

The importance of aquatic carbon fluxes in net ecosystem carbon budgets: a catchment-scale review

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Abstract

The growing importance of resolving ecosystem carbon budgets has resulted in more studies integrating terrestrial and aquatic carbon fluxes. While recent estimates highlight the importance of inland waters in global carbon budgets, the extent to which aquatic pathways contribute to the net ecosystem carbon budget (NECB) of different ecosystems remains poorly understood. Here, we provide a cross-ecosystem review of annual carbon budgets integrating terrestrial and aquatic fluxes. Large variability in the proportion of aquatic carbon offset to terrestrial net ecosystem productivity (NEP) was observed, with aquatic offsets ranging from <1% in a boreal forest to 590% in a freshwater marsh. The total aquatic carbon flux was positively correlated with terrestrial NEP, suggesting highly productive ecosystems will have greater aquatic carbon offsets. However, due to an order of magnitude difference in the range of terrestrial NEP ($\sim 1000 \text{ g C m}^{-2} \text{ yr}^{-1}$) compared to aquatic fluxes ($\sim 100 \text{ g C m}^{-2} \text{ yr}^{-1}$), ecosystems with small NEP's had greater relative aquatic carbon offsets overall in their NECB's. Northern hemisphere peatlands and forests represented 54% of all integrated carbon budget studies collected, indicating a severe ecosystem and spatial bias. Mangroves, agricultural, and disturbed ecosystems were the most underrepresented, yet had extreme ranges in terrestrial NEP and NECB (-638 to $1,170 \text{ g C m}^{-2} \text{ yr}^{-1}$). To improve our mechanistic understanding of the role of aquatic pathways in NECB's, more site-specific integrative studies need to be undertaken across a broader range of climatic regions and ecosystem types.

Keywords

Net ecosystem carbon balance; catchment, aquatic ecosystems, terrestrial ecosystems, carbon accounting, aquatic pathways

Highlights

- The contribution of aquatic fluxes varies widely in ecosystem carbon budgets
- Ecosystems with low terrestrial productivity had greater aquatic carbon offsets
- Net ecosystem carbon budget studies are biased towards northern peatlands and forests

Introduction

Since Cole and others (2007) highlighted that aquatic systems are active interacting components of the carbon cycle, considerable research efforts have focused on constraining carbon fluxes along the aquatic continuum. Although many aquatic systems act as substantial carbon pools (e.g. lakes, ponds and reservoirs, Tranvik and others 2009; Downing 2010), detailed research on the net carbon fluxes has revealed widespread net heterotrophy among aquatic ecosystems (Duarte and Prairie, 2005). Since these revelations, global estimates have suggested that aquatic carbon fluxes can be highly relevant in global carbon cycles. Current global estimates of lateral carbon export, CO₂, and CH₄ evasion amounts to 0.9, 3.8, and 0.075 Pg C yr⁻¹, respectively (Tranvik and others 2009; Ward and others 2017; Stanley and others 2016). Combined, the total aquatic flux amounts to ~4.8 Pg C yr⁻¹ which approaches the upper range of the estimated terrestrial sink of 5 Pg C yr⁻¹ (~4.1 ± 0.9 Pg C yr⁻¹, Le Quere and others 2015).

Integrated ecosystem carbon budgets incorporating both terrestrial and aquatic pathways are rare. This is largely due to the disciplinary nature of science, where methodological constraints tend to enhance the focus on specific components of the carbon balance (Falkowski and others 2000). At the catchment scale, there is currently little consensus or predictable patterns on the relative contribution of aquatic pathways in ecosystem carbon budgets. Consequently, the importance of both aquatic and terrestrial carbon processes and pools at the catchment scale remains underrepresented in discipline-focused ecosystem studies.

The importance of fully integrated carbon budgets has now been demonstrated by numerous studies. Correct accounting of both aquatic and terrestrial carbon fluxes has shifted the source-sink status of ecosystems (Genereux and others 2013; Chu and others 2015; Lundin

and others 2016). Local scale studies (ecosystem-specific at the catchment level) on ecosystem carbon budgets are useful for identifying specific carbon fluxes that contribute to the overall budget. For example, studies measuring both terrestrial and aquatic carbon fluxes were first reported for a lowland temperate peatland catchment (Billet and others 2004) and temperate forest in the early 2000's (Shibata and others 2005). There are now sufficient studies on terrestrial-aquatic carbon budgets at the catchment scale to allow for analyses of broad scale patterns.

Recent reviews support the hypothesis that catchments with higher terrestrial productivity have greater aquatic carbon losses, suggesting that the aquatic component has a more important role in highly productive ecosystems. For example, Maberly and others (2012) found that in 20 lakes over 26 years, lake excess CO₂ was positively correlated with total catchment net primary productivity (NPP). Magin and others (2017) found a positive correlation with total aquatic carbon export (lateral movement) and total catchment NPP across 200 temperate streams. At the continental scale, Butman and others (2016) found a positive correlation between catchment specific aquatic carbon yield (evasion, export and burial) and catchment specific net ecosystem production (NEP) between 19 hydrological regions in the United States. The coupling of terrestrial and aquatic carbon fluxes at these large scales are thought to be explained by annual precipitation, where terrestrial carbon uptake and aquatic carbon fluxes both tend to increase under higher annual rainfall (Hsu and others 2012; Butman and others 2016). However, the response of carbon fluxes to changes in annual precipitation is not consistent between sites and different ecosystems at the catchment scale, which appear to cause greater changes in NEP than to aquatic carbon export (Pumpanen and others 2014; Oquist and others 2014).

Despite recent contributions from these large scale, multiple catchment reviews linking aquatic and terrestrial carbon fluxes, the overall importance of aquatic pathways to ecosystem

carbon budgets remains unresolved. At present, aquatic carbon fluxes are inconsistently evaluated in the context of landscape carbon budgets. This is primarily linked to the terrestrial and aquatic carbon components that are measured and/or included, and the scale at which these fluxes are represented. Butman and others (2016) provide the most complete quantitative assessment of the contribution of aquatic pathways to terrestrial carbon budgets on a regional scale, yet highlight how our ability to model terrestrial-aquatic exchanges is limited by direct measurements. To better understand the contribution of aquatic pathways to land based carbon budgets, attention needs to be directed to smaller scale, ecosystem-specific studies that may provide a more detailed view of aquatic carbon fluxes and drivers.

