

A synthesis of floodplain aquatic ecosystem metabolism and carbon flux using causal criteria analysis

Paul J. McInerney ^{1,2*} Darren P. Giling ^{3,4} Ben Wolfenden,⁵ Ashmita Sengupta⁴

¹CSIRO, Land and Water, Thurgoona, New South Wales, Australia

²Gulbali Institute, Charles Sturt University, Albury, New South Wales, Australia

³Centre for Applied Water Science, Institute for Applied Ecology, Faculty of Science and Technology, University of Canberra, Canberra, Australian Capital Territory, Australia

⁴CSIRO, Land and Water, Canberra, Australian Capital Territory, Australia

⁵New South Wales Department of Planning, and Environment, Parramatta, New South Wales, Australia

Abstract

The transformation of solar energy into organic matter by autotrophs (gross primary production [GPP]) and the use of that energy by autotrophs and heterotrophs (ecosystem respiration [ER]) describe the total energy available to support food webs. Rates of GPP and ER vary with temperature, light, hydrology, nutrients, and organic matter supply and quality yet despite their obvious importance, spatiotemporal variation of metabolic patterns among floodplain habitats, and their relationship to inundation dynamics remain unclear. We set out to review the peer-reviewed literature surrounding the influence of the magnitude, frequency, and duration of floodplain inundation on aquatic ecosystem metabolism and carbon flux by rigorously testing a suite of cause–effect hypotheses using a causal criteria analysis. Causal criteria analysis is a literature synthesis approach developed to address a lack of experimental data and subsequent weak inference of causal relationships. We found support for 3 of the 14 hypotheses we tested relating to putative causal relationships: (1) large floods transfer more carbon from floodplains to the river channel than small floods via the increase in inundation area leading to more overall leaching of floodplain litter, (2) in high turbidity floodplain habitats rates of GPP are reduced by restrictions to photic depth, and (3) a positive correlation between nutrients and GPP—generally GPP in floodplain wetlands increases with nutrient levels. We obtained inconsistent evidence for a causal relationship between macrophytes and aquatic GPP, with studies reporting both a negative influence from decreased light caused by macrophyte shading and a positive influence from structural support provided by macrophytes for periphyton growth. For the remaining 10 hypotheses, there was insufficient evidence to support causal relationships, including for any hypotheses relating to frequency or duration of floodplain inundation. Our results emphasize that despite an apparent wealth of metabolic studies in riverine ecosystems, floodplain metabolic dynamics remain poorly studied, likely due to less investment and increased difficulty compared to lotic waters. The review also highlighted aspects of floodplain aquatic ecosystem metabolism for which there are significant knowledge gaps in the literature, in particular metabolic responses to inundation frequency and duration. Our results call attention to the importance of site specificity and temporal changes when predicting putative cause–effect relationships between floodplain inundation and metabolic patterns.

*Correspondence: paul.mcinerney@csiro.au

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Additional Supporting Information may be found in the online version of this article.

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Regulation of rivers to meet human needs has led to riverine flow regimes that are intrinsically different in character from their natural state, resulting in a wide range of modifications to structure and function of aquatic ecosystems (Reid et al. 2019). In light of these changes to flow regimes, there is a requirement for a comprehensive understanding of quantitative aquatic ecosystem responses to various types and degrees of flow alteration when managing environmental flows (*see* Brisbane Declaration 2007) for rivers and their floodplains (Poff and Zimmerman 2010). One pervasive hydrological change is the disconnection of rivers from their floodplains. River regulation has resulted in a reduced frequency and

magnitude of overbank flow events (Higgsion et al. 2020), degrading wetlands that are critical sites for the maintenance of biodiversity and ecosystem functioning (Kingsford 2000). Therefore, understanding the complex relationship between the functioning of floodplains and rivers has enormous implications for managing flows to maximize benefits for a broad suite of aquatic biota (e.g., the Flood Pulse Concept, Junk et al. 1989).

A fundamental aspect of ecosystems is the generation of new biomass via photosynthesis—the process by which solar energy, water, and carbon dioxide are transformed into reduced carbon compounds that sustain life and form the basis of food webs (Odum 1956). This creation of organic matter by autotrophs is termed as gross primary production (GPP) and the subsequent mineralization of that organic matter by autotrophs and heterotrophs in the system collectively is called ecosystem respiration (ER) (Allan et al. 2021). Net ecosystem production (NEP) is the difference between GPP and ER and specifies how much carbon accrues (ecosystem is autotrophic) or is depleted (ecosystem is heterotrophic). In floodplain wetlands, aquatic GPP is performed by submerged vascular plants, phototrophic bacteria, and by algae (planktonic, benthic and epiphytic), all of which compete for light and nutrients (Wetzel and Ward 1996; Staehr et al. 2012). Metabolic rates govern the supply and transfer of energy through food webs (Bernhardt et al. 2018). Although rates of GPP and ER are not direct estimates of animal energy dynamics, ecological theory and empirical evidence imply that these rates of metabolism and animal secondary productivity are correlated in aquatic ecosystems (Rüegg et al. 2021).

In aquatic environments ecosystem metabolism can be calculated from diel changes in dissolved oxygen that reflect both physical (e.g., reaeration from the atmosphere) and biological processes (e.g., GPP and ER). Aquatic ecosystem metabolism is sensitive to environmental controls (Izagirre et al. 2008) and responds rapidly to organic matter supply and quality, temperature, light, hydrology, and nutrients (Bernhardt et al. 2018). This sensitivity, coupled with recent advances in sensor technology and software, has underscored the utility of ecosystem metabolism as an integrative measure of whole-ecosystem functioning, and the approach is increasingly used in environmental monitoring programs (Jankowski et al. 2021).

Aquatic ecosystem metabolism in floodplain and wetland habitats has received far less attention than in perennial streams and rivers or lakes. In lotic habitats the water column is generally well mixed, such that a single probe can provide a composite sample of activity taking place in the whole ecosystem. In contrast, lentic waters are prone to stratification and spatial heterogeneity in metabolic rates (Giling et al. 2017; Julian et al. 2021), particularly so in floodplain wetlands, where depth, aquatic and terrestrial plant associations, and riverine connectivity are highly dynamic (Shen et al. 2016). These challenges can be addressed in part by the sampling

approach (e.g., benthic chambers or light and dark bottles in specific habitats; Holland et al. 2020), but whole of ecosystem estimates can be difficult to accurately calculate. Consequently, there is less information surrounding aquatic ecosystem metabolism and carbon flux in river floodplains.

As agencies seek to quantify the benefits of environmental flows, and to improve administrative strategies via adaptive management, there is a requirement for quantitative estimates of productivity to inform the development of expected environmental outcomes from management interventions. Approaches that assume that floodplain productivity is largely a function of inundated area, with consistent rates of production in space and time, are likely to be inaccurate given the high level of structural and functional spatial heterogeneity of floodplain wetlands (Molinari et al. 2021). Conceptually, the floodplain landscape can be considered as a mosaic of habitats used by biota at different temporal and spatial scales under various flooding regimes (Ballinger and Mac Nally 2006). Larger flood inundation extents may inundate a greater variety of habitats, creating a more heterogeneous mosaic of physicochemical conditions and concentrations of abiotic resources (e.g., nutrients) for both autotrophs and heterotrophs. Temporal patterns of inundation are also critical. Evidence from intermittent river channels suggests the drying and rewetting of sediments can lead to highly variable metabolic rates (Bernhardt et al. 2018), with aquatic production of course ceasing and instead fueling the terrestrial food web when the water disappears (Ballinger and Mac Nally 2006). Despite ongoing research exploring controls of riverine and terrestrial metabolism (Bernhardt et al. 2022) and development of new remote sensing techniques to estimate floodplain productivity (Ndehedehe et al. 2021), our understanding of the complex relationship between floodplain inundation (e.g., magnitude, frequency, and duration) and spatiotemporal variation in aquatic metabolic dynamics remains poor.

