Reviews and Syntheses: Variable Inundation Across Earth's Terrestrial Ecosystems

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Journal: EGU Biogeosciences
Type of Manuscript: Reviews & Synthesis

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Abstract

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

Introduction

The chemical and biological processes within terrestrial ecosystems hinge on the presence, residence time, volume, and chemistry of water~~.~~ (Schimel et al. 1991, Lohse et al. 2009, Arias-Real et al. 2024). A variety of factors influence water retention, infiltration, flow, and ~~flow~~surface expression within an ecosystem, such as land surface relief, topographic slope, subsurface permeability, evapotranspiration, and human-based modifications of the landscape~~.~~ (Horton 1940, Ribolzi et al. 2011, Appels et al. 2016, McGrane 2016, Orozco-López et al. 2018, McDowell et al. 2023). Water supply is most commonly 'top down' in the form of precipitation and overland flow or 'bottom up' due to rising water tables and transient saturation in the subsurface ~~(Smith et al. 2017).~~(Freeze 1974, Smith et al. 2017, Stewart et al. 2019). Inundation, however, may also occur from lateral inputs, as is common in tidal systems, or from upslope inputs, as in floodplains. Regardless of where water comes from, ~~inundation~~its expression at the land-atmosphere interface occurs when the rate of water supply is greater than the rate of export via infiltration, evapotranspiration, and runoff~~.~~ (Tromp-van Meerveld and McDonnell 2006).

~~Here we define inundation as occurring when there is a near continuous aqueous barrier 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 km^2, 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 km^2, 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 1995)~~**1**). 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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Inundation dynamics are changing due to increased variability and magnitudes of precipitation and evapotranspiration, accelerated sea level rise, and human modifications to the Earth's land surface, including an increase in extreme events ~~(Konapala et al. 2020, Li et al. 2022a). Extreme events such as coastal flooding are increasingly frequent, and while seasonal drying of streams is now more common (Sweet et al. 2014, Zipper et al. 2021), some streams are shifting from non-perennial to perennial (Döll and Schmied 2012, Datry et al. 2018a) while others have fewer no-flow days than they did historically (Zipper et al. 2021). Wetland inundation extent, duration, and seasonal timing are also projected to be altered by climate change (Londe et al. 2022a). Thus, the dynamics of inundation are changing in different ways across different VIEs (Zipper et al. 2021) such that we cannot rely exclusively on historical dynamics to predict future impacts (e.g., on species diversity) of changing inundation dynamics (Culley et al. 2016, Quinn et al. 2018, Rameshwaran et al. 2021, Li et al. 2022b)~~(Konapala et al. 2020, Li et al. 2022a). For example, extreme events such as coastal inundation are increasingly frequent (Vitousek et al. 2017). However, inundation patterns are changing in different ways across different VIEs (Zipper et al. 2021, Londe et al. 2022). For example, in river systems seasonal drying is becoming more common in multiple biomes (Sweet et al. 2014, Zipper et al. 2021). While some rivers are shifting from non-perennial to perennial (Döll and Schmied 2012, Datry et al. 2018a) and others have fewer no-flow days than they did historically (Zipper et al. 2021). Divergence in the direction of change, with some systems inundating less and others inundating more, is likely linked to diverse drivers of change associated with changing climates and/or direct human impacts (Datry et al. 2023). Therefore, researchers and decision makers cannot rely exclusively on historical trends to predict future impacts (e.g., on species diversity) of changing inundation dynamics (Culley et al. 2016, Quinn et al. 2018, Rameshwaran et al. 2021, Li et al. 2022b).

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

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

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

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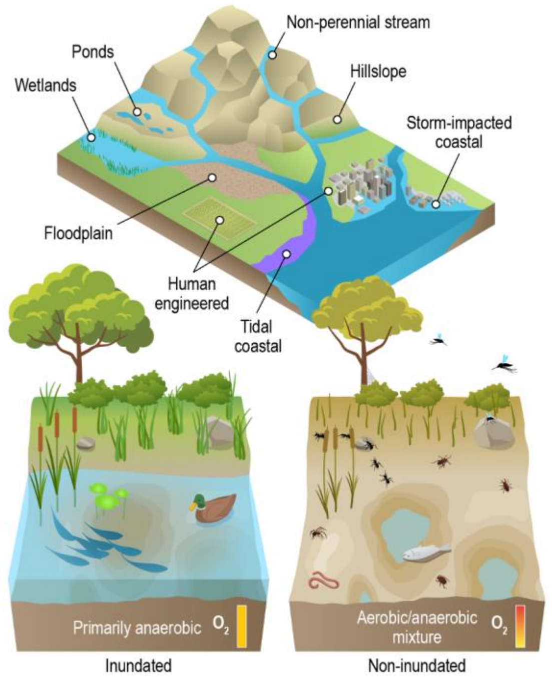

Figure 2. ***Conceptual overview of where different types of VIEs are ~~commonly~~often found within watersheds and some common shifts in system states across inundated and non-inundated conditions.*** *VIEs are found from headwaters to coastal environments (Top) and the impacts of variable inundation 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.*

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

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

~~During inundated periods, biogeochemical processes in VIEs often shift from a dominance of aerobic respiration during drier periods to a diverse suite of anaerobic processes, such as methanogenesis (Datry et al. 2018b, Hondula et al. 2021b). Changes in the frequency of inundation events change the dynamics of dry-wet, hot-cold, and aerobic-anaerobic transitions (Valett et al. 2005). Such dynamics can challenge existing theories. For example, while rates of soil respiration are expected to peak under aerobic conditions, periodic anaerobic conditions can lead to unexpectedly high rates of soil carbon loss (Huang et al. 2021) and the anaerobic process of methanogenesis can be fastest in well-oxygenated dry soils (Angle et al. 2017). More broadly, variable inundation can alter fluxes of greenhouse gasses to the atmosphere such as the common observation of soil rewetting leading to significant carbon loss arising from sudden intensification of soil respiration (Schimel 2018, Shumilova et al. 2019). Variation in inundation also has large impacts on the global CH$_4$ budget (Zhang et al. 2017, Peng et al. 2022) and rewetting of dry sediment in intermittent streams can contribute considerably to the total CO$_2$ emissions from streams (von Schiller et al. 2019). More generally, top down and bottom up hydrologic inundation events broadly influence biogeochemical cycles (Smith et al. 2017) and can result in hysteretic responses to wetting and drying (Patel et al. 2022).~~

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

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Across VIEs, inundation impacts the structure, composition, and function of vegetation communities. Growth and survival can either increase or decrease with inundation depending on local aridity and the impacts on soil hypoxia. Hypoxia kills roots, leading to reduced water uptake, reduced photosynthesis, mortality (Pedersen et al. 2021, McDowell et al. 2022, Cubley et al. 2023), and shifts in vegetation composition. More broadly, inundation dynamics impact organismal ecology (Datry et al. 2023) across all VIEs, such as herbivores responding to inundation-induced shifts in vegetation (De Sassi et al. 2012). Inundation can also alter arthropod communities leading to reductions in diversity, abundance, and biomass (Plum 2005). Changes at the base of food webs can have further, cascading effects (Chen and Wise 1999).