Here, we perform a cross-ecosystem analysis of annual carbon budgets, integrating terrestrial and aquatic fluxes at the catchment scale. Current consensus is that aquatic environments offset a proportion of terrestrial carbon uptake via both lateral transport out of the catchment area and direct loss to the atmosphere (Cole and others 2007; Ward and others 2017). We compiled the literature reporting carbon budgets integrating both terrestrial and aquatic carbon fluxes. We focus on the components of the aquatic carbon flux that most often represent a loss of carbon from the catchment (carbon export and evasion), and include both lentic and lotic systems. Specifically, our objectives were (1) to explore trends in aquatic carbon flux contributions by ecosystem type, terrestrial productivity, and precipitation, (2) review the range in aquatic carbon offsets of terrestrial NEP, and (3) determine the source or sink strength of each ecosystem by looking at the overall net ecosystem carbon budget (NECB). This review is designed to be inclusive of all ecosystem types to highlight the available evidence on terrestrial and aquatic carbon fluxes in NECB's within an interdisciplinary framework. Within this context, we summarise the methodical limitations, major knowledge gaps, and biases in our current knowledge of aquatic-terrestrial carbon budgets and outline future research directions.

Concept of the Net Ecosystem Carbon Budget

The NECB provides a complete, simplified framework for assessing the carbon budget of most land-based ecosystems. Originally proposed by Chapin and others (2006), NECB provides a measure of carbon accumulation rate in ecosystems within a defined boundary. The spatial limits of this boundary is user defined and can be used across all scales, from studies incorporating only aquatic environments (Stets and others 2009) to large watersheds encompassing multiple sub-catchments (Ran and others 2015). The range of different terms used in the literature to determine if an ecosystem is accumulating carbon are often segregated by discipline (Lovett and others 2006), and the NECB can unify different accounting methods from ecology, atmospheric, and aquatic disciplines.

The NECB represents the sum of inputs and outputs from all physical, biological and anthropogenic sources within a defined spatial boundary (Table 1). This equation is best represented by the net fluxes of these components and includes the NEP or net ecosystem exchange (NEE) of CO₂ between the ecosystem and atmosphere from the terrestrial area, net ecosystem CH₄ exchange (F_{CH4}), total aquatic carbon flux (F_{aquatic}), and net lateral transfer of other (non-aquatic) particulate forms of carbon (F_{PC}). The inclusion and relevance of certain pathways will vary between ecosystems. Each term contains specific components as defined in Table 1.

Terrestrial ecosystem production has been defined in terms of gross primary production (GPP), NPP, NEP, and NEE (Lovett and others 2006). The commonly used NPP measure only estimates biomass assimilation within the catchment, and does not represent the true measure of terrestrial productivity. Net ecosystem production (NEP) accounts for both NPP and heterotrophic respiration (soil) and represents the amount of carbon available within the

terrestrial environment for potential storage or export (Lovett and others 2006). GPP and NPP remain the most commonly reported measure of terrestrial production in ecosystems.

However, the reporting of NEP has increased in the last decade thanks to the widespread development of a global network of eddy covariance flux towers, which offers more spatially and temporally resolved measurements of net CO₂ exchanges (Baldocchi and others 2018).

The term net ecosystem exchange (NEE) is essentially a parallel measure of NEP (Kirschbaum and others 2001; Chapin and others 2006). The main difference is that a negative value represents net uptake since the term was conceived by micrometeorologists (seen instead as a CO₂ flux from the atmosphere rather than from the land, Table 1). NEE and NEP are interchangeable, provided that inorganic sources and sinks of CO₂ (fire, UV oxidation, weathering) are negligible (Chapin and others 2006). Here, we use the term NEP to define the terrestrial carbon flux.

The total aquatic carbon flux refers to the amount of carbon released or retained via lateral exchange, evasion (or invasion) to the atmosphere, and accumulation within the aquatic environment (Figure 1). This includes the lateral transfer of dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and particulate organic carbon (POC), and the gaseous flux of CO₂, CH₄ and other volatile gases to the atmosphere. The net CO₂ exchange (flux) between the water and atmosphere represents the balance between aquatic GPP and total respiration, the latter of which is often a mix of aquatic primary producer respiration and allochthonous and autochthonous organic matter decomposition. Additionally, this exchange is also related to abiotic processes including changes in carbonate chemistry and photo oxidation of DOC. Carbon accumulation in sediment is also a component of the total aquatic carbon flux, and is usually important in non-flowing water bodies (lakes and reservoirs, Anas and others 2015; Butman and others 2016). Groundwater input of dissolved carbon into open surface waters can represent one of the major pathways contributing to the total aquatic

carbon flux (Genereux and others 2013; Maher and others 2013). Groundwater carbon inputs are often integrated in surface water carbon export and gaseous evasion measurements, unless groundwater flows across catchments. Here, we assume that groundwater inputs are already included in aquatic carbon measurements reported for surface waters.

We evaluated the NECB's of a variety of ecosystems for which both terrestrial production in the form of NEP and at least one major component of the aquatic carbon flux was reported. We highlight that focusing on these two terms does not always reflect a complete carbon budget, but for most terrestrial-aquatic ecosystems these terms make up the majority of the NECB. It is important to note that "catchment" and "ecosystem" are often used interchangeably in studies that use the NECB framework to describe carbon budgets containing terrestrial and aquatic environments. Here, we refer to ecosystem as used in the broad sense to describe the dominant land cover and defining properties of the area that the NECB was quantified. In most cases, the ecosystem classification will more accurately describe the terrestrial environment, yet encompasses both terrestrial and aquatic components. Catchment is used as a scale measure to describe the spatial extent of the ecosystem, as every NECB requires a defined area at which to constrain all carbon fluxes (Chapin and others 2006).

Methods

We conducted a systematic review on interdisciplinary studies to bring to light the current evidence on the state of terrestrial-aquatic NECB's. Following the guidelines outlined in Pullin and Stewart (2006), we developed the following review protocol to be as inclusive as possible of all ecosystem types while ensuring that all studies included at least one estimate of terrestrial NEP and aquatic carbon flux.

Compiled data were from published studies that report both terrestrial and aquatic carbon flux rates over an annual timeframe and that are or can be represented in the catchment context (i.e. catchment area weighted fluxes). Literature was selected primarily through a Google scholar and Web of Science search using the key terms “net ecosystem carbon budget”, “net ecosystem carbon balance”, and “NECB” with “terrestrial” and “aquatic”, along with citations found in relevant studies. Information collected from each paper included the site description, climate, type of aquatic environment, location, catchment size, annual precipitation, NECB (if reported, otherwise calculated as in Table 1 with the carbon fluxes available), GPP, R_e , aquatic carbon export, aquatic CO₂ flux, CH₄ flux, method used for NEP estimation, carbon species measured or reported in the total aquatic carbon flux, and reference. From each study, individual annual carbon budgets were extracted and classified broadly by ecosystem type based on site description information. If individual carbon budgets are provided for an ecosystem over multiple years, then only one annual carbon budget was included our analysis. This was to avoid overrepresentation of one site. The most climatically representative year was chosen based on the long term average precipitation of the study site.

