. 2012, Hinshaw et al. 2017, Braswell and Heffernan 2019, Cantelon
1086 et al. 2022), we know little of how to predict the future effects of the interacting stressors
1087 associated with climate change (O'Meara et al. 2017, Ward et al. 2020, Arrigo et al. 2020). Our
1088 ability to predict is reliant on our understanding of shifting inundation regimes in the context of
1089 elevated CO₂, nutrient pollution, and coastal development which can generate antagonistic,
1090 synergistic, or additive effects. These knowledge gaps stem from the dynamic and
1091 unpredictable nature of events that drive coastal inundation. Observational data to inform
1092 mechanistic models is limited and governed by where and when events happen (not necessarily
1093 within monitored sites), funding periods, and accessible coastlines. This difficulty is exacerbated
1094 by the fact that 40% of the world's population lives within 100 km of the coast (Maul and Duedall
1095 2019), which heightens social impacts of variable inundation while also adding logistical
1096 difficulty to coastal monitoring. When events do overlap with instrumented sites, the extreme
1097 nature of inundation events threaten the physical integrity of instrumentation. Lastly, high-

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1098 latitude coastlines are also susceptible to coastal inundation, yet few models incorporate
1099 physical, biogeochemical, and ecological implications of inundation on permafrost bound
1100 coastlines and environments (Ekici et al. 2019, Bevacqua et al. 2020). Opportunities of critical
1101 knowledge advancement exist in 1) monitoring events through *in-situ* or remotely sensed
1102 monitoring data, 2) model development that integrates more robust process-based
1103 understanding, and 3) expansion into urban and permafrost-bound coastlines.

1104 **Tidally Driven Coastal Zones**

1105 Tidally-influenced coastal zones exist at the intersection of terrestrial and marine environments
1106 and encompass diverse intertidal ecosystems such as marshes, mangroves, ghost forests, and
1107 beaches (Fig. 9). Globally, tidal wetlands exist on 6 of 7 continents, and are spread across
1108 tropical, temperate, and polar latitudes (Murray et al. 2022a). Tidal flats are predominantly found
1109 along low sloping coastlines with approximately 70% of global tidal flat area existing in Asia,
1110 North America, and South America (Murray et al. 2022b), while beaches encompass 31% of
1111 ice-free shorelines (Luijendijk et al. 2018).

1112 Tidally-driven coastal zones are inundated semi-diurnally (i.e., twice a day) or diurnally (i.e.,
1113 once a day). Unlike VIE systems summarized above, where inundation events may be difficult
1114 to predict, inundation in tidally-driven coastal zones varies primarily based on predictable
1115 drivers. For example, high tide and low tide water levels dictate the spatial extent and duration
1116 of inundation. In addition, intra-annual tidal dynamics are largely controlled by lunar cycles
1117 which drive approximately monthly highest (spring) and lowest (neap) tides, as well as annual
1118 high (king) and low tides. Inter-annual tidal dynamics are linked to sea level rise, which is
1119 shifting the zone of variable inundation inland (Ensign and Noe 2018, Tagestad et al. 2021). We
1120 note that while the timing of king tides is predictable (perigean spring tide), their impacts can be
1121 difficult to predict, as mentioned in the storm-impacted coastal zones section. In addition,
1122 topography (e.g., slope) and other natural physical factors, including wind speed and direction,
1123 waves, and even localized high and low pressure events mediate the lateral extent of surface
1124 water inundation in tidal ecosystems. Human modifications further alter both vertical and
1125 longitudinal extent of tidal ~~flooding~~inundation, via control structures which may exclude tides
1126 (gates, weirs, etc.) and channels that transport tidal waters well inland of the natural intertidal
1127 zone.

1128 The extent of tidal influence, which spans microtidal (< 2 meter tidal range) to macrotidal (>
1129 10 meter tidal range in some locations), controls water quality, terrestrial-aquatic interactions
1130 and resulting biogeochemical and ecological responses [e.g., (Tweedley 2016)]. Estuaries,
1131 where tides mix saltwater and freshwater, are dynamic biogeochemical mixing zones
1132 characterized by sharp chemical gradients that regulate biological activity [e.g., (Crump et al.
1133 2017)]. Shifts in tidal zones associated with sea level rise are predicted to alter the extent of key
1134 intertidal habitats, with potential disruptions to coastal food webs (Rullens et al. 2022). Changes
1135 in duration and extent of inundation associated with tides control soil saturation and salinity,
1136 which influence redox dynamics, and hydrologically driven exchange of carbon, nutrients, and
1137 pollutants (Pozeshki and DeLaune 2012, Bogard et al. 2020, Regier et al. 2021). Biological
1138 activity, including crab burrows that alter hydrologic flow paths (Crotty et al. 2020), also
1139 influence tidal exchanges across the coastal terrestrial-aquatic interface (Crotty et al. 2020).
1140 Increased saltwater exposure due to shifting tidal ranges can alter the stability of coastal soils

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1141 [e.g., (Chambers et al. 2019)], which represent a globally important carbon sink (McLeod et al.
1142 2011). In addition, tidal regimes structure vegetation gradients, where salt-sensitive
1143 communities including low-lying forests and freshwater marsh species are replaced by salt-
1144 tolerant communities including mangroves and saltmarsh species (Kirwan and Gedan 2019,
1145 Lovelock and Reef 2020). This shift in tidal range leads to the creation of ghost forests (Kirwan
1146 and Gedan 2019), which can impact coastal biogeochemical cycles [e.g., (Cawley et al. 2014).
1147 Similarly, sea level rise may lead to mangrove or marsh retreat as inundation patterns change
1148 (Xie et al. 2020)(Tweedley 2016)]. Estuaries, where tides mix saltwater and freshwater, are
1149 dynamic biogeochemical mixing zones characterized by sharp chemical gradients that regulate
1150 biological activity [e.g., (Crump et al. 2017)]. Shifts in tidal zones associated with sea-level rise
1151 are predicted to alter the extent of key intertidal habitats, with potential disruptions to coastal
1152 food webs (Rullens et al. 2022). Changes in duration and extent of inundation associated with
1153 tides control soil saturation and salinity, which influence redox dynamics, and hydrologically
1154 driven exchange of carbon, nutrients, and pollutants (Pezeshki and DeLaune 2012, Bogard et
1155 al. 2020, Regier et al. 2021). Biological activity, including crab burrows that alter hydrologic flow
1156 paths (Crotty et al. 2020), also influence tidal exchanges across the coastal terrestrial-aquatic
1157 interface (Crotty et al. 2020). Increased saltwater exposure due to shifting tidal ranges can alter
1158 the stability of coastal soils [e.g. (Chambers et al. 2019)], which represent a globally important
1159 carbon sink (McLeod et al. 2011). In addition, tidal regimes structure vegetation gradients, where
1160 salt-sensitive communities including low-lying forests and freshwater marsh species are
1161 replaced by salt-tolerant communities including mangroves and saltmarsh species (Kirwan and
1162 Gedan 2019, Lovelock and Reef 2020). This shift in tidal range leads to the creation of ghost
1163 forests (Kirwan and Gedan 2019), which can impact coastal biogeochemical cycles [e.g.,
1164 (Cawley et al. 2014) . Similarly, sea level rise may lead to mangrove or marsh retreat as
1165 inundation patterns change (Xie et al. 2020).