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

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

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

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

Hillslopes with Surface Runoff

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Hillslopes provide water to lower-lying areas, often concentrating the water in gullies and depressions (**Fig. 3**). Hillslopes produce relatively transient VIE features and may often be seen as extensions of other VIEs, such as hillslope seeps co-located with a wetland or the unchannelized swales that contribute to a non-perennial network. In cold regions, snow, ice and permafrost can create an impermeable layer resulting in near-surface soil being inundated for days to weeks during spring thaw ~~(Coles et al. 2017, Patel et al. 2020).~~(Coles et al. 2017, Patel et al. 2020). In dry regions, intense precipitation that exceeds the local infiltration capacity can result in water ponding on the surface of hillslopes or overland flow generation down hillslopes, which can be exacerbated by initial hydrophobicity of dry soil ~~(Kirkby et al. 2002)~~(Kirkby et al. 2002). Exceeding the infiltration capacity is more likely on hillslopes with low-permeability, such as clay-rich soil or when near-surface soils are frozen. This can be exacerbated by restrictive soil horizons located at shallow depths across hillslopes that generate seasonal perched water tables and lead to inundation ~~(McDaniel et al. 2008).~~(McDaniel et al. 2008). Overland flow can be spatially heterogeneous due to variations in soil characteristics as well as flow accumulation, leading to infiltration or exfiltration along the hillslope ~~(Betson and Marius 1969).~~(Betson and Marius 1969).

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

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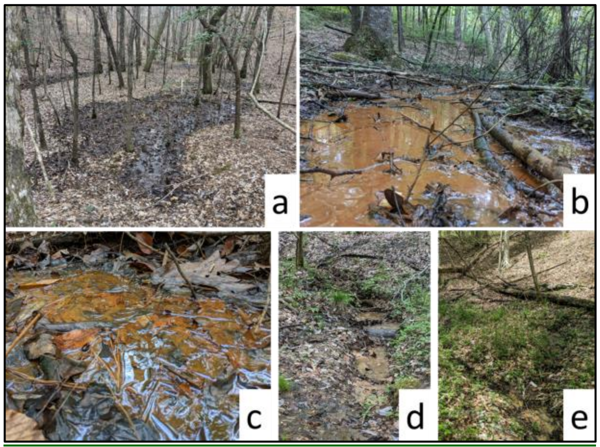

Figure 3. ***Examples of variable inundation along hillslopes.*** *a) looking downslope at an inundated slope; b) ponding with no flow due to microtopography; c) sheet wash with directional flow across the surface of a hillslope; d) rill formation with turbid water from erosion; e) vegetation community 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 (Herndon 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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~~and Li 2020, Stewart et al. 2022). Dry to wet transitions also shift water content and pore space oxygen concentrations (Jarecke et al. 2016, Smyth et al. 2019), often triggering the release of a cascade of solutes produced under anaerobic conditions (Schlesinger and Bernhardt 2020). These entangled, complex interactions among hydrological and biogeochemical processes often challenge the differentiation of individual processes and mechanistic understanding on how variable inundation regulates flow paths, reactions, stream chemistry, and solute and gas export fluxes (Li et al. 2021)~~Shallow soils in hillslopes have abundant organic materials and nutrients (Herndon 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 and Li 2020, Stewart et al. 2022). Dry to wet transitions also shift water content and pore space oxygen concentrations (Jarecke et al. 2016, Smyth et al. 2019), often triggering the release of a cascade of solutes produced under anaerobic conditions (Schlesinger and Bernhardt 2020). These entangled, complex interactions among hydrological and biogeochemical processes often challenge the differentiation of individual processes and mechanistic understanding on how variable inundation regulates flow paths, reactions, stream chemistry, and solute and gas export fluxes (Li et al. 2021).

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

Non-Perennial Streams

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

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~~material to downstream systems (Allen et al. 2020)~~(Busch et al. 2020), are ubiquitous and comprise 50-60% of the global river length (Messager et al. 2021). These systems occur across all continents and biomes (Messager et al. 2021). Streamflow in non-perennial streams ranges from nearly perennial (year-round) flow, to seasonal flow, responding to drivers like snowmelt, to daily or sub-daily flow events responding to rainfall events or evapotranspiration (Price et al. 2021). At the reach scale, non-perennial streams shift between three main states - flowing, ponded/pooled, or no-surface water present (**Fig. 4**). As reaches become hydrologically connected (or disconnected), the spatial footprint/extent of the connected stream network can grow or shrink over sub-daily to seasonal to interannual timescales (Xiao et al. 2019). Spatial and temporal shifts among the three hydrologic states strongly influence the network's capacity to process, transport, and export material to downstream systems (Allen et al. 2020).

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

~~The variable inundation dynamics in non-perennial streams have cascading implications for biogeochemical cycling, water quality, ecosystem function, and community ecology. Under non-flowing conditions, riverbeds are characterized by dry conditions or discontinuous and stagnant water pools, often with high temperatures, low dissolved oxygen levels, and long residence times, functioning more like soils (Arce et al. 2019), as described also in the hillslope section. Pooled, non-flowing conditions can lead to steep redox gradients in the shallow subsurface that drive nutrient processing (Datry and Larned 2008, Gómez-Gener et al. 2021, DelVecchia et al. 2022). During dry/non-flowing states, terrestrial organic matter accumulates in the channel and is subjected to varying degrees of breakdown (Datry et al. 2018c, Del Campo et al. 2021). Rewetting of accumulated substrates can stimulate microbial activity, nutrient attenuation (Saltarelli et al. 2022), and generate pulses of greenhouse gasses such as CO$_2$ and N$_2$O (Datry et al. 2018a, Song et al. 2018). During re-wetting and resumption of flow, non-perennial streams can contain large amounts of terrestrial and aquatic organisms that can be flushed downstream (Corti and Datry 2012, Rosado et al. 2015), with high sediment, dissolved organic carbon, and solutes (Laronne and Reid 1993, Hladyz et al. 2011, Herndon et al. 2018, Wen et al. 2020, Fortesa et al. 2021, Blaurock et al. 2021).~~

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

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

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

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

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The variable inundation dynamics in non-perennial streams have cascading implications for biogeochemical cycling, water quality, ecosystem function, and community ecology. Under non-flowing conditions, riverbeds are characterized by dry conditions or discontinuous and stagnant water pools, often with high temperatures, low dissolved oxygen levels, and long residence times, functioning more like soils (Arce et al. 2019), as described also in the hillslope section. Pooled, non-flowing conditions can lead to steep redox gradients in the shallow subsurface that drive nutrient processing (Datry and Larned 2008, Gómez-Gener et al. 2021, DelVecchia et al. 2022). During dry/non-flowing states, terrestrial organic matter accumulates in the channel and is subjected to varying degrees of breakdown (Datry et al. 2018c, Del Campo et al. 2021). Rewetting of accumulated substrates can stimulate microbial activity, nutrient attenuation (Saltarelli et al. 2022), and generate pulses of greenhouse gasses such as CO_2 and N_2O (Datry et al. 2018a, Song et al. 2018). During re-wetting and resumption of flow, non-perennial streams can contain large amounts of terrestrial and aquatic organisms that can be flushed downstream (Corti and Datry 2012, Rosado et al. 2015), with high sediment, dissolved organic carbon, and solutes (Laronne and Reid 1993, Hladyz et al. 2011, Herndon et al. 2018, Wen et al. 2020, Fortesa et al. 2021, Blaurock et al. 2021).