During the literature search, we confined our collection to sites that had a surface water component, and included aquatic carbon flux estimates from either lotic (streams, rivers, ditches) or lentic (lakes, reservoirs, ponds, pools) systems, excluding those studies that only estimate leaching to groundwater and cross-catchment groundwater discharge. We also only included studies that report the net terrestrial flux represented in its entirety as NEP or NEE, excluding studies that only report a NPP or GPP, unless other components of the NECB are provided so that NEP can be calculated (i.e. autotrophic and heterotrophic respiration). To avoid confusion and maintain comparativeness, NEE estimates were converted to NEP accounting for only the net terrestrial carbon flux, where positive NEP values represent a net carbon sink (Table 1). If aquatic systems were present within the boundary of NEE

measurement (flux tower), then NEE diverges from NEP because aquatic fluxes are also included. In the few studies that had this situation, NEE was adjusted to terrestrial NEE by discounting the aquatic flux, which was reported instead within the total aquatic flux term. Total aquatic carbon fluxes were reported as is from each study, noting that many studies only included export and not evasion (59%), or sometimes evasion and not export (5%) (Table S1).

In this review, we focus more specifically on how aquatic carbon flux components impacts the NECB by comparing it in relative terms to the terrestrial NEP (aquatic carbon offset). These two components were reported in every study included. There may be some inconsistencies between the total carbon fluxes reported from aquatic environments due to hydrological differences, when for example catchments only contain a lateral flux (streams) compared to those that were limited to gaseous evasion (closed lakes). Details on the aquatic environment and aquatic carbon fluxes included in each study are provided in Table S1. To ensure carbon budgets were comparable among studies, all fluxes and final NECB are reported in units $\text{g C m}^{-2} \text{ yr}^{-1}$ which are normalised to catchment area. If catchment area wasn't provided to do these calculations then these studies were excluded from this review. In instances where terrestrial CH_4 fluxes and biomass removal from agriculture are reported we leave these fluxes integrated within the final NECB. Figure 1 illustrates all carbon flux terms included in the theoretical definition of the NECB. In our cross ecosystem assessment of NECB's we focused on the terrestrial and aquatic carbon fluxes most often represented in the studies collected, and excluded aquatic sediment accumulation, DOC deposition from precipitation, soil DOC leaching, and other terrestrial carbon transfers such as erosion and animal movement. For agro-ecosystems, we left biomass harvest in the NECB as this represents a large carbon loss for cropping systems (Smith and others, 2010).

All statistical tests were performed in statistics software R version 3.4.2 (R Core Development Team). To interpret the data, we first explored the influence of some common catchment variables on the annual aquatic carbon flux and terrestrial NEP, all expressed per unit area of catchment. Significant correlations were tested using Pearson's least square regression for linear covariance, with significance implied at 95% confidence interval ($p < 0.05$). Data for many of the variables collected had non-normal distributions, so NEP (excluding negative values), total aquatic carbon flux, and precipitation were \log_{10} transformed to fit the linear regressions. Secondly, we determined the relative importance of carbon fluxes from the aquatic component in offsetting terrestrial NEP by expressing total aquatic carbon fluxes as a percentage of NEP for each study.

To assess the carbon source or sink status of the major ecosystem groups compiled for this review, the NECB of each system was determined based on the equation defined by Chapin and others (2006). The carbon fluxes included in our assessment of NECB between ecosystems is outlined in Figure 1. All studies analysed had NEP and aquatic carbon flux as components of the NECB.

Results and Discussion

Distribution of studies

A total of 41 published studies have reported terrestrial and aquatic carbon fluxes in ecosystems at the catchment-scale that meet our criteria, together making up 59 individual ecosystem carbon budgets (Table 2). All studies were published after 2003, except for Feijtel and others (1985), highlighting that the concept of linking terrestrial and aquatic carbon fluxes is relatively recent. Catchment size ranged from $< 0.1 \text{ km}^2$ to $6,397 \text{ km}^2$ and annual precipitation 233 to $4,321 \text{ mm yr}^{-1}$. A relatively full spectrum of climatic zones were captured

(Table 2), although the majority of studies were conducted in the cooler temperate to sub arctic zones of the northern hemisphere (Figure 2). Overall, seven broad ecosystem types were identified: agro-ecosystem (agricultural), forests, mangroves, mixed catchments (where no dominant ecosystem type was identified), peatlands, rainforest, and wetlands (other than peatlands). Within these ecosystems a number of aquatic environments were identified and included lotic waters such as ditches, streams, rivers, and tidal estuaries, and lentic water bodies such as ponds, lakes, and inundated wetlands. Running waters featured in 95% of all carbon budgets and standing water bodies 25%, demonstrating a bias towards lotic aquatic environments that only represent ~20% of the global inland water area (Raymond and others 2013).

The ecosystems where data are available captured ~60% of the global land area based on the global extent of broad ecosystem types (Table 2). However, the comparative number of studies in each ecosystem is greatly biased towards northern hemisphere natural peatlands, which feature almost twice as frequently as all other ecosystems combined (Table 2). This ecosystem bias greatly limits the scalability of terrestrial-aquatic carbon fluxes. The global extent of peatlands is only 3% of the earth's surface (Waite, 1993) even though they disproportionately contribute to the global carbon budget (Frolking and others 2011). A spatial bias also exists in the distribution of studies and ecosystems, with all but four studies located in the northern hemisphere (Figure 2). NECB's of most peatlands and mixed catchments are concentrated in Europe, while all wetland NECB studies have mostly been carried out in North America (Figure 2). Mangrove and agro-ecosystems are greatly underrepresented, containing only one and three catchment scale carbon budget to date, respectively (Table 2).

NECB across different ecosystems

Agro-ecosystems: Only two studies were collected for agro-ecosystems, one from a subtropical drained floodplain used for sugarcane production (Webb and others, *Under*

review), and two organic pasture sites from Ireland (Barry and others 2016). Although not all agro-ecosystems contain an aquatic component, artificially constructed drainage canals and small reservoirs are abundant in many farmlands (Downing and others 2008; Kaushal and others 2014). Overall, agro-ecosystems demonstrated the highest range in NEP values compared to other ecosystems, ranging from -233 to $900 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Figure 3). Despite the large variation in terrestrial production, aquatic fluxes were similar between each carbon budget (Figure 3). Fluvial carbon losses in the form of dissolved and particulate export can be higher in agro-ecosystems due to a combination of land use change (e.g. removal of riparian vegetation), and enhanced runoff (Nachimuthu and others 2016). On average, agro-ecosystems had the lowest NECB ($-300 \text{ g C m}^{-2} \text{ yr}^{-1}$) of ecosystems (Figure 3). The net carbon loss from these ecosystems is the result of additional carbon losses in the form of biomass removal (harvest, grazing livestock), which does not apply to the NECB of other ecosystems included here (Smith and others 2010). Therefore, terrestrial NEP and biomass removal are likely the major components determining the NECB of agro-ecosystems, which given the high variability have the potential to be carbon sinks (i.e. extremely high $\text{NEP} > 2,000 \text{ g C m}^{-2} \text{ yr}^{-1}$, Anderson and others 2015) or substantial carbon sources (Barry and others 2016).