1166 Due to the frequency of inundation, tidally inundated ecosystems are hydrologically,
1167 biogeochemically, and geomorphologically dynamic, creating challenges for scientists and land
1168 managers seeking accurate estimations of land surface area, elevation, and carbon storage.
1169 These challenges are exacerbated by sea level rise, which exerts heterogeneous and non-linear
1170 influences on tidal ranges (Du et al. 2018). Methodological approaches to assess tidal
1171 ecosystem area and elevation that are based on satellite imagery will be critical for present and
1172 future management and decision making. Similarly, complex feedbacks across three-
1173 dimensional physical space exist among hydrology, biogeochemistry, ecology, and
1174 geomorphology (Xin et al. 2022); these dynamics may need to be considered in future
1175 ecosystem projections. Thus, a deeper understanding of feedbacks and their variability in space
1176 and time in response to tidal activity is needed (Ward et al. 2020). Lastly, with sea level rise,
1177 tidal constituents may change, with nonlinear impacts on tidal range and inundation extent
1178 (Pickering et al. 2017). Tidally inundated VIEs represent the interface between marine and
1179 terrestrial ecosystems, and to predict their future will require understanding bi-directional
1180 connections among physical, chemical, and biological system components.

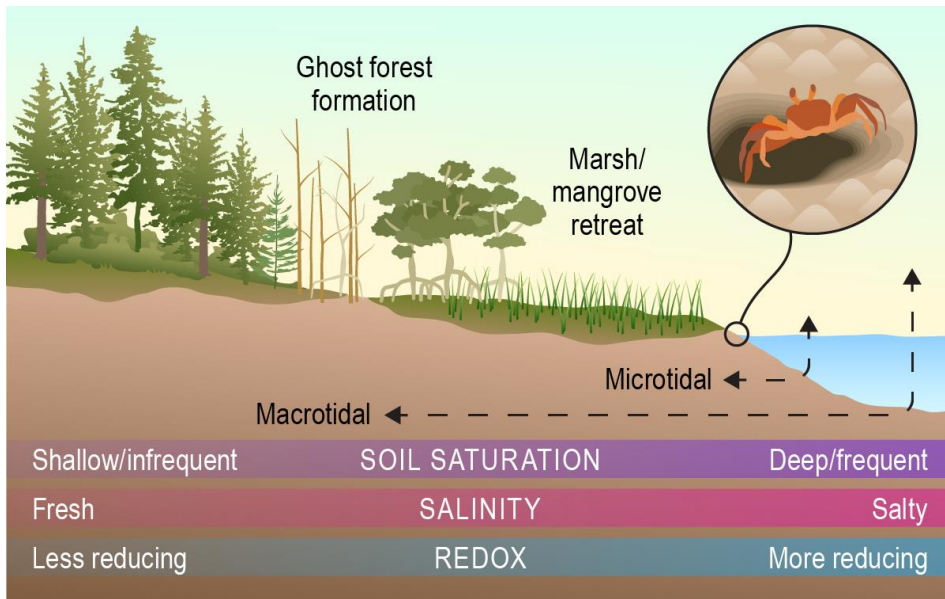
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1183 Due to the frequency of inundation, tidally inundated ecosystems are hydrologically,
1184 biogeochemically, and geomorphologically dynamic, creating challenges for scientists and land

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1185 managers seeking accurate estimations of land surface area, elevation, and carbon storage.
 1186 These challenges are exacerbated by sea level rise, which exerts heterogeneous and non-linear
 1187 influences on tidal ranges (Du et al. 2018). Methodological approaches to assess tidal
 1188 ecosystem area and elevation that are based on satellite imagery will be critical for present and
 1189 future management and decision making. Similarly, complex feedbacks exist among hydrology,
 1190 biogeochemistry, ecology, and geomorphology (Xin et al. 2022); these dynamics may need to
 1191 be considered in future ecosystem projections. Thus, a deeper understanding of feedbacks and
 1192 their variability in space and time in response to tidal activity is needed (Ward et al. 2020).
 1193 Lastly, with sea-level rise, tidal constituents may change, with nonlinear impacts on tidal range
 1194 and inundation extent (Pickering et al. 2017). Tidally inundated VIEs represent the interface
 1195 between marine and terrestrial ecosystems, and to predict their future will require understanding
 1196 bi-directional connections among physical, chemical, and biological system components.
 1197



1198 **Figure 9. Conceptual model of variable inundation in tidal systems.** Tidally driven coastal
 1199 zones span sediments exposed at low tide to marshes and coastal forests inundated at high
 1200 tide. This lateral gradient of tidal exposure is characterized by gradients in vegetation and soil
 1201 characteristics, and modified by the across micro to macro-tidal systems (dotted black lines)
 1202 alters physical- (e.g., particle deposition), biological (e.g., species composition), and chemical,
 1203 and biological- (e.g., nutrient transformations) factors discussed in the tidal systems section.
 1204 Organisms can impact conditions along the gradient, such as flow path alteration by crab
 1205 burrowing. Credit: Nathan Johnson.
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1207 **Human-Engineered Systems**

1208 Human-engineered systems are environments where inundation magnitude, frequency, timing,
1209 and duration are either actively managed or have been dramatically altered by structural
1210 modifications to the landscape (Fig. 10). ~~Human-engineered VIEs rival natural systems in area~~
1211 ~~and extent (Clifford and Heffernan 2018), yet the significance of engineered VIEs in influencing~~
1212 ~~landscape processes is relatively unexplored compared to natural systems (Koschorreck et al.~~
1213 ~~2020) and they are historically excluded from water and nutrient budgets (Abbott et al. 2019).~~
1214 ~~The primary drivers of human-engineered VIE formation explored here are land use change and~~
1215 ~~restoration, though hydrologic modifications impact inundation regimes of the natural VIEs~~
1216 ~~explored earlier in the manuscript. Examples of land-use driven human-engineered VIEs~~
1217 ~~include, but are not limited to, croplands irrigated by flooding (e.g., rice paddies, cranberry~~
1218 ~~bogs); irrigation and drainage canals, stormwater control structures (e.g., roadside ditches,~~
1219 ~~retention ponds), as well as unintentional VIE formation following landscape modification such~~
1220 ~~as “accidental” urban wetlands (Palta et al. 2017) or ponding in agricultural fields (Saadat et al.~~
1221 ~~2020). Whereas the purpose of land-use driven engineered VIEs is to redistribute water for~~
1222 ~~human purposes, the goal of VIEs engineered for restoration is to either replace or enhance~~
1223 ~~ecosystems lost or damaged as a result of human activity. VIE restoration efforts vary in scope~~
1224 ~~and form, spanning local (e.g., residential living shorelines, individual stream reaches,~~
1225 ~~agricultural ditch wetlands) to ecosystem [e.g., adding sediment to degrading marshes~~
1226 ~~(VanZomeren et al. 2018)], to regional (e.g., dam removal) scales. Human-engineered VIEs rival~~
1227 ~~natural systems in area and extent (Clifford and Heffernan 2018), yet the significance of~~
1228 ~~engineered VIEs in influencing landscape processes is relatively unexplored compared to~~
1229 ~~natural systems (Koschorreck et al. 2020) and they are historically excluded from water and~~
1230 ~~nutrient budgets (Abbott et al. 2019). The primary drivers of human-engineered VIE formation~~
1231 ~~explored here are land use change and restoration (including those for nature-based solutions),~~
1232 ~~though hydrologic modifications impact inundation regimes of the natural VIEs explored earlier~~
1233 ~~in the manuscript. Examples of land-use driven human-engineered VIEs include, but are not~~
1234 ~~limited to: croplands irrigated to the point of inundation (e.g., rice paddies, cranberry bogs),~~
1235 ~~canals for irrigation, drainage and stormwater (e.g., roadside ditches, retention ponds), and~~
1236 ~~unintentional VIE formation following landscape modification (e.g., “accidental” urban wetlands~~
1237 ~~(Palta et al. 2017) and ponds in agricultural fields (Saadat et al. 2020). Whereas the purpose of~~
1238 ~~land-use driven engineered VIEs is to redistribute water for human purposes, the goal of VIEs~~
1239 ~~engineered for restoration is to either replace or enhance ecosystems lost or damaged as a~~
1240 ~~result of human activity. VIE restoration efforts vary in scope and form, spanning local (e.g.,~~
1241 ~~residential living shorelines, individual stream reaches, agricultural ditch wetlands) to ecosystem~~
1242 ~~(e.g., adding sediment to degrading marshes), to regional (e.g., dam removal) scales~~
1243 ~~(VanZomeren et al. 2018, Baptist et al. 2021).~~