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Compared to their perennial counterparts, non-perennial streams have received less research and monitoring attention and tend to be undervalued relative to ecological/functional performance of perennial streams (Palmer and Hondula 2014). As such, many of the pressing research needs in non-perennial streams are limited by data availability (Van Meerveld et al. 2020, Zimmer et al. 2022). Non-perennial streams are systematically under-represented in global gaging networks (Messager et al. 2021, Krabbenhoft et al. 2022), leading to major gaps in our understanding of the timing, magnitude, and duration of flow in diverse non-perennial streams. In addition, our ability to predict the onset or cessation of flowing periods is limited by a lack of gaging. Infrequent grab sampling for water chemistry tends to undersample non-perennial streams specifically, leading to an even greater paucity of biogeochemical data from

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Major challenges and opportunities include accurate mapping of non-perennial streams and accurate predictions of flow timing at annual, seasonal, and shorter time scales across scales. Headwaters, which are small, numerous, and often non-perennial (Kampf et al. 2021), are difficult to map and understand hydrologically, leading to knowledge gaps in the hydrological integrity of ecosystems at regional scales (Benstead and Leigh 2012, Dugdale et al. 2022). While challenges remain, the use of drones and thermal infrared remote sensing could connect field observations with modeling to better understand the hydrology of these valuable systems (Dugdale et al. 2022). In addition to mapping issues, limited time series data makes predictions of flow in terms of duration, frequency, and spatial extent challenging. How the timing and frequency of flow will change under climate change remains an open question. It is expected that an increased frequency and duration of droughts will shift streams toward more non-perennial flow states (Döll and Schmied 2012). In contrast, flow permanence may increase in select areas where streams are fed by melting glaciers or snowpack, or where anthropogenic intervention occurs (Datry et al. 2023). The changing frequency of extreme flow events and rapid no-flow/high-flow oscillations also have the potential to further alter streamflow, biogeochemical processes, and organismal ecology in non-perennial streams, necessitating further integrated hydro-biogeochemical studies in these dynamic systems.

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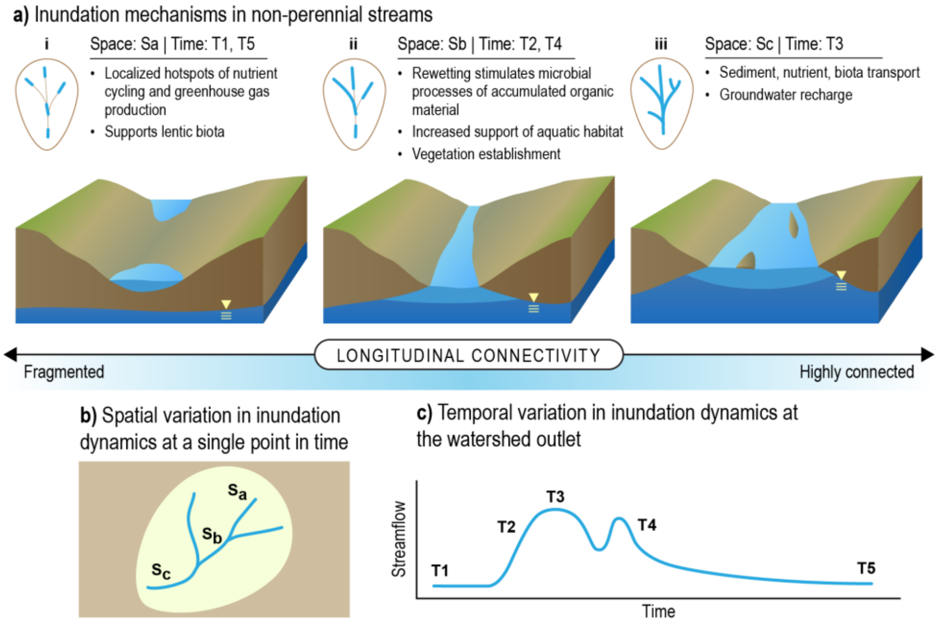

Figure 4. ***Conceptual model of variable inundation in non-perennial streams.*** *a) Water connections between groundwater, near surface, and surface regions at locations within a given network result in varying degrees of longitudinal connectivity with associated biogeochemical processes. b) At a single snapshot in time, water connections result in spatial variation in surface water inundation. c) Under time varying flow states, extent of surface inundation will also vary at a given location. Inundation mechanisms depicted in a) represent a losing system that is transitioning to a flowing state. We acknowledge that in some systems, a low flow fragmented state also occurs in gaining streams with locally connected groundwater. Spatial variation is signified by Sa - Sc and temporal variation is signified by T1 - T5. Credit: Nathan Johnson.*

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

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

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

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

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

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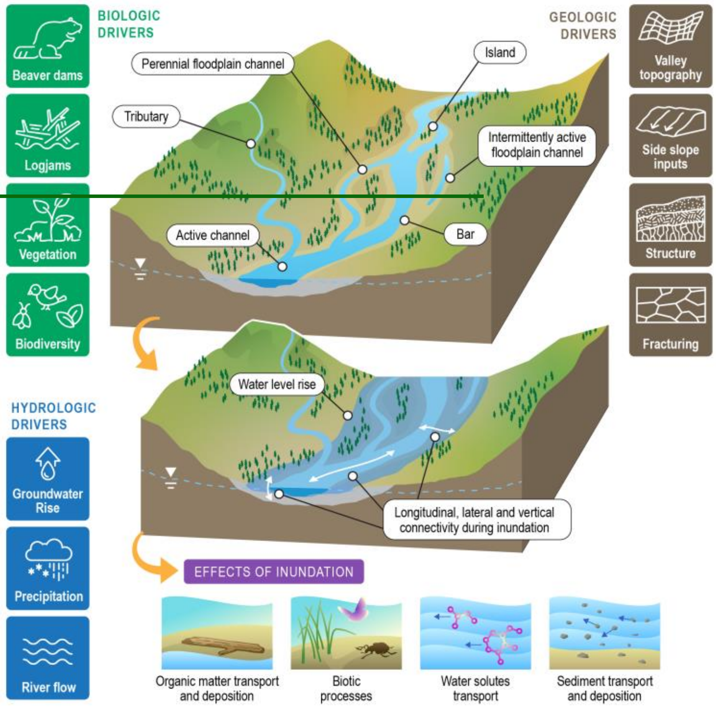
parafluvial zones to adequately represent the physical complexity of variable inundation processes at broad scales, and (ii) developing floodplain/parafluvial functional groups [e.g., ~~(Fryirs and Brierley 2022)~~(Fryirs and Brierley 2022)] that can facilitate understanding of scaling and transferability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



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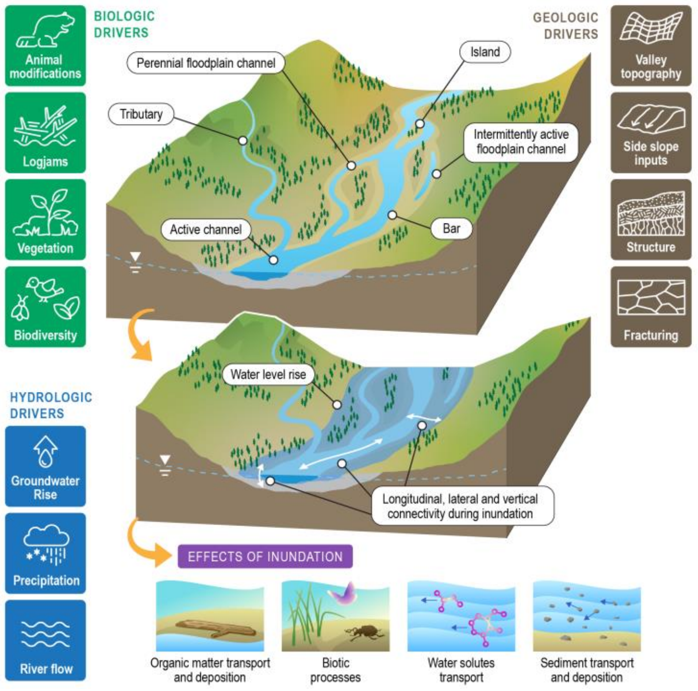