Forests: A total of 12 carbon budgets were collected from the literature survey on forest ecosystems. This included both deciduous and coniferous forests, which despite our broad categorisation, mostly encompassed boreal and cool temperate forests in the northern hemisphere (Figure 2). Average NEP was $196 \text{ g C m}^{-2} \text{ yr}^{-1}$ and all were within the range of 50 to $495 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table S2). The NEP of boreal forests can vary by -100 to $870 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Law and others 2002), so our reviewed integrated carbon budgets capture most of the range in terrestrial production. Total aquatic carbon fluxes were consistently in the lower range ($\sim 9 \text{ g C m}^{-2} \text{ yr}^{-1}$) compared to other ecosystems, and did not vary largely between sites ($1\text{-}20 \text{ g C}$

$\text{m}^{-2} \text{yr}^{-1}$, Figure 3). Of the 12 individual carbon budgets, only three included estimates of POC export and six of CO_2 evasion, although the inclusion of such components did not seem to result in higher total aquatic carbon flux between studies (Table S1). Annual dissolved organic carbon fluxes typically vary over a small range ($0.8\text{--}4.9 \text{ g C m}^{-2} \text{ yr}^{-1}$) in forested catchments relative to terrestrial fluxes (Raymond and Saiers, 2010). Overall, remaining undisturbed forest catchments likely act as consistent carbon sinks as the inclusion of the aquatic carbon flux in the NECB does not substantially offset terrestrial NEP ($\sim 9\%$, Figure 3).

Mangroves: Mangroves were the most underrepresented ecosystems in this review, with only a single integrated carbon budget reported at the catchment scale (Table 2). As a result, no strong conclusions can be drawn on the aquatic carbon contribution to the NECB. Such uncertainty is also reflected in the global scale carbon budgets of mangroves, where the fate of an estimated 50% of terrestrially fixed carbon remains unresolved (Boullion and others 2008). The mangrove site included here had some of the largest terrestrial NEP and total aquatic carbon fluxes of all studies, at $1,170 \text{ g C m}^{-2} \text{ yr}^{-1}$ and $131 \text{ g C m}^{-2} \text{ yr}^{-1}$ respectively. As a result, the NECB exceeded other ecosystems by an order of magnitude (Figure 3). The growing body of recent data for mangrove NEP and aquatic carbon fluxes from isolated studies show that such fluxes appear to be consistently larger than most ecosystems (Lu and others 2017). This likely reflects the increased ecosystem connectivity between terrestrial and aquatic environments due to tidally-driven seawater recirculation in soils (Boullion and others 2008). Despite a similar NEP flux, the current global mangrove carbon budget (inclusive of burial, net algal production and total ecosystem CH_4 fluxes) estimates a much smaller NECB sink compared to the catchment scale study, being ~ 150 and $\sim 1,000 \text{ g C m}^{-2} \text{ yr}^{-1}$ respectively (Troxler and others 2013; Alongi and others 2014, Table S2). Inclusion of all aquatic carbon terms in the global aquatic flux provides a much larger aquatic carbon offset

of 94% compared to 11% in the catchment scale study which estimated aquatic carbon fluxes indirectly (Table S2).

Mixed catchments: Catchments that contain a mixture of ecosystems are difficult to differentiate in terms of their overall carbon functioning. These landscapes differed in their composition and extent of ecosystem elements, including drained and natural peatlands, agricultural land, forests, and wetlands. The seven (Table 2) mixed catchments reported here experienced cool temperate to sub-arctic climates. Surprisingly, the total aquatic flux varied over a relatively narrow range (3-19 g C m⁻² yr⁻¹) between sites (Figure 3), yet the relative contribution ranged between 1- 130% of terrestrial NEP (Table 3). This may be due to the similar Northern European sub arctic climate and precipitation ranges of these studies (Figure 2). Terrestrial NEP and NECB ranges were more variable (4 to 260 g C m⁻² yr⁻¹ and -11 to 257 g C m⁻² yr⁻¹ respectively), and likely reflects the mosaic of ecosystem components that make up the catchment (Figure 3). A modelling study demonstrated how heterogeneity of terrestrial and aquatic environments can substantially shift whole catchment CO₂ and CH₄ fluxes (Premke and others 2016). Many catchment areas worldwide encompass a mixture of ecosystems, highlighting the importance of understanding how individual ecosystems behave in terms of terrestrial and aquatic carbon fluxes to enable scaling that captures whole landscape carbon budgets.

Peatlands: Undisturbed peatlands in the sub arctic zone are the most well represented ecosystems in integrated carbon budgets (Figure 2). Our review revealed that aquatic carbon fluxes in these systems offset on average 40% of the NEP, which is slightly higher than Yu (2012) review of 32%. Excluding one extreme example (293 g C m⁻² yr⁻¹), the total aquatic carbon flux (fluvial and evasion) from peatlands ranged from 3 to 54 g C m⁻² yr⁻¹, which are not noticeably larger than aquatic fluxes in other ecosystems (Figure 3). Average terrestrial NEP was 109 g C m⁻² yr⁻¹ and most peatlands were net carbon sinks with an average NECB

of $69 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Figure 3). The average NECB is higher than the long term accumulation rate estimated for northern peatlands ($\sim 11 \text{ g C m}^{-2} \text{ yr}^{-1}$, Yu, 2012), which may suggest discrepancy among methods (i.e. sediment cores versus direct accounting) or that present day carbon fluxes do not reflect ancient carbon cycles of many peatlands. Although this value is fairly modest compared to the NECB reported for other ecosystems (e.g. forests and mangroves, Figure 3), the relatively low variability in carbon fluxes and consistency in positive NECB values between most studies reinforces the value of peatlands as terrestrial carbon sinks (Limpens and others 2008). In the two peatlands that were a small net carbon source in their annual carbon balance (NECBs = -7.2 and $-7.6 \text{ g C m}^{-2} \text{ yr}^{-1}$), terrestrial NEP was low or negative and the total aquatic flux represented over 100% of NEP (Billet and others 2004; Karlsson and others 2010). Climatic changes including increased precipitation, temperatures, and thawing of permafrost were attributed to the reduced NECBs.