1244 While the full extent of human-engineered VIEs is difficult to quantify, key examples highlight
1245 their significance in the landscape. Agriculture covers nearly 40% of the earth’s land surface
1246 (Siebert et al. 2010)(Siebert et al. 2010), and nearly a quarter of that is variably inundated by
1247 flood irrigation (Wu et al. 2023)(Wu et al. 2023). In urban systems, the extent of stormwater
1248 canal networks rival those of natural systems. For example, the total linear length of residential
1249 canals in North America nearly equals that of the Mississippi River (Waltham and Connolly
1250 2011).(Waltham and Connolly 2011). While restoration efforts are not as widely distributed as

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1251 land-use change, restoration still contributes to extensive VIE creation. For example, restoration
1252 accounts for 14% of areal gain of tidal wetlands globally (Murray et al. 2022b)(Murray et al.
1253 2022b). Inundation regimes in human-engineered VIEs can be driven by natural hydrologic
1254 processes, such as connectivity with the water table or tidal inputs. This is particularly important
1255 in VIEs built for restoration, as establishing natural inundation regimes enhances landscape
1256 connectivity and mediates ecosystem functions (Reis et al. 2017, Jones et al. 2018)(Reis et al.
1257 2017, Jones et al. 2018). However, unlike the previously discussed natural systems, the drivers
1258 and duration of inundation in human-engineered VIEs may be decoupled from natural
1259 hydrologic processes. Controlling drainage, such as for stormwater management, land
1260 reclamation, or effluent releases, is a key motivation for VIE construction and system design,
1261 resulting in inundation periods largely driven by precipitation that persist at event to seasonal
1262 scales depending on local hydrology and climate. Inundation duration may also occur on longer
1263 timescales, such as ~~seasonal flooding~~seasonally, in paddy systems (De Vries et al. 2010)(De
1264 Vries et al. 2010). Finally, direct human interventions, such as floodgates, weirs, and dams, may
1265 affect water residence time at timescales that are asynchronous from natural drivers, such as
1266 seasonality or tides.

1267 Human-engineered VIEs fundamentally alter the landscape, changing the spatial and
1268 temporal patterns of ecosystem processes. Agricultural inundation, such as flood irrigation or
1269 ponding, alters redox conditions, greenhouse gas emissions, groundwater recharge,
1270 evapotranspiration fluxes, plant growth, and pollutant export to natural water bodies (Hale et al.
1271 2015, Pan et al. 2017, Pool et al. 2021, Buszka and Reeves 2021). For example, a recent study
1272 showed that variably inundated depressions in agricultural fields can account for ~30% of
1273 nitrous oxide emissions across cultivated areas despite comprising ~1% of the land surface
1274 (Elberling et al. 2023). The creation of drainage canals increases waterborne carbon fluxes from
1275 VIEs by producing a newly decomposed stock of labile soil carbon to be leached as well as by
1276 increasing the hydrological runoff rate through the soil and receiving canals and ditches (Stanley
1277 et al. 2012). Human-engineered VIEs can also provide ecosystem services that supplement or
1278 replace those of natural VIEs in the landscape (Clifford and Heffernan 2018). For example, they
1279 can enhance habitat (Connolly 2003, Herzon and Helenius 2008), nitrogen removal (Bettez and
1280 Groffman 2012, Reisinger et al. 2016), and recreation (Beckingham et al. 2019). Further, the
1281 services these systems provide can be improved through targeted management [e.g.,
1282 vegetation composition; (Castaldelli et al. 2015)] or restoration practices [i.e., two-stage ditches;
1283 (Speir et al. 2020)(Hale et al. 2015, Pan et al. 2017, Pool et al. 2021, Buszka and Reeves
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1294 improved through targeted management [e.g., vegetation composition; (Castaldelli et al. 2015)]
1295 or restoration practices [i.e., two-stage ditches; (Speir et al. 2020)].

1296 Including human-engineered systems in our conceptualization of VIEs emphasizes the
1297 growing significance of these systems as human landscape modifications continue to alter and
1298 eliminate natural VIEs. Recent efforts have synthesized the role and impacts of human-
1299 engineered VIEs at large scales (Peacock et al. 2021, Li et al. 2022b) but, as with many natural
1300 systems, the majority of studies on human-engineered VIEs are based in North America and
1301 Europe (González et al. 2015, Zhang et al. 2018, Bertolini and da Mosto 2021). Thus, our
1302 knowledge may not reflect the social, political, and economic challenges of developing areas
1303 where the highest rates of VIE modification are occurring (Wantzen et al. 2019). The knowledge
1304 gaps surrounding human-engineered VIEs will become increasingly important to address as
1305 global change continues to alter the spatial and temporal patterns of inundation. Given that
1306 human-engineered VIEs can enhance or disrupt hydrologic connectivity, they potentially
1307 magnify the effects of human driven changes such as sea level rise and impacts of
1308 contamination from anthropogenic “chemical cocktails” (Kaushal et al. 2022). We lack a
1309 baseline standard for how human-engineered VIEs function in the landscape, even as global
1310 change continues to shift existing baselines [e.g., (Palmer et al. 2014)]. Addressing these
1311 knowledge gaps will require the incorporation of human-engineered VIEs into large-scale
1312 synthesis and modeling efforts, particularly those that address hydrologic and biogeochemical
1313 fluxes. Conclusive definitions and inventories of human-engineered VIEs is essential for
1314 estimating their ecological and biogeochemical roles at the global scale. Finally, human-
1315 engineered VIEs need to be conceptualized within an ecological, rather than managerial,
1316 context for integration and comparison with natural systems. Human-engineered VIEs rival the
1317 range of natural VIEs in structure, inundation regime, and global distribution. Understanding
1318 their role in the Earth system is, therefore, critical for understanding both the impacts of and
1319 potential solutions to global change.

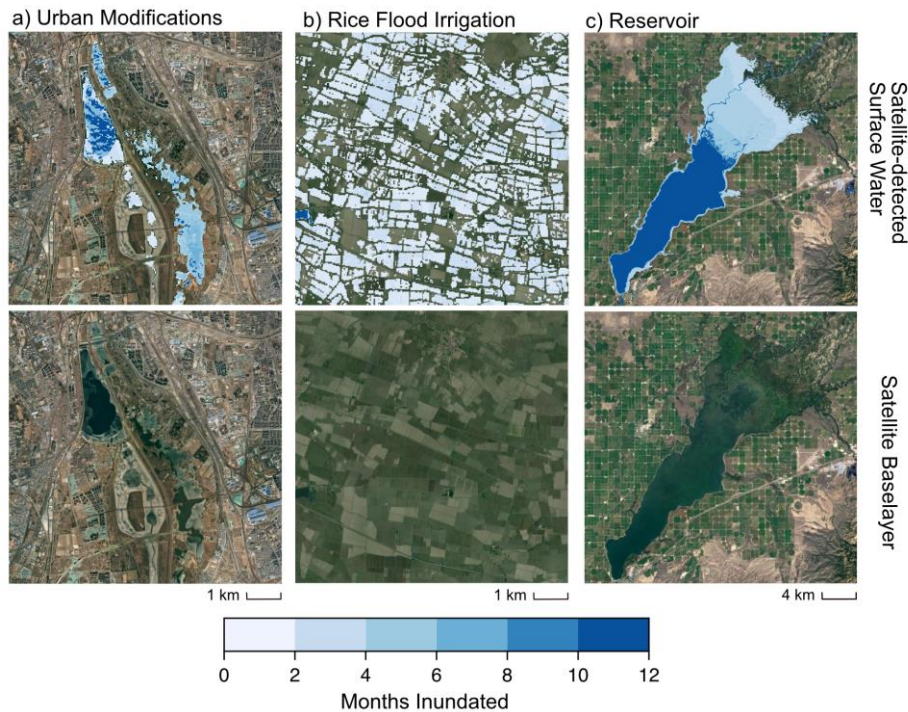
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1322 Including human-engineered systems in our conceptualization of VIEs emphasizes the
1323 growing significance of these systems as human landscape modifications continue to alter and
1324 eliminate natural VIEs. Recent efforts have synthesized the role and impacts of human-
1325 engineered VIEs at large scales (Peacock et al. 2021, Li et al. 2022b) but, as with many natural
1326 systems, the majority of studies on human-engineered VIEs are based in North America and
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1329 where the highest rates of VIE modification are occurring (Wantzen et al. 2019). The knowledge
1330 gaps surrounding human-engineered VIEs will become increasingly important to address as
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1333 magnify the effects of human driven changes such as sea level rise and impacts of
1334 contamination from anthropogenic “chemical cocktails” (Kaushal et al. 2022). We lack a
1335 baseline standard for how human-engineered VIEs function in the landscape, even as global
1336 change continues to shift existing baselines [e.g., (Palmer et al. 2014)]. A baseline
1337 understanding would also enable the restoration and repurposing of engineered VIEs as nature-