Figure 5. ***Conceptual model of variable inundation in floodplain and parafluvial systems.*** *Across floodplains and parafluvial zones a suite of biological, hydrologic, and geologic factors drive inundation regimes in terms of spatiotemporal duration, timing, depth, flow rate, etc. These systems include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

Variably Inundated Wetlands

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

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~~criteria: soil type, hydrophytic vegetation and hydrology (Cowardin and Golet 1995). Alternatively, hydrogeomorphic classification systems propose to exclusively draw on physical drivers, such as geomorphology, hydrology and substrate to allow for cross-site comparisons of biota and serve functional assessments (Brinson 1993, Semeniuk and Semeniuk 1995, 2011, Davis et al. 2013)~~(Arias-Real et al. 2024). Here we focus primarily on wetlands that are similar to swamps, marshes, and bogs (**Fig. 6**). Wetlands cover about 10% of the global land area, and nearly half of global wetland area (46%) is temporarily inundated (Davidson et al. 2018). Generally, wetland inundation regimes are shaped by the wetland's connectivity to surface and subsurface hydrologic sources and landscape position (Åhlén et al. 2022). The landscape position of wetlands is a first order indicator of the water source and chemistry, ranging from headwater depressional locally-fed wetlands, to flow-through and fringing wetlands to groundwater-fed low-lying wetlands (Fan and Miguez-Macho 2011, Tiner 2013). Wetland typologies applied in several national inventories generally rely on a combination of three criteria: soil type, hydrophytic vegetation and hydrology (Cowardin and Golet 1995). Alternatively, hydrogeomorphic classification systems propose to exclusively draw on physical drivers, such as geomorphology, hydrology and substrate to allow for cross-site comparisons of biota and serve functional assessments (Brinson 1993, Semeniuk and Semeniuk 1995, 2011, Davis et al. 2013).

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

The spatial scales of variable inundation are shaped both by wetland size and geomorphology. Wetlands can be shallow over large spatial scales, and thus the size of variably inundated wetland area can range from microtopographic (i.e., hummock/hollow, ~m^2 scales) to larger ecosystem scales. Large wetland areas, especially in the tropics, experience strong seasonal inundation cycles which depend on changes in water balance and local topography ~~(Zhang et al. 2021). While the largest variably inundated wetlands are connected to floodplains, like the 130,000 km^2 Pantanal (Ivory et al. 2019), non-floodplain wetlands surrounded by upland (also known as geographically isolated wetlands) as large as ~6 ha may also experience whole-system drying and rewetting (Lane and D'Amico 2016)~~(Zhang et al. 2021). While the largest variably inundated wetlands are connected to floodplains, like the 130,000 km^2 Pantanal located in Brazil and extending into Bolivia and Paraguay (Ivory et al. 2019), non-floodplain wetlands surrounded by upland (also known as geographically isolated wetlands) as large as ~6 ha may also experience whole-system drying and rewetting (Lane and D'Amico 2016).

~~Embedded within wetland ecosystems, microtopographic structures can create within-system mosaics of inundation regimes. Microtopography in peaty wetlands is particularly pronounced, ranging from several tens of meters [e.g., ridges and sloughs (Larsen et al. 2011)] to meters [e.g. hummock-hollows (Shi et al. 2015)]. These spatial patterns result from dynamic~~

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~~feedbacks between ecological processes (e.g. peat accumulation) and hydrology that reinforce these patterns (Belyea and Baird 2006, Eppinga et al. 2008, Larsen et al. 2011).~~

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

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

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

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

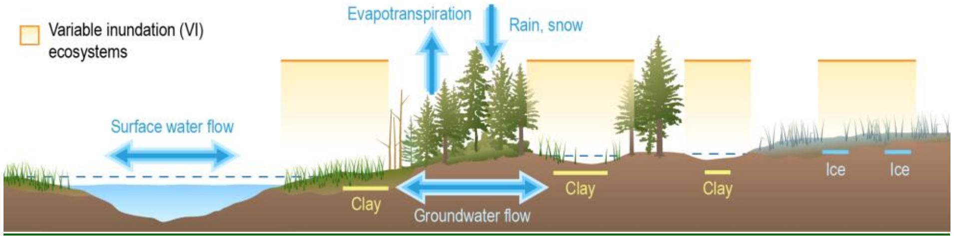

Figure 6. ***Conceptual model of variable inundation in wetland systems.*** *Different wetland types are influenced and shaped by variable inundation. Absence and presence of surface water is driven by (e.g., seasonally) changing water supply and the hydrologic function of the wetland in the landscape.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

Freshwater Ponds

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

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~~techniques (Hayashi et al. 2016, Calhoun et al. 2017, Hill et al. 2021)~~(Davidson et al. 2018, Hill et al. 2021). Ponds are generally small (less than 5 ha) and shallow (less than 5 m), and consequently, are highly sensitive to changes in water levels that can result in highly variable inundation regimes (Gendreau et al. 2021, Richardson et al. 2022a). Pond ecosystems are extremely diverse, and include arctic thermokarst ponds, prairie potholes, vernal pools, playas, rock pools and agricultural dugouts. The numbers of ponds globally are likely underestimated, as their size and ephemeral/temporary nature has meant they are often excluded from physical inventories and they are below the resolution of many remote sensing techniques (Hayashi et al. 2016, Calhoun et al. 2017, Hill et al. 2021).

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

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

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

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

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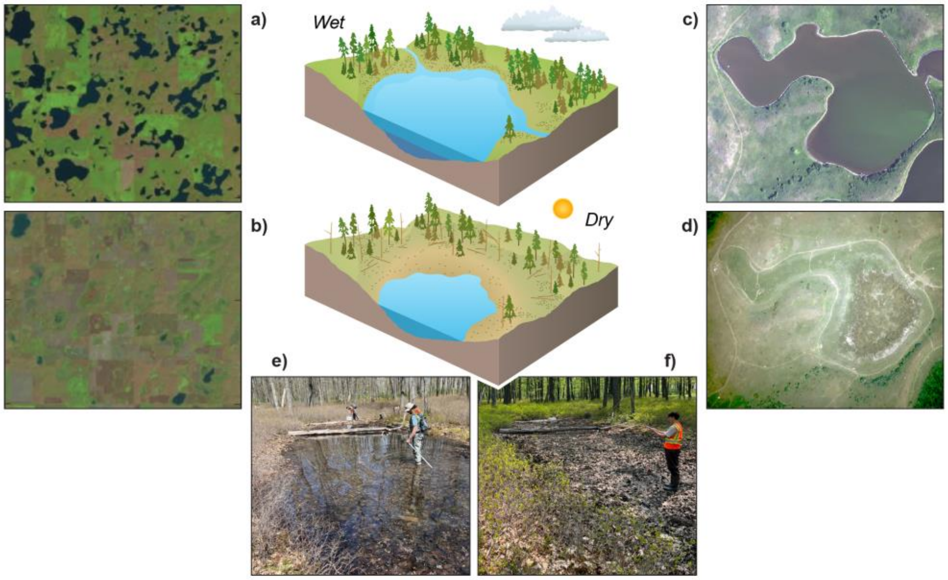