Rainforests: On average rainforests had a NEP of $185 \text{ g C m}^{-2} \text{ yr}^{-1}$, which was lower than that of agro-ecosystems, forests, and mangrove in this review (Figure 3). Although this amount of terrestrial carbon production does not appear to be very large, GPP rates in tropical rainforests are some of the highest globally ($\sim 3,550 \text{ g C m}^{-2} \text{ yr}^{-1}$). Because ecosystem respiration often closely matches GPP in magnitude ($\sim 3,060 \text{ g C m}^{-2} \text{ yr}^{-1}$, Luyssaert and others 2007), NEP (GPP - ER) is relatively low. The rainforests sites included here had the highest annual rainfalls (1,560 to 4,340 mm yr^{-1} ; Table 2). However, the total aquatic carbon flux was not proportionately higher when compared to other ecosystems (Figure 3). Overall, rainforests appeared to be modest carbon sinks, with an average NECB of $145 \text{ g C m}^{-2} \text{ yr}^{-1}$ across the seven studies. One site in the Western Amazon Basin had a negative NECB ($-104 \text{ g C m}^{-2} \text{ yr}^{-1}$) due to an already negative terrestrial NEP (Vihermaa and others 2016), likely due to low annual rainfall during the observation year. Due to the small number of integrated carbon budgets (seven, Table 2) and the sensitivity of NEP to moisture conditions in

rainforests (Zeri and others 2014), the functioning of these ecosystems as sources or sinks needs to be further explored before any conclusive findings are drawn.

Wetlands: NECB wetland studies included maritime wetland forest, tidal freshwater and brackish marshes, and mixed wetland vegetation over seven individual annual carbon budgets (Table 2). Most wetland studies were located in the cool temperate humid climate region, with one set of tidal wetlands located in a subtropical humid climate. Wetlands displayed some of the highest variability in terrestrial NEP (-15 to $301 \text{ g C m}^{-2} \text{ yr}^{-1}$), total aquatic flux (12 to $315 \text{ g C m}^{-2} \text{ yr}^{-1}$), and aquatic carbon to terrestrial NEP offset (12-590%) compared to other ecosystems (Figure 3). On average, the NECB of the wetlands was $45 \text{ g C m}^{-2} \text{ yr}^{-1}$, with sites ranging from large net carbon sources ($-393 \text{ g C m}^{-2} \text{ yr}^{-1}$) to relatively modest net carbon sinks ($265 \text{ g C m}^{-2} \text{ yr}^{-1}$). Findings from these studies also suggest that the aquatic carbon flux is of higher importance in the NECB compared to the other studied ecosystems, as wetlands had the highest average aquatic carbon to NEP ratio of 155%.

The role of wetlands as net carbon sinks or sources is difficult to decipher, yet may become more apparent with further segregation of wetland types as integrated NECB studies increase. Often wetlands exhibit large and variable carbon fluxes across both terrestrial and aquatic pathways (Waletzko and Mitsch, 2013), high terrestrial GPP coupled with high ecosystem respiration (Lu and others 2017), and substantial CH_4 fluxes across terrestrial and aquatic interfaces (Gatland and others 2014; Feijtel and others 1985). The CO_2 sink strength alone estimated from a global database of CO_2 fluxes for inland and coastal wetlands (Lu and others 2016) is 93 and $208 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively, yet may change once other components of the carbon budget are included. Future studies should include wetlands in warmer climates. Subtropical and tropical wetlands are estimated to make up half the total global wetland area (Mitsch and others 2010), are at high risk of climate and anthropogenic

disturbance (Moore and others 2013; Cole and others 2015), and can have some of the highest net carbon retention rates of wetlands (Mitsch and others 2013).

Catchment scale drivers of aquatic carbon fluxes

In spite of the diversity of ecosystems compiled, total aquatic carbon fluxes were significantly, but weakly correlated with terrestrial NEP ($r^2 = 0.074$, $p = 0.046$) (Figure 4). This supports the hypothesis that aquatic environments have higher carbon fluxes in ecosystems with higher terrestrial productivity. Stronger correlations have been observed in other investigations focusing on more restricted geographical boundaries such as Northern Europe and USA (Maberly and others 2013; Butman and others 2016; Magin and others 2017). There are likely many reasons for the relatively weak relationship found here. Firstly, a direct comparison with these studies is limited by the components of the aquatic carbon flux assessed against terrestrial productivity. Lateral export was reported in Magin and others (2017), CO₂ evasion in Maberly and others (2013), and Butman and others (2016) was inclusive of lateral export, evasion and burial. Secondly, we compare individual carbon budgets from different ecosystems and at a much smaller scale, where catchment specific heterogeneity and the different qualities of ecosystems are likely magnified. Thirdly, most studies in our analysis reported carbon fluxes specific to a one year timeframe. Annual climatic variations can impact terrestrial production at a greater magnitude than aquatic carbon fluxes (Tian and others 2000; Oquist and others 2014). In addition, aquatic carbon fluxes may reflect the long-term ecosystem accumulation rate rather than the contemporary carbon budget as in annual NEP (Billet and others 2015; Dean and others 2017; Ratcliffe and others 2017). Lastly, some portion of aquatic carbon can originate from sources that do not represent a component of terrestrial NEP, including groundwater upwelling from origins

outside of the catchment (Oviedo-Vargas and others 2016), autochthonous production (Hotchkiss and others 2015), or weathering.

Annual precipitation had a positive correlation with both the aquatic carbon flux and terrestrial NEP (Figure 5). This is consistent with other studies of terrestrial carbon accounting, where precipitation has been found to be a strong predictor of specific carbon fluxes and pools at catchment (Oquist and others 2014), continental (Merbold and others 2009; Butman and others 2016) and global scales (Sanders and others 2016). The common trend with precipitation most likely reflects the enhanced terrestrial ecosystem carbon assimilation due to increased water availability (Merbold and others 2009), and increased aquatic loadings of terrestrial carbon to aquatic systems during precipitation pulses (Raymond and others 2016). There was considerable variability among ecosystems as represented in the r^2 of 0.32 and 0.26 for Figure 5A and 5B, respectively. This may be due to processes other than precipitation exerting a stronger control over NEP and aquatic carbon fluxes. Such processes include anthropogenic disturbance which increases terrestrial respiration and aquatic fluxes (Raymond and others 2008; Hirano and others 2012), and other hydrological pathways that drive the aquatic flux (e.g. groundwater and tidal exchange, Genereux and others 2013; Santos and others 2012; Sadat-Noori and others 2016).

Contribution of the aquatic carbon flux

The relative magnitude of the aquatic carbon flux offset varied widely across studies, with total aquatic carbon fluxes representing 0.3 – 590% of catchment-scale terrestrial NEP (Figure 6A). There was a consistent decline in the aquatic-NEP flux ratio with increasing NEP (Figure 6A). As terrestrial NEP approaches zero, the relative contribution of the aquatic carbon flux becomes more important. The aquatic carbon flux exceeded 100% NEP only in catchments with low NEP between -15 to 82 g C m⁻² yr⁻¹. Taking only the studies with

positive NEP values, a significant correlation ($p < 0.001$, $r^2 = 0.29$) was found between NEP and the aquatic:NEP ratio (Figure 6B). This implies that even though catchment NEP may have a positive influence on aquatic carbon losses (Figure 4), the greater variability in NEP masks any changes in the aquatic carbon flux that may result from catchment NEP itself or other environmental drivers. Indeed, the total aquatic carbon flux varied over a relatively narrow range between ecosystems compared to terrestrial NEP, between two orders of magnitude ($1\text{-}315 \text{ g C m}^{-2} \text{ yr}^{-1}$) and three orders of magnitude ($-233\text{-}1,170 \text{ g C m}^{-2} \text{ yr}^{-1}$), respectively (Table S2). Given this finding, the relative importance of the aquatic carbon flux in offsetting terrestrial carbon uptake in ecosystems in many cases may be determined by the magnitude difference between terrestrial and aquatic component fluxes.