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1338 based solutions (Clifford and Heffernan 2023)(Clifford et al., 2023). Addressing these
 1339 knowledge gaps will require the incorporation of human-engineered VIEs into large-scale
 1340 synthesis and modeling efforts, particularly those that address hydrologic and biogeochemical
 1341 fluxes. Conclusive definitions and inventories of human-engineered VIEs is essential for
 1342 estimating their ecological and biogeochemical roles at the global scale. Finally, human-
 1343 engineered VIEs need to be conceptualized within an ecological, rather than managerial,
 1344 context for comparison with natural systems and to be integrated into a more continuum-based
 1345 approach for VIE science. Human-engineered VIEs rival the range of natural VIEs in structure,
 1346 inundation regime, and global distribution. Understanding their role in the Earth system is,
 1347 therefore, critical for understanding both the impacts of and potential solutions to global change.
 1348



1349
 1350
 1351 **Figure 10. Examples of human-engineered Variably Inundated Ecosystems.** a) Yongding
 1352 River in Beijing, China; b) Paddy rice fields in northern Italy; c) American Falls Reservoir on the
 1353 Snake River in Idaho, United States. These three examples emphasize significant variation in
 1354 the degree of variable inundation across human-engineered VIEs, with some regions being
 1355 perennially inundated. Top row: Satellite-derived map data on months inundated is derived from
 1356 the “seasonality” product in the Global Surface Water Mapping Layers v1.4 (Pekel et al.
 1357 2016)(Pekel et al. 2016). Credit: Jillian Deines.

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1358 **Inundation Processes are Relevant at the Scale of the Beholder**

1359 VIEs span broad spatiotemporal scales of variable inundation, from microenvironments like small
1360 wetlands and vernal ponds to the floodplains of the world's largest rivers. While examples in the
1361 mini-reviews focus on eight different ecosystems, variably inundated ecosystems are even
1362 broader such as mosses and pore spaces that are periodically covered by droplets of water, ~~to~~
1363 and vast endorheic lakes and rivers. Inundation volumes and surface areas of VIEs vary by at
1364 least sixteen orders of magnitude, from under 10^{-3} L to over 10^{13} L ([https://www.k26.com/lake-](https://www.k26.com/lake-eyre-papers-lake-eyre-basics)
1365 [eyre-papers-lake-eyre-basics](https://www.k26.com/lake-eyre-papers-lake-eyre-basics)), (Bonython and Mason 1953), and 10^6 m² to over 10^{10} m²
1366 (<https://www.guinnessworldrecords.com/world-records/92443-largest-ephemeral-lake>), (Hess et
1367 al. 2015), respectively. The duration of inundation varies by up to eight orders of magnitude,
1368 spanning a few seconds, in the case of droplets, to decades, in the case of endorheic lakes, and
1369 centuries in the case of sea level rise. Non-inundated periods likewise span seconds to
1370 centuries and longer. This variability in spatial and temporal extent has profound consequences
1371 for the ecology and biogeochemistry of VIEs. This section highlights the importance of
1372 considering scale and explores hypotheses regarding how scale drives variability in drivers,
1373 processes, and impacts across VIEs and how we study them.

1374 Spatial and temporal scales of VIEs can be categorized along two axes – extent and
1375 granularity. Extent comprises the total size of the spatial domain or time duration of a defined
1376 system, while granularity pertains to the spatial or temporal intervals of system transitions
1377 ([Ladau and Eloe-Fadrosch 2019](#)), ([Ladau and Eloe-Fadrosch 2019](#)). For example, the dynamics of
1378 water droplets across North America would represent a large extent with fine granularity,
1379 relative to the inundation dynamics of a several square meter desert playa (smaller extent but
1380 coarser grain). The impacts of variable inundation are dependent 'on the scale of the beholder'
1381 relative to the extent and grain of variable inundation, where a 'beholder' may be a molecule,
1382 organism, population, community, land manager, or otherwise- ([Fig. 11](#)). The expressed
1383 metabolism of an individual microbe will be influenced by inundation down to the spatial scale of
1384 water films and on hourly or shorter time scales. An individual microbe may not, however, be
1385 influenced by whether variable inundation occurs only within a square meter or across many
1386 square kilometers because it does not perceive these larger scales. In contrast,
1387 macroinvertebrate behavior is influenced by variable inundation down to scales of meters and
1388 days, and is likely further influenced by larger and longer scales of stream network connectivity
1389 ([Bogan et al. 2017b](#), [Sarremejane et al. 2017](#)), ([Bogan et al. 2017b](#), [Sarremejane et al. 2017](#)).

1390 VIEs can be viewed as habitat patches of different sizes that vary in how long they persist in
1391 a given state and that have dynamic connectivity among patches. Terrestrial and aquatic biota
1392 respond on ecological and evolutionary time scales to the expansion and contraction cycles of
1393 inundation ([Bornette et al. 1998](#), [Ward et al. 2002](#)), ([Bornette et al. 1998](#), [Ward et al. 2002](#)),
1394 Biotic diversity is influenced by productivity, connectivity, disturbance severity and disturbance
1395 frequency, all of which operate at hierarchical scales ([Ward et al. 1999](#)), ([Ward et al. 1999](#)),
1396 Biogeographical and ecological theories posit that patch size (e.g., species area scaling) and
1397 disturbance regimes (e.g., intermediate disturbance hypothesis) are strong determinants of
1398 community composition ([Adler et al. 2005](#), [Svensson et al. 2012](#)), ([Adler et al. 2005](#), [Svensson et](#)
1399 [al. 2012](#)), suggesting that VIE community composition may vary predictably with these factors.
1400 The duration, predictability, and frequency of inundation likely have consistent community-level
1401 consequences that vary predictably with VIE extent and grain. Different extents and grains of

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1402 inundation have the potential to change habitat connectivity in addition to directly selecting for
1403 different groups of organisms. Isolated marshes may, for example, become merged during a
1404 flood, thereby enhancing dispersal of aquatic organisms. The scale of variable inundation has
1405 numerous influences over ecological processes and dynamics that need to be understood.

1406 From a biogeochemical perspective, variable inundation generates spatial and temporal
1407 variation in rates and patterns of biogeochemical processes. This variability is important for
1408 scaling biogeochemical rates because of process nonlinearity and Jensen's inequality (Ruel and
1409 Ayres 1999). (Ruel and Ayres 1999). That is, a rate based on average conditions differs
1410 systematically from the average rate across variable conditions. This is important because the
1411 scales of processes (e.g., microbial activity occurring within pore channels) are typically not
1412 aligned with the scales of measurements and models (e.g., core-scale or above). The lack of
1413 clear understanding for how variable inundation influences variation in biogeochemical
1414 processes and how these relationships change with extent and grain of inundation can,
1415 therefore, lead to unreliable predictions for the scaling of biogeochemical processes.