Figure 7. ***Examples of variable inundation across scales in pond systems.*** *Satellite imagery of the Prairie Pothole Region, North Dakota, USA illustrating decadal variable inundation at a landscape scale a) September 2, 1992; b) May 23, 2013 [modified from ~~(Scientific Investigations Report 2015)~~(Scientific Investigations Report 2015)] and at the pond scale; Aerial Imagery of Pond P1, Cottonwood Lake Study Area, North Dakota c) September, 2002 d) September, 1992 (Images from ~~(U.S. Geological Survey 2017).~~(U.S. Geological Survey 2017). Seasonal changes in a vernal pond in Moshannon State Forest, Pennsylvania, USA) inundated (May 11, 2023) non-inundated (May 23, 2023) (J.N. Sweetman). Conceptual drawings by Nathan Johnson.*

Storm-Impacted Coastal Zones

The coastal zone includes ecosystems and communities (cities/towns) that are adjacent and hydrologically connected to a large water body (e.g., ocean, Great Lakes). These systems influence, are impacted by, and are dependent on coastal zone hydrologic processes, such as ~~flooding, that occur at the interface between terrestrial and aquatic domains. Unlike tidal environments, inundation that affects the coastal zone is driven by temporary, often stochastic events including storms, seiches, and king tides. Depending on the topography of the area, infrastructure of the community, and size of the event, the size of coastal inundation varies from event to event (both geographic impact and aerial extent of inundation; **Fig. 8**). The frequency of these events ranges from multiple times a season to decadal (**Fig. 8**). Tropical storms and cyclones develop in tropical regions during seasonal periods of warm water each year. Due to their high energy and movement, they influence more temperate regions as well (Colbert and Soden 2012). In temperate or cold regions, storms develop in the winter time due to large temperature differences between land and ocean (Liberato et al. 2013). Natural systems will display some form of resilience and recovery to storm impacts (Lugo 2008, Wang et al. 2016), but human settlements and infrastructure are vulnerable to both intense winds and flooding (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, flooding~~inundation, that occur at the interface between terrestrial and aquatic domains. Unlike tidal environments, inundation that affects the coastal zone is driven by temporary, often stochastic events including storms, seiches, and king tides. The impact and areal extent of coastal inundation varies across events, depending on topography, infrastructure, and event size (**Fig. 8**). The frequency of these events ranges from multiple times a season to decadal (**Fig. 8**). Tropical storms and cyclones develop in tropical regions during seasonal periods of warm water each year. Due to their high energy and movement, they influence more temperate regions as well (Colbert and Soden 2012). In temperate or cold regions, storms develop in the winter time due to large temperature differences between land and ocean (Liberato et al. 2013). Natural systems will display some form of resilience and recovery to storm impacts (Lugo 2008, Wang et al. 2016), but human settlements and infrastructure are vulnerable to both intense

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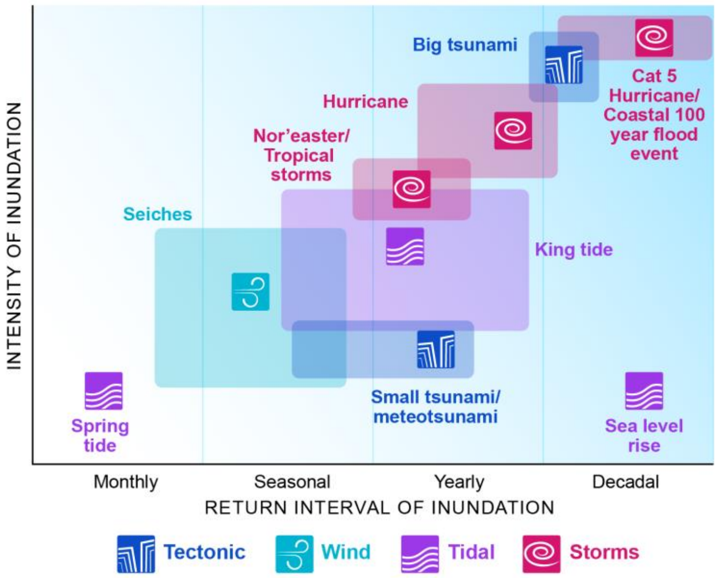

Figure 8. ***Coastal VIEs experience inundation events with different frequencies and intensities.*** *Some events occur rarely, but are very high intensity events (category 5 hurricanes; large tsunamis), increasing the area of inundation and affecting areas that seldom experience ~~flooding~~inundation. 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.*

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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 (Cantelon et al. 2022) quality and mobilizes nutrients through porewater ionic~~

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~~exchange processes (Herbert et al. 2018). Coastal zone inundation as a natural process alters dune systems, which generates a mosaic of habitats that increase biodiversity (Smith et al. 2021) and alter distributions of vegetation and animals. For example, the frequency of overwash events affects plant composition and diversity on sand dunes (Stallins and Parker 2003) and regular inundation is thought to provide necessary habitats for some insects and birds (Smith et al. 2021). Increased salinity and associated geochemical changes alter microbial community diversity and population heterogeneity (Nelson et al. 2015), shifting to more specialized communities as an adaptation to anaerobic conditions, redox fluctuation, and salt stress. Previous studies found high variability in relationships between salinity and ecosystem carbon dioxide fluxes (Morrissey and Franklin 2015, van Dijk et al. 2015, Dang et al. 2019, Hopple et al. 2022)~~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 (Cantelon et al. 2022) quality and mobilizes nutrients through porewater ionic exchange processes (Herbert et al. 2018). Coastal zone inundation as a natural process alters dune systems, which generates a mosaic of habitats that increase biodiversity (Smith et al. 2021) and alter distributions of vegetation and animals. For example, the frequency of overwash events affects plant composition and diversity on sand dunes (Stallins and Parker 2003) and regular inundation is thought to provide necessary habitats for some insects and birds (Smith et al. 2021). Increased salinity and associated geochemical changes alter microbial community diversity and population heterogeneity (Nelson et al. 2015), shifting to more specialized communities as an adaptation to anaerobic conditions, redox fluctuation, and salt stress. Previous studies found high variability in relationships between salinity and ecosystem carbon dioxide fluxes (Morrissey and Franklin 2015, van Dijk et al. 2015, Dang et al. 2019, Hopple et al. 2022).