Our knowledge on the importance of aquatic carbon fluxes in offsetting terrestrial carbon uptake has advanced with recent large scale regional and global studies. Some of these studies were compared to the ecosystem specific catchment scale studies (Figure 6A). Global estimates do not necessarily provide an accurate representation of how the aquatic carbon flux component is scaled in most of the ecosystems reviewed here (Figure 6A). For example, the global carbon flux from inland waters is estimated to be $24.5 \text{ g C m}^{-2} \text{ yr}^{-1}$, representing 140% of the average global terrestrial NEP ($17.4 \text{ g C m}^{-2} \text{ yr}^{-1}$, Table S2). While some of the large scale studies (Gorham 1995; Humborg and others 2010; Butman and others 2016) fall within the same trend as the ecosystem studies, the aquatic versus terrestrial carbon flux for Southeast Asia disturbed peatlands (Wit and others 2015) and the global mangrove estimate (Alongi 2014) deviate greatly (Figure 6A). These studies represent extremes in the range of NEP fluxes (-433 and $1,260 \text{ g C m}^{-2} \text{ yr}^{-1}$) and both have very large aquatic carbon fluxes of 205 and $1,188 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively. Four ecosystem-specific studies also had negative NEP and relatively high aquatic carbon contributions that further offset the terrestrial carbon balance by 30-590% of NEP (Figure 6A, Table S1). Due to the limited number of studies, we

cannot yet predict the importance of the aquatic carbon flux in ecosystems with a net carbon loss, and highlight a need to target tropical and disturbed peatlands and mangroves for integrated carbon budget studies.

The global importance of ecosystems is a product of the aerial extent and intensity of key processes (Downing, 2010). Because aquatic environments often comprise a small spatial area within the landscape they reside in, normalisation of total fluxes to the catchment area decreases the magnitude of variability of aquatic fluxes between ecosystems. In contrast, terrestrial fluxes (NEP) are scaled to the extent of the terrestrial environment, which is often the dominant component of the landscape and therefore normalisation of absolute fluxes is limited. An example of when this is not the case can be demonstrated in one peatland carbon budget, where the aquatic environment made up 10-60% of catchment surface area (D'Acunha, 2017). As a result, the catchment-specific aquatic carbon flux was $290 \text{ g C m}^{-2} \text{ yr}^{-1}$, an order of magnitude greater than all other peatlands in this review. The intensity of carbon cycling in different aquatic environments also becomes less variable when scaled to the landscape. Smaller aquatic environments generally have larger component-specific (aquatic area only) carbon fluxes than large aquatic environments due to higher carbon turnover. This intensity-size scaling was demonstrated by comparison of CO_2 fluxes in small versus large lakes (Premke and others 2016) and headwater streams versus rivers (Butman and Raymond, 2011).

Implications and research directions

Our literature survey on integrative ecosystem carbon budgets revealed that aquatic pathways may play an important yet highly variable role in catchment scale NECB's. In this review, our analysis focused on the two main fluxes terrestrial NEP and the summed aquatic flux, which allowed us to broadly assess how the aquatic component offsets the terrestrial carbon

uptake. We showed that the relative importance of the aquatic carbon flux in proportion to the terrestrial NEP varied greatly between ecosystems. Total aquatic carbon flux appeared to be positively correlated with terrestrial NEP across ecosystems and annual precipitation emerged as a common driver of both aquatic and terrestrial carbon fluxes. However, the relative contribution of the aquatic carbon pathway to the NECB was more strongly determined by the magnitude of the terrestrial NEP flux. In this review, we synthesized studies that provided a bottom-up perspective on the role of aquatic carbon pathways in ecosystem carbon budgets, yet scaling bottom up predictions on ecosystem carbon budgets from catchment scale drivers requires further work. Here, we highlight shortcomings and suggest where future research may be directed.

The theoretical basis for NECB calculation is based on solid principles, however the current literature lacks a formalized framework to effectively integrate the two disciplines of terrestrial and aquatic ecology. We suggest that inconsistencies in reporting components of the NECB is often a major limitation in the literature. Figure 7 summarizes how often four major carbon flux components contributing to the NECB were reported in studies for each ecosystem. As a condition for inclusion in this review, all field studies needed to report terrestrial NEP and at least one major aquatic flux component to allow comparisons between ecosystem types and assess the relative importance of the aquatic flux. The type of aquatic flux reported often varies between studies, with aquatic evasion flux being underrepresented in all ecosystems (Figure 7). CH₄ fluxes were unaccounted for in forest, mangrove, and rainforest studies, yet were reported in over half of the peatland and wetland studies where CH₄ is more likely to be an important contribution to the NECB. While dismissing specific components of the aquatic carbon cycle may be justified in some cases, many datasets are incomplete (Figure 7). Therefore, our meta-analysis underestimates the contribution of aquatic losses to the NECP.

A range of methods were used for terrestrial NEP. This included bottom up scaling of direct measurements for terrestrial NEP using eddy covariance, chambers and changes in biomass inventory (e.g., Feijtel and others 1985; Christensen and others 2007), and non-direct estimates using data from the literature and terrestrial ecosystem models such as MODIS (Ojala and others 2007; McCallister and Giorigio 2012; Table S1). Each method for quantifying CO₂ fluxes between terrestrial ecosystems have uncertainties, which are exacerbated in sites with complex topography and heterogeneous vegetation (Wang et al., 2017). From the studies collected here, 69% reported NEP from eddy covariance measurements. This method arguably provides the best direct estimate of ecosystem-scale NEP in spite of well known uncertainties (Baldocchi, 2003). The eddy flux community have standardized data processing procedures (Papale et al., 2006), which have proven effective in reducing bias across sites (Campioli et al., 2016).