To derive quantitative relationships among the magnitude, frequency, and duration of floodplain inundation and aquatic ecosystem metabolism and carbon flux, and to identify current knowledge gaps to inform future research, we systematically reviewed the literature using a causal criteria analysis. Causal criteria analysis is a literature synthesis method developed to deal with a lack of experimental data (and subsequent weak inference of causal relationships) and was first used in epidemiological research (Hill 1965; Weed 1997). Since then, causal criteria analysis has been used for the assessment of ecological hypotheses that may be relatively weak on their own, but collectively, can compose robust arguments of causality, which can be tested against multiple criteria (Miller et al. 2013; McInerney et al. 2016a). Causal criteria analysis does not require the extraction of effect size information and the subsequent conversion to a standard scale for statistical analysis required for quantitative meta-analysis (Webb et al. 2011), and performs well as an analytical tool when data are limited (Fabricius and De'ath 2004). Due to the dearth of

empirical studies that examine floodplain metabolic dynamics and the difficulty demonstrating causality in ecology more broadly due to a lack of replication, natural variation, confounding factors, and restrictions to experimental design, causal criteria analysis represents a useful tool for our investigation.

Here, we test assumptions surrounding floodplain carbon processing dynamics. We develop a conceptual model of hypothesized cause–effect relationships relating to floodplain inundation and metabolic responses and test these relationships using evidence from the literature with a defensible technique that weights evidence based on the strength of the study's design. Three causal linkages for floodplain carbon processing dynamics were identified that generated 10 hypotheses for inundation magnitude, 2 hypotheses for inundation duration, and 2 hypotheses relating to inundation frequency. Using causal criteria analysis, we synthesize patterns of floodplain aquatic ecosystem metabolism and carbon flux and explore the implications for riverine productivity at broad spatial scales.

Methods

Causal criteria analysis

The causal criteria analysis method tests evidence items against a series of criteria and can be used to construct a case for causality through the cumulative strength of evidence items (Greet et al. 2011). Unlike meta-analysis, which synthesizes studies to determine an overall effect size associated with a given treatment, causal analysis provides a clear, repeatable, approach to quantify (putative) cause–effect linkages (Norris et al. 2012). The causal criteria analysis was applied using Eco Evidence, a freely available eight-step framework that includes an online database of evidence and supporting software (Norris et al. 2008; Norris et al. 2012) (available from <https://toolkit.ewater.org.au>). The method requires the reviewer to first define the overarching question being addressed and associated context, before developing a conceptual model of hypothesized cause–effect relationships. Our overarching question was “How does inundation influence floodplain carbon flows?”

The cause–effect hypotheses then guide the reviewer through a systematic literature review to extract “evidence items” from studies that link a putative cause (in this case floodplain inundation) to reported effects. Multiple “evidence items” may be sourced from each individual primary research study with each item classified according to relevant criteria, including the specific cause and effect relationships from the conceptual model, the nature of association between them (including its trajectory—increase (↑), decrease (↓), change (Δ), no change (NC), and the experimental design and replication; Nichols et al. 2011).

Following extraction, the evidence items relating to each hypothesized cause and effect relationship (ecological

responses) are weighted and synthesized (Norris et al. 2012). Each evidence item is weighted according to the study design (“Spatial gradient,” “Temporal gradient,” “Before–After,” “Control–Impact,” “Before–After/Control–Impact [BACI],” or “After–impact only”) and the number of independent control and impact sampling units. Weights range from 1 to 10, with studies that better control for confounding variables or with greater replication receiving higher scores (weights applied in this analysis are provided in Supporting Information Table S1). These individual weights are summed for all evidence items that support a given hypothesis and for all evidence items that refute the hypothesis. The two sums are compared to a default threshold value of 20 points that defines the point at which sufficient evidence for (or against) the hypothesis exists to give adequate support for (or against) the presence of a causal relationship (Norris et al. 2008). The threshold (and study weights) may be varied by the user, but such changes need to be documented with sufficient justification, and here we apply the default values following (Greet et al. 2011). Although collation of evidence in favor of the hypothesis with a total sum of study weights of 20 or more is deemed as providing support for a cause–effect relationship, if a summed study weight of 20 or more for studies that do not show support for the hypothesis is also attained, it represents a lack of consistency for the cause–effect association (possible causal criteria analysis outcomes and their interpretation are provided in Supporting Information Table S2). Thus, causal criteria analyses result in one of four conclusions: support for hypothesis, support for alternate hypothesis, inconsistent evidence, and insufficient evidence (Nichols et al. 2011).

Literature review method

We developed a conceptual model of aquatic carbon processing on inundated floodplains that identifies 14 relevant and testable hypotheses drawn from assumptions commonly used to explain metabolic patterns in floodplain wetlands (Fig. 1). All hypotheses refer to the cause (floodplain inundation), while the effect varies for each hypothesis, acknowledging the interdependence of many hypotheses. We separated our hypotheses into three broad aspects of floodplain inundation: (1) magnitude, (2) duration, and (3) frequency. Hypotheses relating to magnitude and duration describe short-term or single events while hypotheses relating to frequency describe long-term or decadal inundation patterns. Following the methods outlined by Eco Evidence, we generated 14 hypotheses (H1–H14, Fig. 2).

The scope of the review was confined to published, peer-reviewed studies that investigated ecosystem metabolism and carbon flux in floodplain habitats, and riverine studies were excluded. The one exception to this rule was for inclusion of some Australian arid zones studies that investigated non-flowing riverine pools, since these habitats more closely resemble floodplain wetland systems when disconnected. Studies from all geographic regions were considered, although

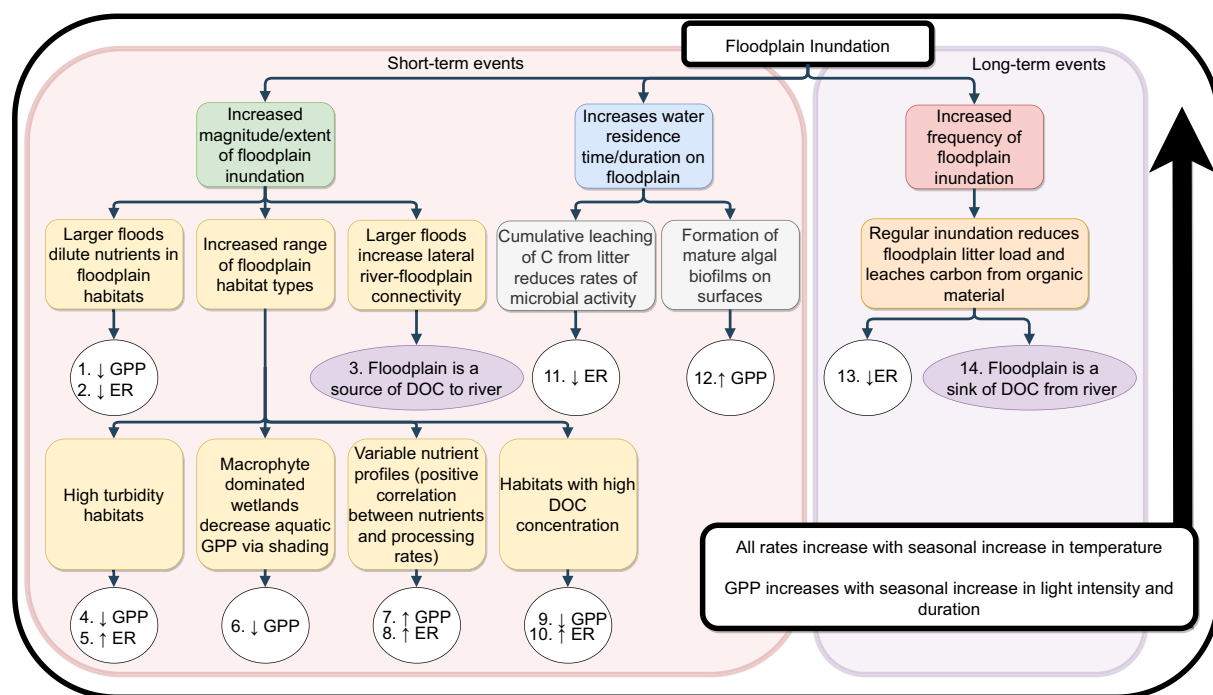


Fig. 1. Putative causal relationships among flood magnitude, duration, and frequency and effects on floodplain aquatic metabolism with hypotheses to be tested (\uparrow = increase, \downarrow = decrease).