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

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~~While we understand many of the linkages between the ecology, biogeochemistry, hydrology, and geomorphology that regulate ecosystem structure and function in coastal systems (Fagherazzi et al. 2012, Hinshaw et al. 2017, Braswell and Heffernan 2019, Cantelon et al. 2022), we know little of how to predict the future effects of the interacting stressors associated with climate change (O'Meara et al. 2017, Ward et al. 2020, Arrigo et al. 2020). Our ability to predict is reliant on our understanding of shifting inundation regimes in the context of elevated~~ ~~CO_2~~~~, nutrient pollution, and coastal development which can generate antagonistic, synergistic, or additive effects. These knowledge gaps stem from the dynamic and unpredictable nature of events that drive coastal inundation. Observational data to inform~~

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

~~Tidally Driven Coastal Zones~~

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

~~Tidally-driven coastal zones are inundated semi-diurnally (i.e., twice a day) or diurnally (i.e., once a day). Unlike VIE systems summarized above, where inundation events may be difficult to predict, inundation in tidally-driven coastal zones varies primarily based on predictable drivers. For example, high tide and low tide water levels dictate the spatial extent and duration of inundation. In addition, intra-annual tidal dynamics are largely controlled by lunar cycles which drive approximately monthly highest (spring) and lowest (neap) tides, as well as annual high (king) and low tides. Inter-annual tidal dynamics are linked to sea level rise, which is shifting the zone of variable inundation inland (Ensign and Noe 2018, Tagestad et al. 2021)~~While we understand many of the linkages between the ecology, biogeochemistry, hydrology, and geomorphology that regulate ecosystem structure and function in coastal systems (Fagherazzi et al. 2012, Hinshaw et al. 2017, Braswell and Heffernan 2019, Cantelon et al. 2022), we know little of how to predict the future effects of the interacting stressors associated with climate change (O'Meara et al. 2017, Ward et al. 2020, Arrigo et al. 2020). Our ability to predict is reliant on our understanding of shifting inundation regimes in the context of elevated CO_2, nutrient pollution, and coastal development which can generate antagonistic, synergistic, or additive effects. These knowledge gaps stem from the dynamic and unpredictable nature of events that drive coastal inundation. Observational data to inform mechanistic models is limited and governed by where and when events happen (not necessarily within monitored sites), funding periods, and accessible coastlines. This difficulty is exacerbated by the fact that 40% of the world's population lives within 100 km of the coast (Maul and Duedall 2019), which heightens social impacts of variable inundation while also adding logistical difficulty to coastal monitoring. When events do overlap with instrumented sites, the extreme nature of inundation events threaten the physical integrity of instrumentation. Lastly, high-latitude coastlines are also susceptible to coastal inundation, yet few models incorporate physical, biogeochemical, and ecological implications of inundation on permafrost bound coastlines and environments (Ekici et al. 2019, Bevacqua et al. 2020). Opportunities of critical knowledge advancement exist in 1) monitoring events through *in-situ* or remotely sensed monitoring data, 2) model development that integrates more robust process-based understanding, and 3) expansion into urban and permafrost-bound coastlines.

Tidally Driven Coastal Zones

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

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

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

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

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

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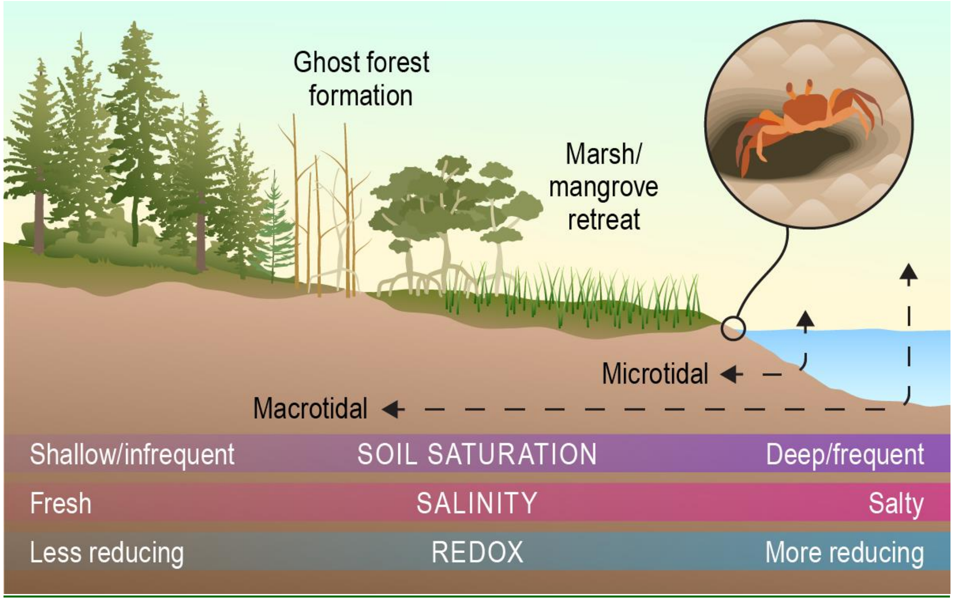

Figure 9. ***Conceptual model of variable inundation in tidal systems.*** *Tidally driven coastal zones span sediments exposed at low tide to marshes and coastal forests inundated at high tide. This lateral gradient of tidal exposure ~~is characterized by gradients in vegetation and soil characteristics,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

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Human-Engineered Systems

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

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

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

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

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

Including human-engineered systems in our conceptualization of VIEs emphasizes the growing significance of these systems as human landscape modifications continue to alter and eliminate natural VIEs. Recent efforts have synthesized the role and impacts of human-engineered VIEs at large scales (Peacock et al. 2021, Li et al. 2022b) but, as with many natural systems, the majority of studies on human-engineered VIEs are based in North America and Europe (González et al. 2015, Zhang et al. 2018, Bertolini and da Mosto 2021). Thus, our knowledge may not reflect the social, political, and economic challenges of developing areas where the highest rates of VIE modification are occurring (Wantzen et al. 2019). The knowledge gaps surrounding human-engineered VIEs will become increasingly important to address as global change continues to alter the spatial and temporal patterns of inundation. Given that human-engineered VIEs can enhance or disrupt hydrologic connectivity, they potentially magnify the effects of human driven changes such as sea level rise and impacts of contamination from anthropogenic "chemical cocktails" (Kaushal et al. 2022). We lack a baseline standard for how human-engineered VIEs function in the landscape, even as global change continues to shift existing baselines [e.g., (Palmer et al. 2014)]. A baseline understanding would also enable the restoration and repurposing of engineered VIEs as nature-

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

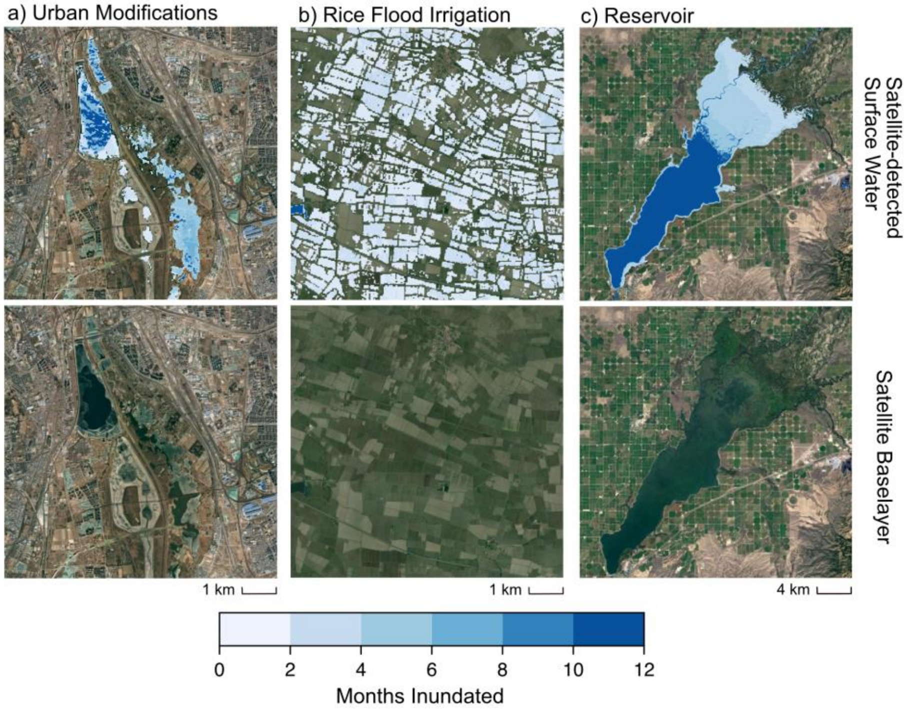

Figure 10. ***Examples of human-engineered Variably Inundated Ecosystems.*** *a) Yongding River in Beijing, China; b) Paddy rice fields in northern Italy; c) American Falls Reservoir on the Snake River in Idaho, United States. These three examples emphasize significant variation in the degree of variable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