Very few studies reported all major aquatic carbon flux components together. Although the number of studies reporting aquatic CO₂ and CH₄ evasion with more direct methodologies has greatly increased in recent years (Bastviken and others 2015; Webb and others 2016), the representation of this flux is poor in integrative carbon budgets as only ~40% of studies reported aquatic evasion in this review. Other potentially important pathways such as the net ecosystem CH₄ flux, carbon burial, groundwater flux, and DOC input from rain, were also rarely reported in the integrated carbon budgets (Figure 1). For groundwater, this may include delivery of old carbon to surface waters, the age of which does not reflect the contemporary carbon budget and must be corrected for in the total aquatic carbon flux (Billet and others 2015; Maher and others 2017). Such methodological shortcomings greatly limits how we evaluate both the role of the aquatic flux in offsetting terrestrial NEP and the overall NECB between separate studies of different ecosystems.

Another understudied aspect of carbon flux is the role of some aquatic environments as fluvial and gaseous carbon sinks. For the studies collected here, inclusion of sediment carbon accumulation in the aquatic environment was rarely reported and therefore was excluded in the total aquatic carbon flux term (Figure 1). Although most aquatic environments behave as net carbon sources, inclusion of sediment carbon accumulation may switch the total aquatic carbon flux to a net gain term in the NECB (Feijtel and others 1985). Some aquatic environments can also act as net CO₂ sinks. In hardwater lakes, a combination of increased biological and chemical uptake has resulted in an increased catchment scale CO₂ uptake of 5 g C m⁻² yr⁻¹ over the last decade (Finlay and others 2015). Net CO₂ uptake has also been observed in estuaries where significant communities of seagrasses and macro-algae exist (e.g. Maher and others 2012). The role of these terms on the aquatic carbon flux needs to be further explored across a wider range of aquatic environments, and further reflects the spatial and ecosystem bias inherent in most integrated carbon budgets.

There is a clear need to expand the database of integrated NECB studies in other ecosystems across other climatic regions. Our current understanding on the importance of the aquatic carbon flux scaled to the landscape is limited mostly to sub arctic (boreal) peatlands, which had aquatic carbon fluxes offsetting on average 40% of terrestrial NEP. The average aquatic to terrestrial carbon offset from other ecosystems ranged from 9% in forests to 155% in wetlands, demonstrating the high variability between and within ecosystems that needs to be further explored. Ecosystems including tropical peatlands, natural floodplains, agricultural ecosystems, marshes, grasslands, and mangroves are currently the most underrepresented in NECB studies. Tropical forests, wetlands and mangroves in particular seem to be large players in terrestrial-aquatic carbon cycling with NEP up to 2,142 g C m⁻² yr⁻¹ and aquatic exports of 144 g C m⁻² yr⁻¹ (Alongi 2011; Zhou and others 2013).

Furthermore, tropical forests and tropical grasslands together make up 59% of total biome

GPP globally (Beer and others 2010). This major spatial and ecosystem bias represents a knowledge gap that inhibits an accurate evaluation of the role of aquatic systems in catchment scale carbon budgets.

The need to study underrepresented ecosystems is further exemplified by the anthropogenic and climatic impacts that many ecosystems are currently experiencing. Agriculture and urbanisation have driven increases in terrestrial carbon loss via rivers of around 70% and 80% since pre-disturbance (Regnier and others 2013; Noacco and others 2017). Disturbed forests and peatlands in the tropical latitudes are of particular concern, as they represent large areas of unquantified ecosystems that may have large negative NECBs. For example, terrestrial NEP has been shown to shift to large negative fluxes due to increases in soil respiration (Hirano and others 2009), and tropical peatlands have 50% higher fluvial organic carbon exports than intact peatlands (Moore and others 2013). Changes in ecosystem-scale disturbances such as precipitation intensity and frequency and wildfire regimes are anticipated to impact the magnitude of both terrestrial and aquatic carbon fluxes (Hirano and others 2009; Gatland and others 2014). In our review, four studies reported negative terrestrial NEP fluxes, suggesting that these sites are likely experiencing or recovering from some kind of disturbance event. Explicit comparison of aquatic carbon fluxes across varying degrees of land use disturbance from different ecosystems will provide a more direct measure of how such disturbances have impacted the role of the aquatic pathway in NECB's.

Continuous long term measurement of both NEP and aquatic carbon flux is required to monitor inter annual changes in NECB of ecosystems. Many studies included in this review noted the large variability in NEP between years (Chu and others 2015; Oquist and others 2014; Leach and others 2016) and how the aquatic carbon flux remains a more consistent and permanent carbon flux that needs to be included in ecosystem carbon budgets, regardless of its contributing importance. The relative importance of the aquatic carbon flux increases

when terrestrial NEP decreases (Figure 6), and therefore may ultimately determine the direction of the NECB's when terrestrial NEP is near neutral. This type of finding along with the observed variability in NEP highlights the importance of enabling continuous long term measurement of both NEP and aquatic carbon fluxes, simultaneously, to monitor inter annual changes in NECBs. Some long term assessments already exist for boreal peatlands and forests, including the Auchencorth catchment in Scotland and the Krycklan catchment in Northern Sweden (Billet and others 2004; Dinsmore and others 2010; Oquist and others 2014). As such, these sites have refined carbon flux estimates between the terrestrial and aquatic components, and have identified important environmental drivers that operate over longer time scales, such as precipitation.

Conclusion

Previous reviews on terrestrial-aquatic carbon accounting have demonstrated how the aquatic carbon flux can significantly offset terrestrial carbon sinks on a global scale (Cole and others 2007; Raymond and others 2013; Regnier and others 2013). Our analysis identifies the need to reassess the importance of aquatic carbon flux to catchment scale ecosystem carbon budgets. We show that a spatial and ecosystem bias towards Northern Hemisphere boreal peatlands and forests currently exists in NECB's integrating aquatic and terrestrial fluxes. Consequently, this hinders our understanding on the relative importance of aquatic carbon fluxes in NECB's. Building on from earlier work by focusing on a global distribution of catchment scale investigations, we demonstrated (1) a wide range in the aquatic carbon offset of terrestrial NEP from an average of 9% in forests to 155% in wetlands, (2) a scattered yet significant positive correlation between catchment normalised aquatic carbon fluxes and terrestrial NEP, and (3) a correlation between aquatic carbon losses and terrestrial NEP with rainfall that holds true across the 59 catchments. Despite the generally higher total aquatic

fluxes associated with productive terrestrial ecosystems, the aquatic carbon flux is proportionately more important in the NECB of ecosystems with very low NEP. The finding that precipitation may be a common driving factor for catchment scale aquatic and terrestrial fluxes provides an initial framework that may eventually evolve into bottom up estimates of global aquatic carbon fluxes when more ecosystem-specific investigations are available. We suggest future studies explore the contribution of aquatic carbon fluxes across ecosystems that encompass a broad range of NEP fluxes to capture the full range of terrestrial productivity.

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Tables

Table 1: Definitions of common terms used in carbon accounting

Table 2: Summary of literature surveyed and catchment characteristics. Values presented represent the average (min-max) of all budgets for each ecosystem.