1416 Understanding the biogeochemical influences of variable inundation across a broad range of
1417 scales is important for informing a diverse suite of needs across models, decision makers, and
1418 other interested parties. Our ability to inform these needs depends on our ability to rigorously
1419 understand and predict influences of variable inundation across scales. This is a challenge as
1420 variable inundation likely has direct, but unknown, influences over the scaling of biogeochemical
1421 function. For example, cumulative metabolism in streams is predicted to increase faster than
1422 their upstream drainage area for perennial stream networks (Wollheim et al. 2022). ~~The
1423 influence of variable inundation on biogeochemical processes cannot yet be accounted for in
1424 such scaling theory. More generally, perturbations like variable inundation can drive systems
1425 away from steady-state assumptions from which scaling relationships are derived (McCarthy et
1426 al. 2019)(Wollheim et al. 2022). The influence of variable inundation on biogeochemical
1427 processes cannot yet be accounted for in such scaling theory. More generally, perturbations like
1428 variable inundation can drive systems away from steady-state assumptions from which scaling
1429 relationships are derived (McCarthy et al. 2019),~~ therefore, we expect significant changes in
1430 scaling behavior across inundation regimes. A research frontier is to quantify the direction,
1431 magnitude, and duration of changes in scaling patterns in response to variable inundation and
1432 to modified variable inundation regimes wrought by climate, land-use, and other environmental
1433 changes.

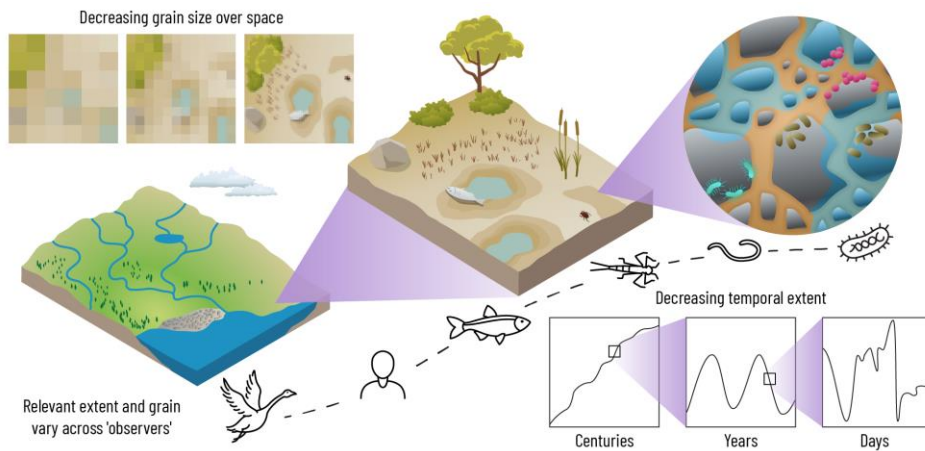
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1435
 1436 **Figure 11. Variable inundation can be observed at different spatiotemporal granularities**
 1437 **and extents.** (Upper left) Granularity is based on the resolution of observations in space or
 1438 time. (Lower right) Extent is based on the cumulative breadth of observations in space or time.
 1439 (Middle panels) Granularity and extent of observations are often correlated, such as barely
 1440 resolving individual trees when extent spans a watershed and resolving individual microbes
 1441 when extent spans a few soil particles. A given beholder observes variable inundation at a given
 1442 scale and will, in turn, make changes to behavior, physiology, and/or aspects of life history. For
 1443 example, migratory waterfowl select habitats based on inundation state as they move across
 1444 watersheds, humans plan cities based on regional patterns, fish move across stream reaches
 1445 based on continuity of inundation, macroinvertebrates lay eggs on individual rocks based on
 1446 inundation state, nematodes experience variable inundation as they move through porous
 1447 media, and soil microbes separated by microns likely experience vastly different inundation
 1448 dynamics linked to water films on soil particles.

1449 **Summary of Primary Methods used to Study VIEs**

1450 The multi-scale nature of VIE systems has led to experimental and observational studies that
 1451 span from point-scale lab-based characterization, to reach- or watershed-scale monitoring
 1452 networks, and to regional- and global-scale remote sensing. Point-scale measurements at the
 1453 smallest scales help reveal processes that underlie larger scale dynamics. For example, point
 1454 measures of water presence, water absence, and low flow detection within a watershed are
 1455 increasingly available with the development of small, inexpensive, and easily deployable
 1456 sensors, meters, and time-lapse cameras [e.g., (Soupir et al. 2009, Chapin et al. 2014, Costigan
 1457 et al. 2017, Zimmer et al. 2020)] (Fig. 11(Soupir et al. 2009, Chapin et al. 2014, Costigan et al.
 1458 2017, Zimmer et al. 2020)] (Fig. 12). While these measurements are easy to take and can
 1459 provide a long temporal dataset for little effort, they are not always detailed and require regular
 1460 calibrations.

1461 A broad range of methods can be used to link the hydrologic dynamics to ecological and
 1462 biogeochemical responses. Standardized field surveys and biomolecular methods (e.g., isotopic

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1463 ratios, including compound specific analyses) are commonly used to study organismal,
1464 population, and community ecology across multiple taxa [e.g., (Ode et al. 2016, Gates et al.
1465 2020)] and can be standardized for both inundated and non-inundated states. There is
1466 increasing use of crowdsourcing for biogeochemical characterization to consistently obtain
1467 samples across diverse systems (von Schiller et al. 2019, Garayburu-Caruso et al. 2020).
1468 Sample collection can be followed by a variety of laboratory measurements of properties (e.g.,
1469 carbon content, redox potential and redox-active elements, microbial genetic potential, sediment
1470 grain size) and processes, such as CO₂ production and methanogenesis related to variable
1471 inundation. Point-scale measurements often operate at instantaneous to daily scales.
1472 Conversely, larger scale measurements integrate across finer scale processes to quantify
1473 ecosystem dynamics and properties, but without necessarily revealing the governing the
1474 processes. Spatially distributed monitoring networks using *in situ* sensors (e.g., the United
1475 States Geological Survey, USGS, gage network) can connect event-scale responses across
1476 hydrologically linked locations as well as reveal long-term trends [e.g., (Zipper et al. 2021)].
1477 Long-term field manipulations are another complementary *in situ* technique that can reveal
1478 mechanisms underlying system responses to changes in inundation state. There are numerous
1479 configurations of such experiments that directly or indirectly impact inundation dynamics, such
1480 as intentional inundation (Hopple et al. 2023), water exclusion (Kundel et al. 2018) and heating
1481 (Hanson et al. 2017)(Ode et al. 2016, Gates et al. 2020)] and can be standardized for both
1482 inundated and non-inundated states. There is increasing use of crowdsourcing for
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1496 directly or indirectly impact inundation dynamics, such as intentional inundation (Hopple et al.
1497 2023), water exclusion (Kundel et al. 2018) and heating (Hanson et al. 2017). Despite the
1498 plethora of data produced by such large scale projects, these are expensive and require deep
1499 buy-in of researchers and landowners.