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Inundation Processes are Relevant at the Scale of the Beholder

VIEs span broad spatiotemporal scales of variable inundation, from ~~microenvironments like~~small wetlands and vernal ponds to the floodplains of the world's largest rivers. While examples in the mini-reviews focus on eight different ecosystems, variably inundated ecosystems are even broader such as mosses and pore spaces that are periodically covered by droplets of water~~, to~~ and vast endorheic lakes and rivers. Inundation volumes and surface areas of VIEs vary by at least sixteen orders of magnitude, from under 10^{-3} L to over 10^{13} L ~~(https://www.k26.com/lake-eyre-papers-lake-eyre-basics).~~(Bonython and Mason 1953), and 10^{-6} m^2 to over 10^{10} m^2 ~~(https://www.guinnessworldrecords.com/world-records/92443-largest-ephemeral-lake),~~(Hess et al. 2015), respectively. The duration of inundation varies by up to eight orders of magnitude, spanning a few seconds, in the case of droplets, to decades, in the case of endorheic lakes, and centuries in the case of sea level rise. Non-inundated periods likewise span seconds to centuries and longer. This variability in spatial and temporal extent has profound consequences for the ecology and biogeochemistry of VIEs. This section highlights the importance of considering scale and explores hypotheses regarding how scale drives variability in drivers, processes, and impacts across VIEs and how we study them.

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

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

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

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

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

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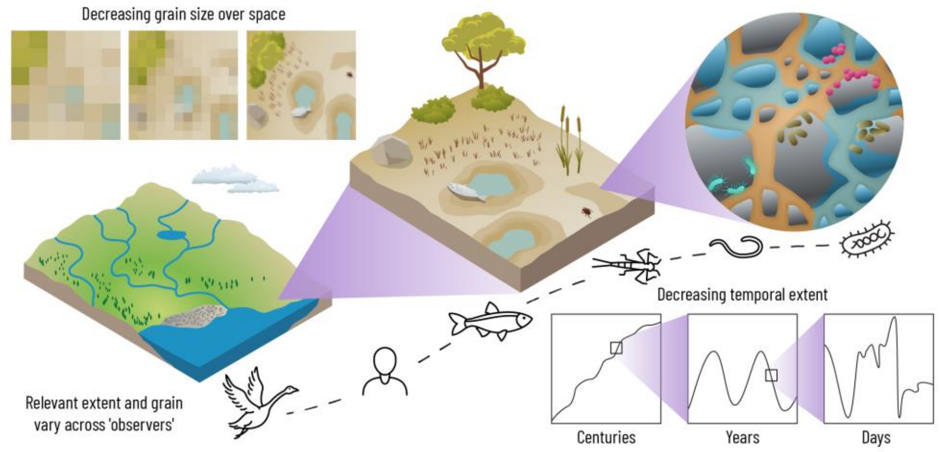

Figure 11. ***Variable inundation can be observed at different spatiotemporal granularities and extents.*** *(Upper left) Granularity is based on the resolution of observations in space or time. (Lower right) Extent is based on the cumulative breadth of observations in space or time. (Middle panels)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

Summary of Primary Methods used to Study VIEs

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

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

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ratios, including compound specific analyses) are commonly used to study organismal, population, and community ecology across multiple taxa [e.g., ~~(Ode et al. 2016, Gates et al. 2020)] and can be standardized for both inundated and non-inundated states. There is increasing use of crowdsourcing for biogeochemical characterization to consistently obtain samples across diverse systems (von Schiller et al. 2019, Garayburu-Caruso et al. 2020). Sample collection can be followed by a variety of laboratory measurements of properties (e.g., carbon content, redox potential and redox-active elements, microbial genetic potential, sediment grain size) and processes, such as CO$_2$ production and methanogenesis related to variable inundation. Point-scale measurements often operate at instantaneous to daily scales. Conversely, larger scale measurements integrate across finer-scale processes to quantify ecosystem dynamics and properties, but without necessarily revealing the governing the processes. Spatially distributed monitoring networks using *in situ* sensors (e.g., the United States Geological Survey, USGS, gage network) can connect event-scale responses across hydrologically linked locations as well as reveal long-term trends [e.g., (Zipper et al. 2021)]. Long-term field manipulations are another complementary *in situ* technique that can reveal mechanisms underlying system responses to changes in inundation state. There are numerous configurations of such experiments that directly or indirectly impact inundation dynamics, such as intentional inundation (Hopple et al. 2023), water exclusion (Kundel et al. 2018) and heating (Hanson et al. 2017)~~(Ode et al. 2016, Gates et al. 2020)] and can be standardized for both inundated and non-inundated states. There is increasing use of crowdsourcing for biogeochemical characterization to consistently obtain samples across diverse systems (von Schiller et al. 2019, Garayburu-Caruso et al. 2020). Sample collection can be followed by a variety of laboratory measurements of properties (e.g., carbon content, redox potential and redox-active elements, microbial genetic potential, sediment grain size) and processes, such as CO$_2$ production and methanogenesis related to variable inundation. Point-scale measurements often operate at instantaneous to daily scales. Conversely, larger scale measurements integrate across finer-scale processes to quantify ecosystem dynamics and properties, but without necessarily revealing what governs those processes. Spatially distributed monitoring networks using *in situ* sensors (e.g., the United States Geological Survey, USGS, gage network) can connect event-scale responses across hydrologically linked locations as well as reveal long-term trends [e.g., (Zipper et al. 2021)]. Long-term field manipulations are another complementary *in situ* technique that can reveal mechanisms underlying system responses to changes in inundation state. There are numerous configurations of such experiments that directly or indirectly impact inundation dynamics, such as intentional inundation (Hopple et al. 2023), water exclusion (Kundel et al. 2018) and heating (Hanson et al. 2017). Despite the plethora of data produced by such large scale projects, these are expensive and require deep buy-in of researchers and landowners.