marine and tidal/estuarine studies were excluded. Search terms (Table 1) specific to each hypothesis were entered into Web of Science (09 August 2020). Searches returned between 80–390 hits depending on the hypothesis under review. It was not feasible to review every study uncovered and after reading titles and abstracts of the first 100 items for each hypothesis, we found that < 5% were relevant to the search topic among items 90–100. As such, we confined our search to the first 100 studies returned from the Web of Science search for each hypothesis. Many studies that were returned from our search criteria explored terrestrial productivity rather than aquatic responses and a great many more focused on metabolic dynamics of flowing waters or large lakes, which we also dismissed. Although our literature search identified more than 2000 studies with potentially useful information, filtering reduced that number to less than 50 studies that provided useable evidence items meeting our criteria for inclusion. Final filtering returned 41 peer-reviewed publications, providing 55 individual evidence items that contributed to the testing of our 14 hypotheses.

Results and discussion

We found evidence to support 3 hypotheses, inconsistent evidence for 1 hypothesis, and insufficient evidence to support our remaining 10 hypotheses (Table 2). Individual study weights are provided in the Supporting Information (Table S3). The evidence used in this study is available for reuse from the Eco Evidence database (<https://toolkit.ewater.org.au>). Some studies provided evidence for multiple

hypotheses and the evidence points for and against our hypotheses are provided in Table 2. A summary of quantitative relationships between causal linkages and floodplain aquatic metabolism is provided in Table 3, and a detailed summary of results from individual studies is provided in Supporting Information Appendix S1.

Causal linkages relating to inundation magnitude are as follows.

Larger floods dilute nutrients in floodplain habitats H1–H2

With only three studies providing evidence for H1 and H2 combined, there was insufficient evidence to support our hypotheses that larger floods dilute nutrients on floodplains, leading to lower rates of GPP and ER in aquatic habitats. Patterns in nutrient delivery among the studies were highly context dependent and related to the nutrient profiles of the adjacent rivers delivering flood waters and the antecedent nutrient status of wetlands prior to flooding. For example, two studies described how large floods diluted floodplain wetland nutrient concentrations (Lindholm et al. 2007; Weilhoefer et al. 2008) while the other described how nutrients and inorganic matter from large floods elevated the nutrient status of floodplain habitats (Gallardo et al. 2012). Lindholm et al. (2007) reported that significantly lower concentrations of nutrients in a large flood resulted in an almost 50% reduction in floodplain GPP compared to a small flood. Similarly, Weilhoefer et al. (2008) reported that high-magnitude floods in North American river diluted floodplain wetland nutrient

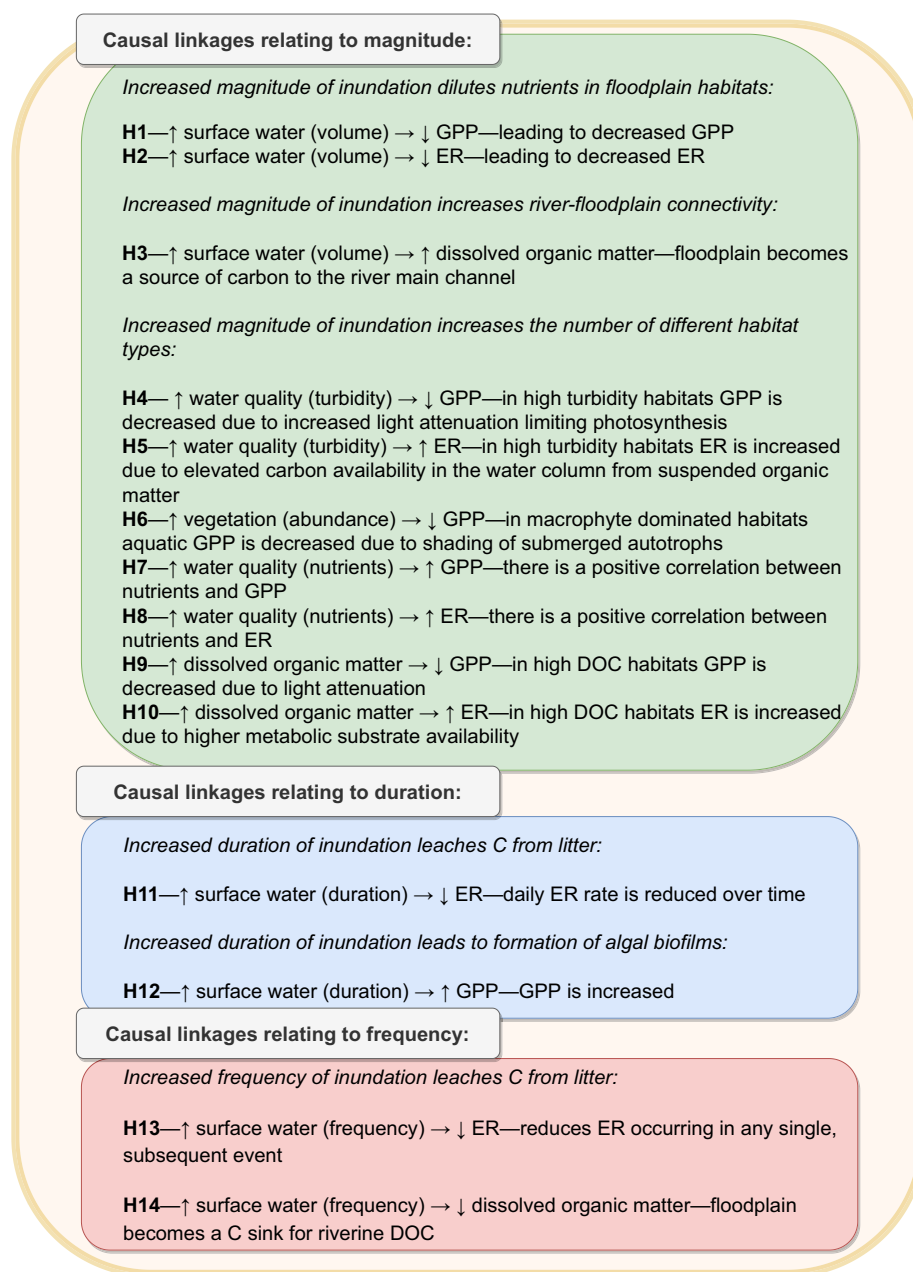


Fig. 2. Hypotheses generated for effects of flood magnitude, duration, and frequency on floodplain aquatic metabolism.

concentrations, leading to a reduction of algal production. In contrast, in a European river system Gallardo et al. (2012) reported that increases in floodplain lake nutrients following a large flood led to rates of NEP well above stable conditions. Gallardo et al. (2012) also provided evidence in refutation of H2, reporting that the input of organic matter and nutrients caused by the river flood was likely responsible for fueling heterotrophic consumption and increasing respiration rates. The low number of studies and the high variability in patterns suggest that more empirical field studies are required to better understand the relationship between the magnitude of floodplain inundation, nutrients and metabolic responses.

Larger floods increase DOC export to the river channel H3

There was sufficient evidence in the literature to support our hypothesis that larger floods increase DOC export to the river channel, with 14 out of 15 evidence items supporting our hypotheses. The primary mechanism by which this occurred was via the increase in inundation area leading to more overall leaching of floodplain litter, increasing DOC concentration of floodwaters and the subsequent carbon-rich water returning from the floodplain to the river (Baldwin et al. 2013; Wolfenden et al. 2018). We expect the pattern to be magnified in ecosystems where floodplain litter generation is high (Nielsen et al. 2016) and indeed, much of the literature

Table 1. Terms used to implement literature searches, targeting 14 hypothesized effects of flood magnitude, duration, and frequency on floodplain aquatic metabolism.