1500 Remote sensing can complement *in situ* measurements to facilitate more spatially
1501 continuous characterization of surface water dynamics and their impacts. There are different
1502 types of remote sensing techniques that can capture different aspects of VIEs. For example, soil
1503 surface saturation may be captured through passive microwave radiometer as well as C and L-
1504 band radar backscatter, which can also penetrate through thin canopies, clouds, and through
1505 the top few centimeters of the soil (Schumann and Moller 2015). Recent missions such as the
1506 Surface Water and Ocean Topography (SWOT) mission provide increased capabilities for

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1507 monitoring changes in surface water over time with radar data (Biancamaria et al. 2016), while
1508 NASA's forthcoming NISAR mission will allow for detection of inundation even under tree
1509 canopy. Thermal infrared measurements can indirectly reveal saturation at very high
1510 spatiotemporal resolutions, as well as evapotranspiration associated with water table depth, soil
1511 moisture, and rooting depth (Fisher et al. 2020, Lalli et al. 2022). Long time series from
1512 moderate resolution (~30 m) optical satellites can document multi-decadal open water trends
1513 and seasonal regimes across the globe (Pekel et al. 2016), while some combinations of indices
1514 have shown success in detecting mixed vegetation and inundation cover (Jones 2019).
1515 Recently launched satellite constellations provide daily global imagery at < 4 m resolution,
1516 enabling monitoring of more dynamic water bodies [e.g., Arctic lakes, (Cooley et al. 2017) and
1517 forested wetlands (Hondula et al. 2021a)]. Finally, deep groundwater and changes in the total
1518 water column storage are detectable through measurements of gravitational anomalies at very
1519 high precision but low spatial resolution (Bloom et al. 2010, 2017, Richey et al. 2015, Pascolini-
1520 Campbell et al. 2021).

1521
1522
1523 Remote sensing can complement *in situ* measurements to facilitate more spatially
1524 continuous characterization of surface water dynamics and their impacts. There are different
1525 types of remote sensing techniques, from drones to satellites and optical to microwave sensors,
1526 that can capture different aspects of VIEs. For example, soil surface saturation may be captured
1527 by a passive microwave radiometer as well as C and L-band radar backscatter, which can also
1528 penetrate through thin canopies, clouds, and through the top few centimeters of the soil
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1541 Deep groundwater and changes in the total water column storage are detectable through
1542 measurements of gravitational anomalies at very high precision but low spatial resolution
1543 (Bloom et al. 2010, 2017, Richey et al. 2015, Pascolini-Campbell et al. 2021). Fine-scale
1544 inundation dynamics, which have been historically hard to measure, can be captured using
1545 unmanned aerial vehicles (UAVs), which are often useful during or immediately after a
1546 significant inundation event (Perks et al. 2016), to capture small-scale spatial dynamics that are
1547 difficult to detect with satellite or airborne methods (Manfreda et al. 2018, Dugdale et al. 2022),
1548 or to derive detailed data for input into hydrologic models and surface water calculations
1549 (Acharya et al. 2021).

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1551 **Figure 44-12. Monitoring inundation regimes is increasingly possible via in situ sensors.**
 1552 *Stream Temperature, Intermittency, and Conductivity Sensors (STICs)* (Chapin et al.
 1553 ~~2014~~)(Chapin et al. 2014), one of the types of increasingly available sensors to measure water
 1554 presence/absence in an inexpensive and easily deployable manner. These sensors can be used
 1555 across all types of VIEs. Credit: Amy Burgin.

1557
 1558 To advance predictive understanding requires integration of data with models. Process-
 1559 based models can be used to simulate hydrological and biogeochemical processes under dry
 1560 and wet conditions (Fatichi et al. 2016, Li et al. 2017). These models are often built upon mass
 1561 conservation principles, with ordinary or partial differential equations that describe coupled
 1562 hydrological, ecological, and biogeochemical processes. They rely on existing knowledge on
 1563 processes, including, for example, theories or empirical relationships between discharge and
 1564 water storage (Wittenberg 1999), biogeochemical reaction rate dependence on temperature and
 1565 water content (Davidson et al. 1998, Mahecha et al. 2010) and redox reactions (Borch et al.
 1566 2010). Among process-based models, there are spatially distributed models that couple surface
 1567 and subsurface flow dynamics explicitly (Kollet and Maxwell 2006, Coon et al. 2020). This class
 1568 of models has recently been extended to include reactive transport (Wu et al. 2021), which may
 1569 be considered as a set of tools to understand the biogeochemical effects of variable inundation
 1570 (Molins et al. 2022). However, spatial resolution and data requirements for the integrated
 1571 surface and subsurface models are high, which places practical limits on the spatial scales that
 1572 can be addressed. Semi- or fully distributed models with coarse spatial resolution are able to
 1573 work at larger scales, but require theories or empirical relationships to represent processes and
 1574 impacts at subgrid scales. Data-driven machine learning methods present new opportunities to
 1575 blend models with various levels of mechanistic representations into hybrid models (Reichstein
 1576 et al. 2019). Increases in the volume of observational data sets combined with advances in high
 1577 performance computing have triggered a shift towards machine learning applications for
 1578 capturing inundation dynamics. More recently, integration of physics-based models with
 1579 machine learning have improved the interpretability of machine learning methods and increased
 1580 their ability to model complex ecosystem processes (Sun et al. 2022). (Fatichi et al. 2016, Li et
 1581 al. 2017). These models are often built upon mass conservation principles, with ordinary or
 1582 partial differential equations that describe coupled hydrological, ecological, and biogeochemical
 1583 processes. They rely on existing knowledge on processes, including, for example, theories or
 1584 empirical relationships between discharge and water storage (Wittenberg 1999).

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1585 biogeochemical reaction rate dependence on temperature and water content (Davidson et al.
1586 1998, Mahecha et al. 2010) and redox reactions (Borch et al. 2010). Among process-based
1587 models, there are spatially distributed models that couple surface and subsurface flow dynamics
1588 explicitly (Kollet and Maxwell 2006, Coon et al. 2020). This class of models has recently been
1589 extended to include reactive transport (Wu et al. 2021), which may be considered as a set of
1590 tools to understand the biogeochemical effects of variable inundation (Molins et al. 2022).
1591 However, spatial resolution and data requirements for the integrated surface and subsurface
1592 models are high, which places practical limits on the spatial scales that can be addressed.
1593 Semi- or fully-distributed models with coarse spatial resolution are able to work at larger scales,
1594 but require theories or empirical relationships to represent processes and impacts at subgrid-
1595 scales. Data-driven machine learning methods present new opportunities to blend models with
1596 various levels of mechanistic representations into hybrid models (Reichstein et al. 2019).
1597 Increases in the volume of observational data sets combined with advances in high
1598 performance computing have triggered a shift towards machine learning applications for
1599 capturing inundation dynamics. More recently, integration of physics-based models with
1600 machine learning have improved the interpretability of machine learning methods and increased
1601 their ability to model complex ecosystem processes (Sun et al. 2022b). These hybrid
1602 approaches have the potential to optimize the characterization and prediction of inundation
1603 dynamics by incorporating the strengths of multiple models to achieve predictions with
1604 minimized uncertainty and greater accuracy than either model alone.

1605 Coordinated integration (~~Patel et al. 2023~~)(Patel et al. 2023) between model development
1606 and data generation is key to deepening our understanding of VIEs and increasing our ability to
1607 predict their future ecosystem function and ecological integrity. More specifically, we promote
1608 iterating between model-guided data generation and observation-informed model development.
1609 This iterative cycle between models and 'experiments' (i.e., real-world data generation) has
1610 previously been termed 'ModEx' (~~Atchley et al. 2015~~) and is similar to approaches used in
1611 'ecological forecasting' (Dietze et al. 2017, 2018).(Atchley et al. 2015) and is similar to
1612 approaches used in 'ecological forecasting' (Dietze et al. 2017, 2018). It also aligns generally
1613 with the scientific method based on continuous iteration between conjectures (hypotheses /
1614 models) and refutation (falsification of hypothesis using observations and data) to drive scientific
1615 discovery and knowledge growth (~~Popper 2014~~).(Popper 2014). The ModEx approach often
1616 starts by using experimental or field data to parameterize and calibrate models and/or generate
1617 new data based on known model input needs. This can be expanded whereby models generate
1618 hypotheses via *in silico* experiments, and field or lab studies can be designed to test those
1619 hypotheses. Models can also be used to optimize the design of real-world experiments by
1620 indicating when, where, and what to measure to provide the strongest hypothesis evaluation.