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

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

Remote sensing can complement *in situ* measurements to facilitate more spatially continuous characterization of surface water dynamics and their impacts. There are different types of remote sensing techniques, from drones to satellites and optical to microwave sensors, that can capture different aspects of VIEs. For example, soil surface saturation may be captured by a passive microwave radiometer as well as C and L-band radar backscatter, which can also penetrate through thin canopies, clouds, and through the top few centimeters of the soil (Schumann and Moller 2015). Recent satellite missions such as the Surface Water and Ocean Topography (SWOT) mission provide increased capabilities for monitoring changes in surface water over time with radar data (Biancamaria et al. 2016), while NASA's forthcoming NISAR mission will allow for detection of inundation even under tree canopy. Thermal infrared measurements can indirectly reveal saturation at very high spatiotemporal resolutions, as well as evapotranspiration associated with water table depth, soil moisture, and rooting depth (Fisher et al. 2020, Lalli et al. 2022). Long time series from moderate resolution (~30 m) optical satellites can document multi-decadal open water trends and seasonal regimes across the globe (Pekel et al. 2016), while some combinations of indices have shown success in detecting mixed vegetation and inundation cover (Jones 2019). Commercial satellite constellations provide daily global imagery at < 4 m resolution, enabling monitoring of more dynamic water bodies [e.g., Arctic lakes, (Cooley et al. 2017) and forested wetlands (Hondula et al. 2021a)]. Deep groundwater and changes in the total water column storage are detectable through measurements of gravitational anomalies at very high precision but low spatial resolution (Bloom et al. 2010, 2017, Richey et al. 2015, Pascolini-Campbell et al. 2021). Fine-scale inundation dynamics, which have been historically hard to measure, can be captured using unmanned aerial vehicles (UAVs), which are often useful during or immediately after a significant inundation event (Perks et al. 2016), to capture small-scale spatial dynamics that are difficult to detect with satellite or airborne methods (Manfreda et al. 2018, Dugdale et al. 2022), or to derive detailed data for input into hydrologic models and surface water calculations (Acharya et al. 2021).

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Figure ~~11~~12. *Monitoring inundation regimes is increasingly possible via in situ sensors.* *Stream Temperature, Intermittency, and Conductivity Sensors (STICs)* ~~*(Chapin et al. 2014)*~~(Chapin et al. 2014)*, one of the types of increasingly available sensors to measure water presence/absence in an inexpensive and easily deployable manner. These sensors can be used across all types of VIEs. Credit: Amy Burgin.*

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

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

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

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

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

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

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Towards Cross-VIE Transferable Understanding

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

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

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

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

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

While many environmental variables could be used in this conceptual model (**Fig. 13**), here we propose using inundation return interval and topographic slope, as both are well known to impact ecological communities. For example, inundation return interval has been shown to alter plant composition (Arim et al. 2023) and biogeochemical function such as CH_4 fluxes (Batson et al. 2015). We view it as an integrated proxy for variables with direct impacts (e.g., desiccation) that are linked to the temporal scale of non-inundated conditions. The other axis of our conceptual model is topographic slope (**Fig. 13**), which we also view as an integrated proxy, but for variables linked to how much time water spends in a system (Anderson and Burt 1978, McGuire et al. 2005). Slope and the variables it represents ~~a key component of the continuum of inundation regimes and may be considered as a forcing factor. Topographic slope represents a~~ (e.g., water residence time and velocity) are also well known to influence ecological communities (e.g., by altering fish composition, as in (Bain et al. 1988)) and biogeochemistry (e.g., by altering nitrate reductions as in (Gomez et al. 2012)).

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

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

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

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

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

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

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

Cross-VIE knowledge and models are needed to address human impacts to environments across the globe. Humans both directly (i.e., dams, weirs, surface water and groundwater abstraction, channelization, draining, invasive species introduction and spread, etc.) and indirectly (i.e., climate change) alter VIEs~~.~~ (Maris et al. 2016, Pumo et al. 2016, Kiss et al. 2019). As climate change and other anthropogenic impacts increasingly alter these already dynamic systems, it is imperative that knowledge and models transcend VIEs. Future environmental change can alter the position of a given VIE within environmental space, including what is depicted in our conceptual model (**Fig.** ~~12~~13) (e.g., ~~by~~increasing frequency of storm surges changing the inundation return interval). The ability to predict impacts of such environmental change can be facilitated by mechanistic knowledge that is transferable across the environmental space occupied by VIEs. We hypothesize that ~~use of the continuum approach proposed here~~unifying VIEs across environmental continuums can ~~be an effective approach to achieving~~help achieve this mechanistic, transferable knowledge.

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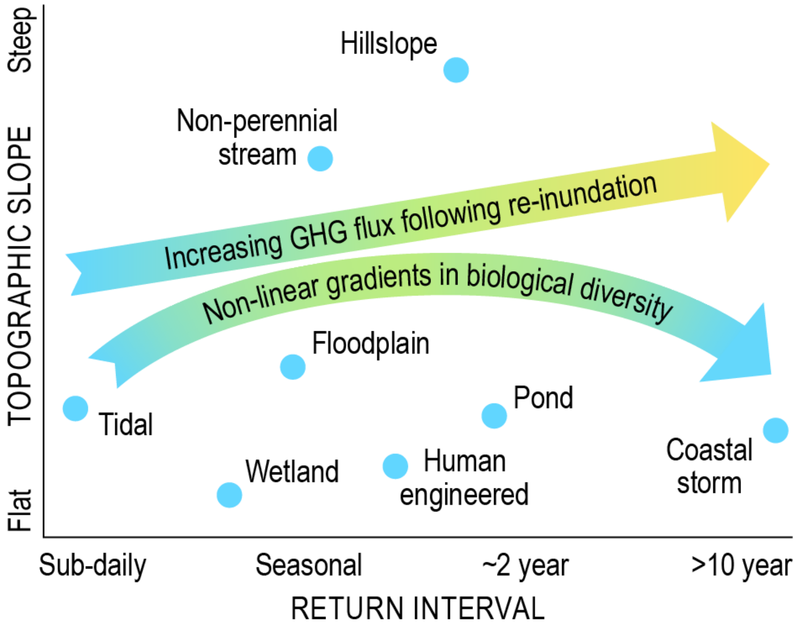

Figure ~~12~~13. ***We encourage ~~a continuum perspective for VIE science whereby~~unifying conceptual models of VIEs based on hypotheses linked to continuous environmental axes, across which these systems ~~are~~can be studied ~~across broad ranges of key controlling variables~~ without regard for what system names may be attached to a given studied place and time.*** *~~Two potential axes~~In our proposed conceptual model, two key are topographic slope and inundation return interval. Points represent approximate locations of where each VIE type may lie. Each VIE type spans a range of slopes and inundation return intervals, but we do not define these ranges as the ~~continuum perspective~~conceptual model is based on how study systems fall across the environmental space represented here, rather than within specific nomenclature. Two priority research directions are greenhouse gas (GHG) fluxes and biological diversity, and the arrows represent possible hypotheses that could be evaluated with cross-VIE studies. We propose that knowledge and models that are transferable across VIEs can be achieved through evaluation of such hypotheses across broad ~~environmental extents tied to key environmental variables, such as~~ranges in slope and return interval. Credit: Nathan Johnson.*

Acknowledgements

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The research described in this paper was supported by the Earth & Biological Sciences Program Development Office at Pacific Northwest National

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Laboratory, a multiprogram national laboratory operated by Battelle for the U.S. Department of Energy. We thank Jon Chorover, Sarah Godsey, Jesus Gomez-Velez, Wei Huang, Roser Matamala, Hyun Song and Kristen Underwood for contributions to the conceptual directions of this manuscript. This manuscript was an outgrowth of the VIE Workshop and we greatly thank the participants for their contributions.

Competing Interests: The authors declare that they have no conflict of interest.

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