Effect (hypotheses)	Search terms TS = ((floodplain OR “temporary wetland” OR “ephemeral wetland” OR wetland OR riparian) AND (“metabolism” OR “primary producti*” OR “GPP” OR “community respiration” OR “CR” OR “ecosystem respiration” OR ER) AND (flow OR flood OR flooding OR “environmental flows” OR “environmental water” OR inundation))	Web of Science literature search hits
H1—↑ surface water (volume) → ↓ GPP	AND (magnitude OR dilution OR nutrients))	392
H2—↑ surface water (volume) → ↓ ER	AND (magnitude OR dilution OR nutrients))	
H3—↑ surface water (volume) → ↑ dissolved organic matter	AND (magnitude OR “dissolved organic carbon”))	172
H4—↑ water quality (turbidity) → ↓ GPP	AND (magnitude OR turbidity))	101
H5 - ↑ water quality (turbidity) → ↑ ER	AND (magnitude OR turbidity))	
H6—↑ vegetation (abundance) → ↓ GPP	AND (magnitude OR macrophytes OR shading))	194
H7—↑ water quality (nutrients) → ↑ GPP	AND (magnitude OR nutrients))	386
H8—↑ water quality (nutrients) → ↑ ER	AND (magnitude OR nutrients))	
H9—↑ dissolved organic matter → ↓ GPP	AND (magnitude OR “dissolved organic carbon” OR “light attenuation”))	174
H10—↑ dissolved organic matter → ↑ ER	AND (magnitude OR “dissolved organic carbon” OR leaching))	191
H11—↑ surface water (duration) → ↓ ER	AND (duration OR leaching OR labile))	125
H12—↑ surface water (duration) → ↑ GPP	AND (duration OR “algae biomass”))	80
H13—↑ surface water (frequency) → ↓ ER	AND (frequency OR litter))	143
H14—↑ surface water (frequency) → ↓ dissolved organic matter	AND (frequency OR “dissolved organic carbon”))	164
	Total	2122

that provided evidence for this hypothesis was focused on river systems where elevated DOC from floodplains has led to hypoxic blackwater events that have resulted in fish mortality (Howitt et al. 2007; Whitworth et al. 2012). Although strong relationships among litter loads, floodplain inundation area, and DOC concentration in adjacent rivers have been established, the dynamic relationships between antecedent conditions and flooding frequency and the ability to predict responses are an active area of research. Our review has demonstrated that this hypothesis was well represented in the literature, and we are confident that an increase in flood magnitude will generally lead to increased export of carbon to the river channel in floodplain rivers. Here, we provide support for one aspect of the Flood Pulse Concept (Junk et al. 1989), finding strong evidence that floodplains can be a source of dissolved carbon for river channels.

Increased habitat heterogeneity H4–H10

For hypotheses 4–10, we assumed that larger floods increase the number of different habitat types (Fig. 1) simply by increasing wetted area. We acknowledge this may not always be the case, but since inundation magnitude is one mechanism by which the number of habitat types may be increased, we proceeded to test putative causal linkages of a range of

likely habitat variables that can influence aquatic metabolic dynamics. Evidence for how GPP and ER respond in different floodplain habitats that generate distinct biotic and abiotic conditions was variable and highly context specific, with enough evidence to support two hypotheses (H4 and H7), inconsistent evidence for one hypothesis (H6), and insufficient evidence for the remaining four hypotheses.

Influence of turbidity on ecosystem metabolism H4–H5

Five studies conducted in Australia, United States, and Canada provided enough evidence to support our hypothesis that photic depth limitation in high turbidity habitats reduces GPP, with only one study providing evidence not in favor of this hypothesis. Although many studies have shown clear relationships between turbidity and GPP in riverine ecosystems (Roach et al. 2014; Hall et al. 2015; Honious et al. 2021), and light strongly influences rates of autotrophic production, direct comparisons in floodplain ecosystems are less studied, possibly due to problems associated with high spatial variation and stratification within lentic waters making accurate measurement difficult (Van de Bogert et al. 2007). Despite finding few studies that examine turbidity–GPP relationships in floodplain habitats, we found sufficient evidence in the literature to support this hypothesis, suggesting that H4 can be applied to

Table 2. Summary of the number of evidence items and the weight of evidence either supporting or refuting our 14 testable hypotheses.

Inundation driver	Causal linkage	Number of evidence items	Evidence points		Conclusion	Support for hypothesis	Support for alternative hypothesis
			Supporting hypothesis	Refuting hypothesis			
Magnitude	H1—↑ surface water (volume) → ↓ GPP	3	16	6	Insufficient evidence	Lindholm et al. (2007), Weilhöfer et al. (2008)	Gallardo et al. (2012)
	H2—↑ surface water (volume) → ↓ ER	1	0	6	Insufficient evidence		Gallardo et al. (2012)
	H3—↑ surface water (volume) → ↑ dissolved organic matter	15	94	6	Support for hypothesis	Baldwin et al. (2013), Fellman et al. (2013), Howitt et al. (2007), Nielsen et al. (2016), Preiner et al. (2008), Rees et al. (2020), Robertson et al. (1999), Tockner et al. (1999), Vorobyev et al. (2019), Wallace and Furst (2016), Whitworth et al. (2012), Wolfenden et al. (2018), Zuijgeest et al. (2015, 2016)	Maynard et al. (2014)
Duration	H4—↑ water quality (turbidity) → ↓ GPP	6	43	9	Support for hypothesis	Bunn et al. (2003), Fellows et al. (2009), Maynard et al. (2012), Squires and Lesack (2001), Squires et al. (2009)	Squires et al. (2009)
	H5—↑ water quality (turbidity) → ↑ ER	2	15	0	Insufficient evidence	Maynard et al. (2014), Maynard et al. (2012)	
Frequency	H6—↑ vegetation (abundance) → ↓ GPP	9	26	30	Inconsistent evidence	Ahn and Mitsch (2002), Marotta and Enrich-Prast (2015), Squires et al. (2009)	Pettit et al. (2016), Reeder (2011), Squires et al. (2009), Stanley et al. (2003), Thomas et al. (2006), Ward et al. (2016)
	H7—↑ water quality (nutrients) → ↑ GPP	7	41	5	Support for hypothesis	Cronk and Mitsch (1994a,b), Gallardo et al. (2012), Kobayashi et al. (2013), Maynard et al. (2016), Shen et al. (2016)	Alvarez-Cobelas et al. (2011)
Duration	H8—↑ water quality (nutrients) → ↑ ER	3	17	5	Insufficient evidence	Kobayashi et al. (2013), Maynard et al. (2012)	Opsahl (2005)
	H9—↑ dissolved organic matter → ↓ GPP	1	5	0	Insufficient evidence	Martinez et al. (2017)	
Duration	H10—↑ dissolved organic matter → ↑ ER	1	5	0	Insufficient evidence	Martinez et al. (2017)	
	H11—↑ surface water (duration) → ↓ ER	2	7	6	Insufficient evidence	Fuell et al. (2013)	McInerney et al. (2016b)
Frequency	H12—↑ surface water (duration) → ↑ GPP	1	6	0	Insufficient evidence	McInerney et al. (2016b)	
	H13—↑ surface water (frequency) → ↓ ER	2	9	3	Insufficient evidence	Howitt et al. (2007)	Jenkins et al. (2009)
Duration	H14—↑ surface water (frequency) → ↓ dissolved organic matter	2	6	9	Insufficient evidence	Rees et al. (2020)	O'Connell et al. (2000)

Table 3. Summary of quantitative relationships between causal linkages and floodplain aquatic metabolism.