1621 In the context of VIEs, we expect ModEx to touch scales ranging from molecular
1622 microbiology to landscape ecology to regional ecosystem function to Earth system elemental
1623 cycles. ~~Key to enabling this~~As a landscape-scale example of ModEx, physical models could first
1624 be used to predict variable inundation across a watershed. Spatial and/or temporal uncertainty
1625 in those predictions could then be used to optimize collection of commercial remote sensing
1626 data. Those data would, in turn, be used to evaluate model predictions, leading to updated
1627 guidance from the model on where/when to collect additional remote sensing data. Further
1628 cycles could be pursued and model uncertainties could also guide collection of in situ data on

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1629 variable inundation, organismal ecology, and/or biogeochemical processes. Many other
1630 examples across a variety of scales can be envisioned, and key to enabling this approach is the
1631 further development of models and measurement techniques that can capture system states in
1632 both inundated and non-inundated conditions. Techniques/models designed for specific kinds of
1633 ecosystems (e.g., perennial rivers) may be difficult to adapt. This emphasizes a need to do
1634 ModEx using models and measurements intentionally designed to span inundated and non-
1635 inundated system states.

1636 Across the continuum of ModEx, it is important to consider the scales at which models and
1637 measurements operate, as discussed above. The issues around scale could, in part, be
1638 addressed by Integrated Coordinated Open Networked (ICON) science principles (Goldman et
1639 al. 2022)(Goldman et al. 2022). ICON is based on intentional design of research efforts to be
1640 Integrated across disciplines and scales, Coordinated across research efforts via consistent
1641 methods, Open throughout the research lifecycle, and Networked across stakeholders to
1642 understand collective needs. We propose using ICON principles for *in situ* data generation and
1643 remote sensing, jointly guided by model-generated predictions (i.e., ModEx). Embedding ICON
1644 throughout the research life cycle can help to ensure that new data are at the right scale and
1645 can be used to link disciplines (e.g., hydrology, biogeochemistry, and community ecology). This
1646 can also ensure that data are interoperable across VIEs, are available to everyone and
1647 connected to deep metadata, and are useful to a broad range of stakeholders with interests
1648 spanning different types and locations of VIEs. The use of ICON in cross-VIE science could
1649 bridge existing data across multiple spatial and temporal scales, and potentially bridge gaps
1650 among VIEs.

1651 **Towards Cross-VIE Transferable Understanding**

1652 We propose that a key goal for VIE science is the development and open sharing of knowledge,
1653 models, algorithms, and data that transcend individual system types. This can enhance our
1654 capacity to predict and protect the future of VIE function and integrity. Knowledge that crosses
1655 VIE systems will inherently span scales and levels of certainty from predictable, sub-daily
1656 inundation regimes to rare extreme events; integrating perspectives of these dynamic systems
1657 can aid in understanding and anticipating tipping points of physical, chemical, and biological
1658 components across VIEs. Development of such knowledge should be done via ModEx
1659 approaches coupled with ICON principles, which can generate models that can be used across
1660 VIEs with different physical settings and hydrologic dynamics. We suggest this can be achieved
1661 by taking a continuum approach based on key physical characteristics of VIEs (Fig. 12). While
1662 the categorical approach in the above mini-review sections was used to emphasize the breadth
1663 of VIE systems, we encourage research efforts to move beyond those artificial bins by invoking
1664 this continuum approach. For example, a dynamic, unified classification model has been
1665 proposed in wetlands, including a suite of temporally variable ecological and geomorphological
1666 characteristics (Lisenby et al. 2019). This framework has improved the understanding of human
1667 impacts on wetlands and led to more effective management (Wierzbicki et al. 2020, Mandishona
1668 and Knight 2022). Knowledge that crosses VIE systems will inherently span scales and levels of
1669 certainty from predictable, sub-daily inundation regimes to rare extreme events; integrating
1670 perspectives of these dynamic systems can aid in understanding and anticipating tipping points

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1671 of physical, chemical, and biological components across VIEs. Development of such knowledge
1672 should be done via ModEx approaches coupled with ICON principles, which can generate
1673 models that can be used across VIEs. Similar to the perspectives of Arias-Real et al. (2024), we
1674 suggest this can be facilitated through the development of conceptual models based on
1675 continuous environmental axes that modulate system responses to re-inundation (e.g.,
1676 greenhouse gas production and changes in biological diversity).

1677 Such continuum-based conceptual models necessitate going beyond discrete VIE
1678 categories by treating key physical characteristics as continuous variables that influence all VIE
1679 systems. One realization of such a conceptual model is summarized in Figure 13. Related
1680 approaches that are based on a suite of temporally variable ecological and geomorphological
1681 characteristics have proven useful for wetlands (Euliss et al. 2004, Lisenby et al. 2019). These
1682 wetlands frameworks have improved the understanding of human impacts on wetlands and led
1683 to more effective management (Wierzbicki et al. 2020, Mandishona and Knight 2022). These
1684 successes emphasize the potential effectiveness of continuum-based conceptual models for
1685 cross-VIE science.

1686 The impacts of variable inundation depend on multiple characteristics of the inundation
1687 regimes (e.g., return interval and duration) and factors that influence those regimes (e.g.,
1688 subsurface permeability, topography, climate, and vegetation) (Banach et al. 2009, De Jager
1689 et al. 2012). Furthermore, there are dynamic attributes that influence process rates (e.g., such
1690 as water residence time and hydrologic connectivity), which can create additional feedback to
1691 the impacts of inundation variation that influence process rates (Covino 2017). We hypothesize
1692 that despite this complexity, cross-VIE science can make progress towards transferable
1693 understanding by studying through the evaluation of conceptual models that focus on impacts of
1694 variable inundation across relatively simple physical variables that can be easily measured. Two
1695 such variables are inundation return interval and topographic slope (Fig. 12).

1696 Inundation-13). As suggested above, we encourage studies that examine responses to
1697 variable inundation (e.g., biogeochemical rates and ecological community composition) across
1698 VIEs that collectively span a broad range of return intervals and slopes.

1699 While many environmental variables could be used in this conceptual model (Fig. 13), here
1700 we propose using inundation return interval and topographic slope, as both are well known to
1701 impact ecological communities. For example, inundation return interval has been shown to alter
1702 plant composition (Arim et al. 2023) and biogeochemical function such as CH₄ fluxes (Batson et
1703 al. 2015). We view it as an integrated proxy for variables with direct impacts (e.g., desiccation)
1704 that are linked to the temporal scale of non-inundated conditions. The other axis of our
1705 conceptual model is topographic slope (Fig. 13), which we also view as an integrated proxy, but
1706 for variables linked to how much time water spends in a system (Anderson and Burt 1978,
1707 McGuire et al. 2005). Slope and the variables it represents a key component of the continuum of
1708 inundation regimes and may be considered as a forcing factor. Topographic slope represents a
1709 (e.g., water residence time and velocity) are also well known to influence ecological
1710 communities (e.g., by altering fish composition, as in (Bain et al. 1988)) and biogeochemistry
1711 (e.g., by altering nitrate reductions as in (Gomez et al. 2012)).