Causal linkages	Empirical values	Source
Nutrient metabolism relationships	50% reduction in GPP attributed to reduction in nutrients; nutrients; 1 mg L ⁻¹ (nitrogen) and 10 µg L ⁻¹ (phosphorous)—GPP; 125 mg C m ⁻³ d ⁻¹ compared to nutrients; 2.5 mg L ⁻¹ (nitrogen) and 1 mg L ⁻¹ (phosphorous)—GPP; 200 mg C m ⁻³ d ⁻¹	Lindholm et al. (2007)
	Mean NEP 292.3 and 119.9 mg O ₂ m ⁻³ h ⁻¹ prior to flooding and 462.8 mg O ₂ m ⁻³ h ⁻¹ after flooding attributed to higher nutrient concentrations. NEP minimum of -33.6 mg O ₂ m ⁻³ h ⁻¹ attributed to a lack of inorganic nutrients. Increase in ER (reflected by decreases in NEP) from ~ 140 to ~ 40 mg O ₂ m ⁻³ h ⁻¹ and ~ 290 to ~ 0 mg O ₂ m ⁻³ h ⁻¹	Gallardo et al. (2012)
	Mean GPP in high nutrient habitats of 69–84 kJ m ⁻² d ⁻¹ compared to 46–73 kJ m ⁻² d ⁻¹ in low nutrient habitats	Cronk and Mitsch (1994a)
	Epiphytic productivity highest in high nutrient habitats; range 2–85 g C m ⁻² yr ⁻¹	Cronk and Mitsch (1994b)
	Positive correlation between nutrients and metabolic rates: TN range; 682.0–14,700.0 mg m ⁻³ , TP ranged 48.0–405.0 mg m ⁻³ , GPP range; 3.7–405.5 mg C m ⁻³ h ⁻¹ (mean 89.4 mg C m ⁻³ h ⁻¹) ER range; 1.5–251.6 mg C m ⁻³ h ⁻¹ (mean 43.2 mg C m ⁻³ h ⁻¹)	Kobayashi et al. (2013)
	Mean GPP range; 6.41–13.69 g O ₂ m ⁻² d ⁻¹ , greatest in high nutrient zones, mean ER range; 4.85–9.79 g O ₂ m ⁻² d ⁻¹	Maynard et al. (2012)
	GPP range; 0.04–49.78 mg O ₂ L ⁻¹ d ⁻¹ variation attributed to nutrients, water depth, salinity, pH, and turbidity	Shen et al. (2016)
	GPP range; 18–186 mg C m ⁻³ h ⁻¹ and not influenced by nutrients	Alvarez-Cobelas et al. (2011)
Turbidity GPP relationships	Elevated turbidity (Secchi depths ranging from 6 to 15 cm) restricted photic depth and limited GPP (e.g., < 90 mg C m ² d ⁻¹ in deep channels)	Bunn et al. (2003)
Macrophyte GPP relationships	Low GPP of 6.66 g O ₂ m ⁻² d ⁻¹ coincident with high turbidity values 116.6 NTU	Maynard et al. (2012)
	100% cover by floating aquatic macrophytes—lowest pelagic chlorophyll <i>a</i> (< 2 µg L ⁻¹) and primary production (< 2.5 mg O ₂ L ⁻¹ d ⁻¹)	Marotta and Enrich-Prast (2015)
	Emergent vegetation; mean GPP = 7.58 g O ₂ m ⁻² d ⁻¹ , open-water wetlands; mean GPP = 6.95 g O ₂ m ⁻² d ⁻¹ , submerged vegetation wetlands; mean GPP = 5.48 g O ₂ m ⁻² d ⁻¹	Reeder (2011)
Litter inundation duration metabolism relationships	Maximum ER obtained after 84 d (~ 1.2–1.7 mg O ₂ g ⁻¹ h ⁻¹), minimum at 300 d	Fuell et al. (2013)
	Maximum GPP obtained after 16 d (3125 mg C m ⁻² d ⁻¹), maximum ER obtained after 16 d (1633 mg C m ⁻² d ⁻¹), minimum on day 7 (266 mg C m ⁻² d ⁻¹) (NB. Trial ended after day 16)	McInerney et al. (2016b)

floodplains generally, regardless of context specific variables. In contrast, there was insufficient evidence to support our hypothesis that higher turbidity elevates rates of ER (H5), with only two studies providing support. Both of these studies were conducted in the same Californian location where high turbidity was caused by inorganic particulate sediment resuspension resulting from wind-induced turbulence and benthic bioturbation that also elevated organic carbon concentration, causing a shift of the system towards heterotrophy (Maynard et al. 2012; Maynard et al. 2014). We expect the nature of this relationship to be highly context dependent and relate strongly to the relative percentage of organic carbon that contributes to turbidity, for example, in habitats or flow events where elevated turbidity is caused mainly by suspended fine inorganic sediments and clays with low organic carbon content, we expect the relationship to be poor.

Influence of macrophytes on GPP H6

Evidence was inconsistent for our hypothesis that shading limits GPP in macrophyte dominated habitats (H6), with three studies in favor and six studies providing evidence not in favor of our hypothesis. There appears to be a balance between the negative influence on aquatic autotrophs of decreased light from macrophyte shading (Ahn and Mitsch 2002; Marotta and Enrich-Prast 2015) and the positive influence of structural support provided by macrophytes for periphyton growth (Ward et al. 2016). The contribution to aquatic GPP by different autotrophic groups (e.g., submerged macrophytes and planktonic, benthic, and epiphytic algae) is dynamic and it is likely that the importance of each driver will co-vary strongly with a range of other variables. For example, Squires et al. (2009) provided evidence both for and against (H6). Squires et al. (2009) reported that in lakes with lower

turbidity macrophyte beds afford more surface area for epiphyton production, but when macrophyte biomass is very high, epiphyton, and phytoplankton production is limited strongly by shading. Squires et al. (2009) demonstrated that epiphytic productivity was dependent on the distribution and biomass of macrophytes, but benthic algae production was regulated by macrophyte shading and inorganic turbidity. Ward et al. (2016) showed that open-water areas without emergent or floating macrophytes contain the greatest abundance of submerged macrophytes and that these areas have the highest periphyton productivity. In contrast, constructed wetlands investigated by Reeder (2011) displayed higher net primary production and GPP in wetlands with emergent vegetation than in open-water wetlands and wetlands dominated by submerged vegetation. Both Thomas et al. (2006) and Stanley et al. (2003) provided evidence that macrophyte presence had a negligible influence on the magnitude of algal production, with the latter study showing that increased macrophyte shading did not significantly change rates of algal GPP up to 98% shade levels. We expect H6 to be highly context specific and to vary widely between individual wetlands and floodplain systems, relating to the type of macrophytes, their structural complexity and the amount of light that they allow to penetrate the water surface, along with water quality parameters such as turbidity and nutrient status. Thus, the high level of context dependency and complexity of responses for H6 suggests that more empirical data might not necessarily lead to support for this hypothesis.

Influence of elevated nutrients on ecosystem metabolism H7–H8

There was strong evidence to support our hypothesis that nutrients regulate GPP (H7), with six studies providing evidence from four continents. Quantitative relationships between nutrients and metabolic rates collated from the literature are supplied in Table 3 and provide useful information for predicting metabolic responses to floodplain inundation. Only one study provided evidence not in favor of our hypothesis for H7, with Alvarez-Cobelas et al. (2011) reporting that nutrients did not influence net primary production which was controlled by different size fractions of phytoplankton biomass at different wetland sites. The authors note that despite nutrients patterns displaying distinct seasonality, the system was hypertrophic due to long-term nutrient additions, and no relationships were found between nutrient concentrations and phytoplankton biomass. However, we believe H7 has low context dependency and can be applied broadly to floodplain ecosystems globally—generally GPP in wetlands increases with nutrients. In contrast, we found less evidence to support relationships between nutrients and ER, with only three studies providing evidence. Kobayashi et al. (2013) showed clear and similar relationships between nutrients and both GPP and ER in non-channel floodplain habitats, although they reported that in floodplain channel habitats metabolic patterns were

best predicted by concentrations in DOC, highlighting a need for more empirical evidence. We did not assess interactions, but it is possible that GPP responses will depend on the relative changes in nutrient and light availability that are caused by inundation events of a particular magnitude, as has been suggested in lake pelagic zones (Kelly et al. 2018).