1712 At a high-level, return interval and slope are two key component of the continuum of VIE
1713 characteristics that influence how VIE systems respond to inundation based forcing. In turn,
1714 dimensions of temporal scale: how long it takes water to return and how long a parcel of water

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1715 ~~spends in the system. Similarly, these two variables can~~ variables encompass differences across
1716 ~~spatial scales, capturing differences in timing of inundation and how water flows through and is~~
1717 ~~connected to different components of VIEs (e.g., differences in drying across branches of a river~~
1718 ~~network). While these two components should jointly influence nearly every physical, chemical,~~
1719 ~~and biological aspect of VIEs. We through time and across space, we do not, however, imply~~
1720 ~~that these two variables will capture all relevant processes. Other variables such as~~
1721 ~~sediment/soil mineralogy and climate also have strong influences over biogeochemistry and~~
1722 ~~community ecology of VIEs (e.g., Pumo et al. 2016). We may learn that additional axes are~~
1723 ~~needed and these may be linked to other conceptual models, such as whether inundation~~
1724 ~~emerges through infiltration-excess (Hortonian flow generation) or through saturation-excess~~
1725 ~~(Dunnian flow generation) (Freeze 1974). Nonetheless, we propose that significant progress~~
1726 ~~can be made towards cross-VIE understanding of the controls over biogeochemistry and~~
1727 ~~community ecology by pursuing further developing and testing the continuum approach via high-~~
1728 ~~level conceptual model proposed here linked to inundation return interval and topographic~~
1729 ~~slope. In doing so, we encourage careful attention towards the spatial and temporal scales of~~
1730 ~~modeling and data generation efforts linked to return interval and slope.~~

1731 The continuum approach can be applied to questions representing science challenges that
1732 span all VIEs, such as how greenhouse gas fluxes and biological diversity respond to variable
1733 inundation (Fig. 12). Similarly, metabolism research has suggested using a continuum of flow
1734 predictability and light availability to better unify river metabolism research (Bernhardt et al.
1735 2022). In this approach there is no need to bin VIEs into discrete categories, many of which
1736 have varying definitions and levels of overlap. Rather, we can observe and study continuous
1737 response surfaces across multiple physical axes and identify patterns within this quantitative
1738 space. In addition to generating transferable understanding, bringing all VIEs together via the
1739 continuum approach could help raise awareness of VIE diversity, importance, vulnerabilities,
1740 and how they may change in the future. This may, in turn, help address the fact that VIEs are
1741 often overlooked in terms of conservation and monitoring efforts (Calhoun et al. 2017, Hill et al.
1742 2018, Krabbenhoft et al. 2022, Zimmer et al. 2022). The continuum approach can also be used
1743 to learn where, along environmental continuums, functional thresholds exist that could help with
1744 categorizations important for policy and management (Richardson et al. 2022b).

1745 Cross-VIE understanding of the drivers, patterns, and processes linking inundation to
1746 system responses can greatly improve with increased collaboration and communication across
1747 scientific fields and systems. Our conceptual model can be used to frame and
1748 study questions representing science challenges that span all VIEs, such as how greenhouse
1749 gas fluxes and biological diversity respond to variable inundation (Fig. 13). Similarly,
1750 metabolism research has suggested using a continuum of flow predictability and light availability
1751 to better unify river metabolism research (Bernhardt et al. 2022). In this approach there is no
1752 need to bin VIEs into discrete categories (Euliss et al. 2004), many of which have varying
1753 definitions and levels of overlap. A given system may also not fit clearly into a single VIE
1754 category and/or may transition across categories through time and across space. Rather, we
1755 can observe and study continuous response surfaces across multiple physical axes and identify
1756 patterns within this quantitative space.

1757 In addition to generating transferable understanding, bringing all VIEs together via studies
1758 focused on unifying conceptual models could help raise awareness of VIE diversity, importance,

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1759 vulnerabilities, and how they may change in the future. This may, in turn, help address the fact
1760 that VIEs are often overlooked in terms of conservation and monitoring efforts (Calhoun et al.
1761 2017, Hill et al. 2018, Krabbenhoft et al. 2022, Zimmer et al. 2022). Studying diverse VIEs
1762 across broad ranges of key environmental axes can also be used to learn where, along
1763 environmental continuums, functional thresholds exist that could help with categorizations
1764 important for policy and management (Richardson et al. 2022b).

1765 Cross-VIE understanding of the drivers, patterns, and processes linking inundation to
1766 system responses can greatly improve with increased collaboration and communication across
1767 scientific fields and systems. Our experience is that communities working in VIEs are scattered
1768 across different societies and funding programs. Studying VIEs together via ~~the continuum~~
1769 ~~approach~~unifying conceptual models tied to environmental continuums, can bring these science
1770 communities together. To this end, we encourage training and collaborations focused on
1771 consistent data generation methods that may be adopted across the VIE community and in
1772 pursuit of ~~the continuum approach~~.conceptual unification. In addition, disciplinary conferences
1773 could also recognize VIE commonalities with special sessions to bring people together from
1774 across the VIE continuum to discuss research needs.

1775 Cross-VIE knowledge and models are needed to address human impacts to environments
1776 across the globe. Humans both directly (i.e., dams, weirs, surface water and groundwater
1777 abstraction, channelization, draining, invasive species introduction and spread, etc.) and
1778 indirectly (i.e., climate change) alter VIEs. (Maris et al. 2016, Pumo et al. 2016, Kiss et al. 2019).
1779 As climate change and other anthropogenic impacts increasingly alter these already dynamic
1780 systems, it is imperative that knowledge and models transcend VIEs. Future environmental
1781 change can alter the position of a given VIE within environmental space, including what is
1782 depicted in our conceptual model (Fig. 4213) (e.g., by increasing frequency of storm surges
1783 changing the inundation return interval). The ability to predict impacts of such environmental
1784 change can be facilitated by mechanistic knowledge that is transferable across the
1785 environmental space occupied by VIEs. We hypothesize that use of the continuum approach
1786 proposed hereunifying VIEs across environmental continuums, can be an effective approach to
1787 achievinghelp achieve, this mechanistic, transferable knowledge.

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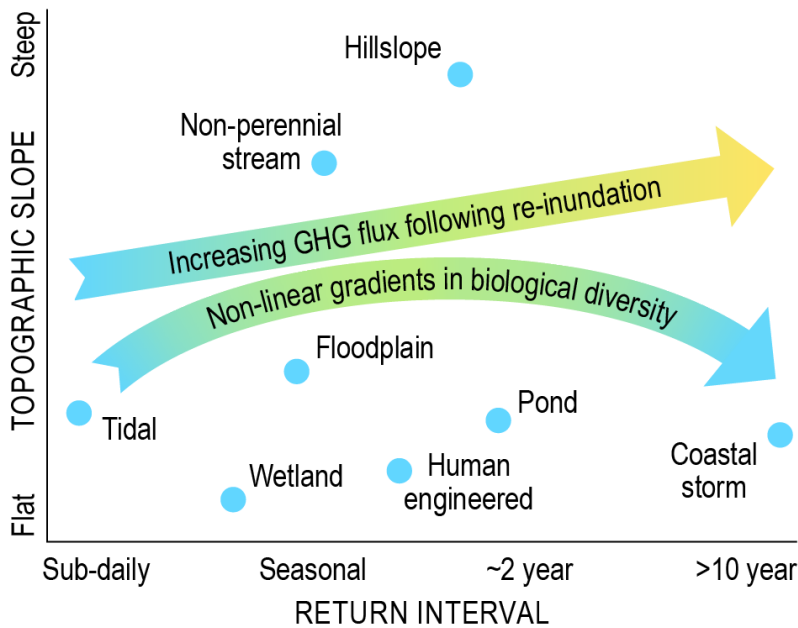
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1790 **Figure 4213.** We encourage a continuum perspective for VIE science whereby unifying
 1791 conceptual models of VIEs based on hypotheses linked to continuous environmental
 1792 axes, across which these systems are can be studied across broad ranges of key
 1793 controlling variables, without regard for what system names may be attached to a given
 1794 studied place and time. Two potential axes In our proposed conceptual model, two key are
 1795 topographic slope and inundation return interval. Points represent approximate locations of
 1796 where each VIE type may lie. Each VIE type spans a range of slopes and inundation return
 1797 intervals, but we do not define these ranges as the continuum perspective conceptual model is
 1798 based on how study systems fall across the environmental space represented here, rather than
 1799 within specific nomenclature. Two priority research directions are greenhouse gas (GHG) fluxes
 1800 and biological diversity, and the arrows represent possible hypotheses that could be evaluated
 1801 with cross-VIE studies. We propose that knowledge and models that are transferable across
 1802 VIEs can be achieved through evaluation of such hypotheses across broad environmental
 1803 extents tied to key environmental variables, such as ranges in slope and return interval. Credit:
 1804 Nathan Johnson.

1805
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1817
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