Influence of elevated DOC concentration H9 and H10

The remaining two hypotheses with causal linkages relating to magnitude concern the influence of elevated DOC concentrations on patterns of metabolism (H9 and H10). We found insufficient evidence for support, with only a single study providing evidence for both hypotheses. Martinez et al. (2017) incubated biofilms in differing concentrations of *Eucalyptus* leachate and measured metabolic responses, providing evidence to support both H9—elevated DOC decreases GPP via decreased light attenuation and H10—elevated DOC increases ER due to more available carbon for microbial activity. Although we found abundant evidence in the literature surrounding the relationship between inundation and litter leaching rates and generation of DOC, few studies explicitly explored patterns of ER in high DOC water. The low number of studies identified in our literature search that provide evidence for this facet of floodplain metabolic dynamics highlights a clear knowledge gap that requires further empirical support.

Causal linkages relating to inundation duration are as follows.

Cumulative leaching of C from litter reduces rates of microbial activity H11

Only two studies provided evidence for our hypothesis that ER decreases with the duration for which litter is inundated (H11), one was in favor (Fuell et al. 2013) and the other provided evidence not in favor of our hypothesis (McInerney et al. 2016b). However, it is likely that incongruent evidence provided by each study pertained to the length of the studies rather than any real discrepancies. For example, Fuell et al. (2013) reported that maximum respiration rates of microbial respiration assays (conducted in the laboratory) of leaves retrieved from wetlands were obtained after 84 d of litter submersion. By 300 d, Fuell et al. (2013) reported that rates declined to a minimum, thus providing evidence that ER declined with duration after 84 d. Despite also examining metabolic dynamics of leaves collected from wetlands in the laboratory, McInerney et al. (2016b) reported that respiration rates did not decline with the time that the leaves were immersed in water, but this study only examined a 16 d inundation duration. The results highlight the difficulty in determining consistent patterns from studies conducted over contrasting temporal and spatial scales and identify a requirement for more empirical field studies that examine the relationship between litter leaching and respiration rates. Results from H11 also identify a need for greater temporal precision when

setting out putative causal linkages and generating hypotheses to test, for example, hypothesis testing of casual linkages relating to duration may need to be more specifically time-bound.

Increased duration of inundation leads to formation of algal biofilms that increase GPP H12

McInerney et al. (2016b) also provided the only evidence that GPP increased with inundation duration (H12) via formation of algal dominated biofilms on leaf surfaces. We expect that GPP will reach a maximum before declining again, but as discussed above, this study was probably not of sufficient length for a maximum to be reached. Although maximum primary productivity of biofilms in rivers has been shown to occur after 29 d of inundation, and after 75 d heterotrophic biofilms begin to dominate (Ryder 2004), our synthesis has shown that there is a lack of information specific to addressing aquatic metabolic variation among floodplain wetlands. The findings emphasize the importance of the temporal resolution of individual metabolic studies when interpreting results. Furthermore, since both studies providing evidence for duration patterns were conducted within a laboratory setting, they highlight a lack of empirical floodplain field data and a need for studies that examine changes in metabolic patterns over longer inundation periods.

Causal linkages relating to inundation frequency are as follows.

Regular inundation reduces floodplain litter load and leaches carbon from organic material H13 and H14

We found insufficient evidence from the literature to support our two hypotheses relating to inundation frequency (H13 and H14), with only four studies providing evidence. The one study in support of H13 by Howitt et al. (2007) does not provide any empirical evidence, but presents a predictive model for water quality during flooding of lowland river forests (as does an updated version of the model, not included as a separate study here—Whitworth and Baldwin 2016). The model assumes that no readily degradable litter remains on the flooded portion of the floodplain at the end of the previous flood and for any flooded area that was not inundated during the previous flood, 1 yr is added to the litter accumulation period, for example, thus more frequent flooding results in less carbon for microbial respiration in subsequent events. The predictive model is compared with empirical water quality data from actual floods and provides an accurate estimation of water quality dynamics, although the authors note that drying and rewetting of litter during subsequent flooding may release additional carbon that would not have been available for leaching without a drying phase between. The remaining study that provided evidence not in favor of H13 did not explicitly measure ER, but used soil carbon as a proxy for ER potential (Jenkins et al. 2009), again highlighting a lack of information relating to putative causal linkages for inundation frequency.

Similarly, for our hypothesis that increased frequency of inundation causes floodplains to become a sink for riverine dissolved organic carbon (H14), only one study provided evidence in support (Rees et al. 2020) and one in refute (O'Connell et al. 2000). The former study provided evidence that a floodplain shifted from being a source of carbon to the river channel to a sink during subsequent flooding, but only examined two floods over a short temporal scale. The latter study by O'Connell et al. (2000) examined the position of litter on floodplain as a proxy for flood history, and also only compared two flooding histories. Here, we identify a clear gap in our knowledge surrounding the impact of flooding frequency on floodplain metabolic dynamics that is also lacking in empirical data.

Conclusions

Although we found strong evidence to support three of our 14 hypotheses, we identified clear knowledge gaps in our understanding for 11 hypotheses relating to floodplain metabolic dynamics and carbon flux. Our systematic review revealed a high level of context dependency for many of our hypotheses, being highly site and co-variate specific, making unified predictions for metabolic responses difficult. Not all studies that provided evidence presented field or laboratory derived metabolic values to support their findings (e.g., proxy estimates or model predictions) making weighting of the evidence difficult in some cases. Nonetheless, here we provide a synthesis of current quantitative relationships between putative causal linkages relating to floodplain metabolic dynamics. We establish an obvious requirement for further empirical field studies to address knowledge gaps and identify specific aspects of aquatic floodplain productivity that should comprise the focus of future research. We found enough evidence in the literature to confirm that larger floods transfer more carbon from floodplains to the river channel than small floods, that high turbidity in floodplain habitats reduces GPP and that nutrient concentrations govern patterns of GPP. Future empirical studies need to focus on deriving quantitative relationships between aquatic metabolism and frequency and duration of floodplain inundation, for which information is lacking. When planning floodplain watering actions, the high level of context dependency (e.g., inconsistent evidence for macrophyte influence) for many aspects of floodplain metabolism identified in this review needs to be considered in a local perspective. Thus, we acknowledge that more experimental data might not lead to support for general principles, but it will increase our knowledge and understanding of complex floodplain ecosystems.

Data availability statement

Data are available by request.

References

- Ahn, C., and W. J. Mitsch. 2002. Scaling considerations of mesocosm wetlands in simulating large created freshwater marshes. *Ecol. Eng.* **18**: 327–342.
- Allan, J. D., M. M. Castillo, and K. A. Capps. 2021. Carbon dynamics and stream ecosystem metabolism, p. 421–452. *In* *Stream ecology: Structure and function of running waters*. Springer International Publishing.
- Alvarez-Cobelas, M., D. G. Angeler, C. Rojo, and S. Cirujano. 2011. The importance of phytoplankton production for carbon budgets in a semiarid floodplain wetland. *An. Jard. Bot. Madr.* **68**: 253–267.
- Baldwin, D. S., and others. 2013. Provisioning of bioavailable carbon between the wet and dry phases in a semi-arid floodplain. *Oecologia* **172**: 539–550.
- Ballinger, A., and R. Mac Nally. 2006. The landscape context of flooding in the Murray–Darling basin. *Adv. Ecol. Res.* **39**: 85–105.
- Bernhardt, E. S., and others. 2018. The metabolic regimes of flowing waters. *Limnol. Oceanogr.* **63**: S99–S118.
- Bernhardt, E. S., and others. 2022. Light and flow regimes regulate the metabolism of rivers. *Proc. Natl. Acad. Sci.* **119**: e2121976119.
- Brisbane Declaration. 2007. The Brisbane Declaration: Environmental flows are essential for freshwater ecosystem health and human well-being, p. 3–6. *In* 10th International River Symposium, Brisbane, Australia.
- Bunn, S. E., P. M. Davies, and M. Winning. 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshw. Biol.* **48**: 619–635. doi:10.1046/j.1365-2427.2003.01031.x
- Cronk, J. K., and W. J. Mitsch. 1994a. Aquatic metabolism in 4 newly constructed fresh-water wetlands with different hydrologic inputs. *Ecol. Eng.* **3**: 449–468. doi:10.1016/0925-8574(94)00012-3
- Cronk, J. K., and W. J. Mitsch. 1994b. Periphyton productivity on artificial and natural surfaces in constructed freshwater wetlands under different hydrologic regimes. *Aquat. Bot.* **48**: 325–341. doi:10.1016/0304-3770(94)90024-8
- Fabricius, K. E., and G. De'ath. 2004. Identifying ecological change and its causes: A case study on coral reefs. *Ecol. Appl.* **14**: 1448–1465.
- Fellman, J. B., N. E. Pettit, J. Kalic, and P. F. Grierson. 2013. Influence of stream-floodplain biogeochemical linkages on aquatic foodweb structure along a gradient of stream size in a tropical catchment. *Freshw. Sci.* **32**: 217–229. doi:10.1899/11-117.1
- Fellows, C. S., S. E. Bunn, F. Sheldon, and N. J. Beard. 2009. Benthic metabolism in two turbid dryland rivers. *Freshw. Biol.* **54**: 236–253. doi:10.1111/j.1365-2427.2008.02104.x
- Fuell, A. K., S. A. Entrekin, G. S. Owen, and S. K. Owen. 2013. Drivers of leaf decomposition in two wetland types in the Arkansas River valley, USA. *Wetlands* **33**: 1127–1137.
- Gallardo, B., C. Espanol, and F. A. Comin. 2012. Aquatic metabolism short-term response to the flood pulse in a Mediterranean floodplain. *Hydrobiologia* **693**: 251–264.
- Giling, D. P., and others. 2017. Delving deeper: Metabolic processes in the metalimnion of stratified lakes. *Limnol. Oceanogr.* **62**: 1288–1306.
- Greet, J., A. J. Webb, and R. D. Cousens. 2011. The importance of seasonal flow timing for riparian vegetation dynamics: A systematic review using causal criteria analysis. *Freshw. Biol.* **56**: 1231–1247.
- Hall, R. O., Jr., and others. 2015. Turbidity, light, temperature, and hydropeaking control primary productivity in the Colorado River, Grand Canyon. *Limnol. Oceanogr.* **60**: 512–526.
- Higgisson, W., B. Higgisson, M. Powell, P. Driver, and F. Dyer. 2020. Impacts of water resource development on hydrological connectivity of different floodplain habitats in a highly variable system. *River Res. Appl.* **36**: 542–552.
- Hill, A. B. 1965. The environment and disease: Association or causation? *Proc. R. Soc. Med.* **58**: 295–300.
- Holland, A., P. J. McInerney, M. E. Shackleton, G. N. Rees, N. R. Bond, and E. Silvester. 2020. Dissolved organic matter and metabolic dynamics in dryland lowland rivers. *Spectrochim. Acta A Mol. Biomol. Spectrosc.* **229**: 117871.
- Honious, S. A., R. L. Hale, J. J. Guiling, B. T. Crosby, and C. V. Baxter. 2021. Turbidity structures the controls of ecosystem metabolism and associated metabolic process domains along a 75-km segment of a semiarid stream. *Ecosystems* **25**: 1–19.
- Howitt, J. A., D. S. Baldwin, G. N. Rees, and J. L. Williams. 2007. Modelling blackwater: Predicting water quality during flooding of lowland river forests. *Ecol. Model.* **203**: 229–242.
- Izagirre, O., U. Agirre, M. Bermejo, J. Pozo, and A. Elozegi. 2008. Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams. *J. North Am. Benthol. Soc.* **27**: 252–268.
- Jankowski, K. J., F. H. Mejia, J. R. Blaszcak, and G. W. Holtgrieve. 2021. Aquatic ecosystem metabolism as a tool in environmental management. *WIREs Water* **8**: e1521.
- Jenkins, K., R. Kingsford, and D. Ryder. 2009. Developing indicators for floodplain wetlands: Managing water in agricultural landscapes. *Chiang Mai J. Sci.* **36**: 224–235.
- Julian, P., T. Z. Osborne, R. K. Bhomia, and O. Villapando. 2021. Knowing your limits: Evaluating aquatic metabolism in a subtropical treatment wetland. *Hydrobiologia* **848**: 3969–3986.
- Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.* **106**: 110–127.
- Kelly, P. T., C. T. Solomon, J. A. Zwart, and S. E. Jones. 2018. A framework for understanding variation in pelagic gross primary production of lake ecosystems. *Ecosystems* **21**: 1364–1376.

- Kingsford, R. T. 2000. Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. *Austral Ecol.* **25**: 109–127.
- Kobayashi, T., T. J. Ralph, D. S. Ryder, and S. J. Hunter. 2013. Gross primary productivity of phytoplankton and planktonic respiration in inland floodplain wetlands of southeast Australia: Habitat-dependent patterns and regulating processes. *Ecol. Res.* **28**: 833–843.
- Lindholm, M., D. O. Hessen, K. Mosepele, and P. Wolski. 2007. Food webs and energy fluxes on a seasonal floodplain: The influence of flood size. *Wetlands* **27**: 775–784.
- Marotta, H., and A. Enrich-Prast. 2015. Catastrophic shifts in the aquatic primary production revealed by a small low-flow section of tropical downstream after dredging. *Braz. J. Biol.* **75**: 804–811.
- Martinez, A., J. S. Kominoski, and A. Larranaga. 2017. Leaf-litter leachate concentration promotes heterotrophy in freshwater biofilms: Understanding consequences of water scarcity. *Sci. Total Environ.* **599**: 1677–1684.
- Maynard, J. J., R. A. Dahlgren, and A. T. O'Geen. 2012. Quantifying spatial variability and biogeochemical controls of ecosystem metabolism in a eutrophic flow-through wetland. *Ecol. Eng.* **47**: 221–236.
- Maynard, J. J., R. A. Dahlgren, and A. T. O'Geen. 2014. Autochthonous and allochthonous carbon cycling in a eutrophic flow-through wetland. *Wetlands* **34**: 285–296.
- McInerney, P. J., G. N. Rees, B. Gawne, and P. Suter. 2016a. Implications of riparian willow invasion to instream community structure and function: A synthesis using causal criteria analysis. *Biol. Invasions* **18**: 2377–2390.
- McInerney, P. J., G. N. Rees, B. Gawne, and P. Suter. 2016b. Invasive *Salix fragilis*: Altered metabolic patterns in Australian streams. *Hydrobiologia* **767**: 267–277.
- Miller, K. A., J. A. Webb, S. C. de Little, and M. J. Stewardson. 2013. Environmental flows can reduce the encroachment of terrestrial vegetation into river channels: A systematic literature review. *Environ. Manag.* **52**: 1202–1212.
- Molinari, B., B. Stewart-Koster, T. J. Malthus, and S. E. Bunn. 2021. Assessing spatial variation in algal productivity in a tropical river floodplain using satellite remote sensing. *Remote Sens.* **13**: 1710.
- Ndehedehe, C. E., A. O. Onojeghuo, B. Stewart-Koster, S. E. Bunn, and V. G. Ferreira. 2021. Upstream flows drive the productivity of floodplain ecosystems in tropical Queensland. *Ecol. Indic.* **125**: 107546.
- Nichols, S., A. Webb, R. Norris, and M. Stewardson. 2011. Eco evidence analysis methods manual: A systematic approach to evaluate causality in environmental science. eWater Cooperative Research Centre. Available from <https://toolkit.ewater.org.au>
- Nielsen, D. L., R. A. Cook, N. Ning, B. Gawne, and R. Petrie. 2016. Carbon and nutrient subsidies to a lowland river following floodplain inundation. *Mar. Freshw. Res.* **67**: 1302–1312.
- Norris, R., and others. 2008. Causal criteria analysis methods manual: A systematic approach to evaluate causality in environmental science. eWater Cooperative Research Centre; [accessed 2015 October 20]. Available from https://www.usbr.gov/uc/progact/amp/twg/2010-11-15-twg-meeting/Attach_14.pdf.
- Norris, R. H., J. A. Webb, S. J. Nichols, M. J. Stewardson, and E. T. Harrison. 2012. Analyzing cause and effect in environmental assessments: Using weighted evidence from the literature. *Freshw. Sci.* **31**: 5–21.
- O'Connell, M., D. S. Baldwin, A. I. Robertson, and G. Rees. 2000. Release and bioavailability of dissolved organic matter from floodplain litter: Influence of origin and oxygen levels. *Freshw. Biol.* **45**: 333–342.
- Odum, H. T. 1956. Primary production in flowing waters. *Limnol. Oceanogr.* **1**: 102–117.
- Opsahl, S. P. 2005. Organic carbon composition and oxygen metabolism across a gradient of seasonally inundated limesink and riparian wetlands in the southeast Coastal Plain, USA. *Biogeochemistry* **76**: 47–68. doi:10.1007/s10533-005-2074-5
- Poff, N. L., and J. K. H. Zimmerman. 2010. Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Freshw. Biol.* **55**: 194–205.
- Reeder, B. C. 2011. Assessing constructed wetland functional success using diel changes in dissolved oxygen, pH, and temperature in submerged, emergent, and open-water habitats in the Beaver Creek Wetlands Complex, Kentucky (USA). *Ecol. Eng.* **37**: 1772–1778.
- Rees, G. N., R. A. Cook, N. S. P. Ning, P. J. McInerney, R. T. Petrie, and D. L. Nielsen. 2020. Managed floodplain inundation maintains ecological function in lowland rivers. *Sci. Total Environ.* **727**: 138469.
- Reid, A. J., and others. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* **94**: 849–873.
- Roach, K. A., K. O. Winemiller, and S. E. Davis III. 2014. Autochthonous production in shallow littoral zones of five floodplain rivers: Effects of flow, turbidity and nutrients. *Freshw. Biol.* **59**: 1278–1293.
- Robertson, A. I., S. E. Bunn, P. I. Boon, and K. F. Walker. 1999. Sources, sinks and transformations of organic carbon in Australian floodplain rivers. *Mar. Freshw. Res.* **50**: 813–829. doi:10.1071/mf99112
- Rüegg, J., and others. 2021. Thinking like a consumer: Linking aquatic basal metabolism and consumer dynamics. *Limnol. Oceanogr. Lett.* **6**: 1–17.
- Ryder, D. S. 2004. Response of epixylic biofilm metabolism to water level variability in a regulated floodplain river. *J. North Am. Benthol. Soc.* **23**: 214–223.
- Shen, X. M., T. Sun, S. Tang, and W. Yang. 2016. Short-term response of aquatic metabolism to hydrologic pulsing in the coastal wetlands of Yellow River delta. *Wetlands* **36**: S81–S94.

- Squires, M. M., and L. F. W. Lesack. 2001. Benthic algal response to pulsed versus distributed inputs of sediments and nutrients in a Mackenzie Delta lake. *J. North Am. Benthol. Soc.* **20**: 369–384. doi:10.2307/1468035
- Squires, M. M., L. F. W. Lesack, R. E. Hecky, S. J. Guildford, P. Ramlal, and S. N. Higgins. 2009. Primary production and carbon dioxide metabolic balance of a lake-rich arctic river floodplain: Partitioning of phytoplankton, epipelon, macrophyte, and epiphyton production among lakes on the Mackenzie delta. *Ecosystems* **12**: 853–872.
- Staehr, P. A., J. M. Testa, W. M. Kemp, J. J. Cole, K. Sand-Jensen, and S. V. Smith. 2012. The metabolism of aquatic ecosystems: History, applications, and future challenges. *Aquat. Sci.* **74**: 15–29.
- Stanley, E. H., M. D. Johnson, and A. K. Ward. 2003. Evaluating the influence of macrophytes on algal and bacterial production in multiple habitats of a freshwater wetland. *Limnol. Oceanogr.* **48**: 1101–1111.
- Thomas, S., E. E. Gaiser, and F. A. Tobias. 2006. Effects of shading on calcareous benthic periphyton in a short-hydroperiod oligotrophic wetland (Everglades, FL, USA). *Hydrobiologia* **569**: 209–221.
- Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer, and J. V. Ward. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). *Freshw. Biol.* **41**: 521–535. doi:10.1046/j.1365-2427.1999.00399.x
- Van de Bogert, M. C., S. R. Carpenter, J. J. Cole, and M. L. Pace. 2007. Assessing pelagic and benthic metabolism using free water measurements. *Limnol. Oceanogr. Methods* **5**: 145–155.
- Vorobyev, S. N., O. S. Pokrovsky, L. G. Kolesnichenko, R. M. Manasyrov, L. S. Shirokova, J. Karlsson, and S. N. Kirpotin. 2019. Biogeochemistry of dissolved carbon, major, and trace elements during spring flood periods on the Ob River. *Hydrol. Process.* **33**: 1579–1594. doi:10.1002/hyp.13424
- Wallace, T. A., and D. Furst. 2016. Open water metabolism and dissolved organic carbon in response to environmental watering in a lowland river-floodplain complex. *Mar. Freshw. Res.* **67**: 1346–1361. doi:10.1071/mf15318
- Ward, D. P., N. E. Pettit, M. Adame, M. M. Douglas, S. A. Setterfield, and S. E. Bunn. 2016. Seasonal spatial dynamics of floodplain macrophyte and periphyton abundance in the Alligator Rivers region (Kakadu) of northern Australia. *Ecohydrology* **9**: 1675–1686.
- Webb, J. A., S. J. Nichols, R. H. Norris, M. J. Stewardson, S. R. Wealands, and P. Lea. 2011. Ecological responses to flow alteration: Assessing causal relationships with Eco Evidence. *Wetlands* **32**: 203–213.
- Weed, D. L. 1997. On the use of causal criteria. *Int. J. Epidemiol.* **26**: 1137–1141.
- Weilhoefer, C. L., Y. D. Pan, and S. Eppard. 2008. The effects of river floodwaters on floodplain wetland water quality and diatom assemblages. *Wetlands* **28**: 473–486.
- Wetzel, R., and A. Ward. 1996. Primary production. Blackwell Science.
- Whitworth, K. L., and D. S. Baldwin. 2016. Improving our capacity to manage hypoxic blackwater events in lowland rivers: The blackwater risk assessment tool. *Ecol. Model.* **320**: 292–298.
- Whitworth, K. L., D. S. Baldwin, and J. L. Kerr. 2012. Drought, floods and water quality: Drivers of a severe hypoxic blackwater event in a major river system (the southern Murray-Darling Basin, Australia). *J. Hydrol.* **450**: 190–198.
- Wolfenden, B. J., S. M. Wassens, K. M. Jenkins, D. S. Baldwin, T. Kobayashi, and J. Maguire. 2018. Adaptive management of return flows: Lessons from a case study in environmental water delivery to a floodplain river. *Environ. Manag.* **61**: 481–496.
- Zuijgeest, A., S. Baumgartner, and B. Wehrli. 2016. Hysteresis effects in organic matter turnover in a tropical floodplain during a flood cycle. *Biogeochemistry* **131**: 49–63. doi:10.1007/s10533-016-0263-z
- Zuijgeest, A. L., R. Zurbrugg, N. Blank, R. Fulcri, D. B. Senn, and B. Wehrli. 2015. Seasonal dynamics of carbon and nutrients from two contrasting tropical floodplain systems in the Zambezi River basin. *Biogeosciences* **12**: 7535–7547. doi:10.5194/bg-12-7535-2015

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Conflict of Interest

None declared.

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