Table 1

Term	Definition
NECB	Net ecosystem carbon budget: $NECB = NEP - F_{CH_4} - F_{aquatic} - F_{PC}$, where all fluxes are represented in the same spatial and temporal integrated units; as a rate (year) over the land surface area (m ²) considered (g C m ⁻² yr ⁻¹). A positive NECB indicates carbon accumulation and a negative value represents a carbon loss.
GPP	Gross primary production. Represents the gross assimilation of CO ₂ via photosynthesis.
NPP	Net primary production: $NPP = GPP - R_a$, refers to the net production of organic carbon by plants, which is a net measure of biomass growth over a certain time frame.
NEP	Net ecosystem production: $NEP = GPP - R_e$, represents the inorganic carbon exchange (CO ₂) of an ecosystem caused by gross primary production and ecosystem respiration originating from biological sources. A positive value represents a net carbon input into the ecosystem
NEE	Net ecosystem exchange: $NEE = R_e - GPP$, defined as the difference between the total quantities of CO ₂ leaving and entering the atmosphere, which is generally interpreted as R _e and GPP. Within the ecosystem, this includes biological and abiotic pathways of CO ₂ release and uptake. A negative sign indicates a loss from the atmosphere, and a gain by the ecosystem.
F _{aquatic}	Total aquatic carbon flux: $F_{aquatic} = F_{DOC} + F_{DIC} + F_{POC} + F_{aq-CO_2} + F_{aq-CH_4} - S$, where F _{DOC} , F _{DIC} and F _{POC} refer to the movement of dissolved and particulate carbon via hydrological discharge, F _{aq-CO₂} and F _{aq-CH₄} are the atmospheric fluxes of aquatic CO ₂ and CH ₄ , and S is the carbon accumulation in sediment. In this review, a positive value represents a net carbon output (loss from ecosystem) for this flux, and S was excluded when referring to F _{aquatic} as most studies did not report this value.
R _a	Autotrophic respiration. Refers to the CO ₂ lost via internal plant metabolism
R _h	Heterotrophic respiration. Refers to the CO ₂ respired via organisms other than plants. This mostly includes the decomposition of organic matter in soils.
R _e	Total ecosystem respiration: $R_e = R_a + R_h$, the sum of autotrophic and heterotrophic respiration.
F _{CH₄}	Net ecosystem exchange of CH ₄ . Refers to the exchange CH ₄ between the atmosphere and ecosystem, where a negative value indicates a loss from the atmosphere and gain by the ecosystem.
F _{PC}	Net lateral transfer of particulate carbon by other processes, often ecosystem specific (e.g. soot emission, animal movement, erosion and deposition, agricultural biomass removal or addition)

1 **Table 2**

Ecosystem	Global extent (km²)	Climate	Number of studies	Catchment size (km²)	Rainfall (mm yr⁻¹)	Literature Reference^a
Agro-ecosystem	48,390,000 ^a	Cool temperate, sub tropical	3	2.24 (1-2.9)	1338 (1081-1740)	1-2
Forest	18,310,000 ^a	Sub arctic, cool temperate, warm temperate	12	998 (0.12-3454)	899 (360-2300)	3-13
Mangrove	160,000 ^b	Tropical	1	n.d	1550	14
Mixed catchment		Sub arctic, cool temperate	7	1551 (1.6-6397)	460 (233-645)	4-5, 15-18
Peatland	4,000,000 ^c	Sub arctic, cool temperate, warm temperate, tropical	21	236 (0.2-3025)	1024 (303-2235)	5, 19-35
Rainforest	16,300,000 ^a	Cool temperate, tropical	7	5 (0.23-8.24)	2178 (1557-4341)	21, 36-39
Wetland	3,000,000 ^d	Cool temperate, sub tropical	7	481 (0.6-1791)	1337 (602-1600)	4, 21, 40-41
Total	90,160,000		59			41

2 *References: ¹Barry and others (2016); ²Webb and others, (In Press); ³Argerich and others (2016); ⁴Buffam and others (2011); ⁵Christensen and others (2007); ⁶Deirmenjian
3 and others (2017); ⁷McCallister and Giorigio (2012); ⁸Oquist and others (2014); ⁹Polsenaere and others (2013); ¹⁰Pumpanen and others (2014); ¹¹Shibata and others (2005);
4 ¹²Wallin and others (2013); ¹³Jonsson and others (2007); ¹⁴Troxler and others (2013); ¹⁵Huotari and others (2013); ¹⁶Juutinen and others (2013); ¹⁷Lundin and others (2013);
5 ¹⁸Ojala and others 2007; ¹⁹Billet and others (2004); ²⁰D'Acunha (2017); ²¹D'Amore and others (2016); ²²Dinsmore and others (2010); ²³Goodrich and others (2017);
6 ²⁴Hendriks and others (2007); ²⁵Jammet and others (2017); ²⁶Karlsson and others (2010); ²⁷Koehler and others (2011); ²⁸Leach and others (2017); ²⁹Levy and Gray (2015);
7 ³⁰Lloyd (2010); ³¹Nilsson and others (2007); ³²Olefeldt and others (2012); ³³Roulet and others (2007); ³⁴Wilson and others (2016); ³⁵Worrall and others (2009); ³⁶Genereux
8 and others (2013); ³⁷Viherrmaa and others (2016); ³⁸Waterloo and others (2006); ³⁹Zhou and others (2013); ⁴⁰Chu and others (2015); ⁴¹Feijtel and others (1985).
9 ^aPongratz and others (2008); ^bAlongi (2009); ^cWaite (1993); ^dTotal wetland area from Mitsch and others (2010) excluding peatland area from Waite (1993)

10 **Figures**

11 Figure 1: Conceptual diagram illustrating components of the NECB. Carbon flux components
12 that were included in our cross-ecosystem assessment are shown in bold lines and arrows,
13 and those that were excluded are highlighted by dashed lines and arrows. Refer to Table 1 for
14 definitions.

15 Figure 2: Global distribution of NECB studies integrating an aquatic flux represented by
16 ecosystem type. Map was sourced from the World borders shapefile available under the
17 Creative Commons Attribution-Share Alike Licence and plotted using ggplot2 in RStudio
18 version 3.4.2

19 Figure 3: Boxplots for terrestrial NEP, total aquatic carbon fluxes (sum of export and evasion,
20 where reported), aquatic carbon offset of terrestrial NEP, and annual net ecosystem carbon
21 budget (NECB, where positive values represent a carbon sink) for different ecosystems from
22 the studies reviewed. Boxes span the interquartile range (25-75% quartiles), whiskers 5-95%
23 of observations, horizontal line the median, and circle points represent outliers. Letters
24 indicate significant differences between the mean of ecosystems (Tukey post-hoc tests, $p <$
25 0.05). Values above boxes represent the sample number for each ecosystem. Details on the
26 exact values and ranges of carbon flux components presented here are summarised in Table
27 S2.

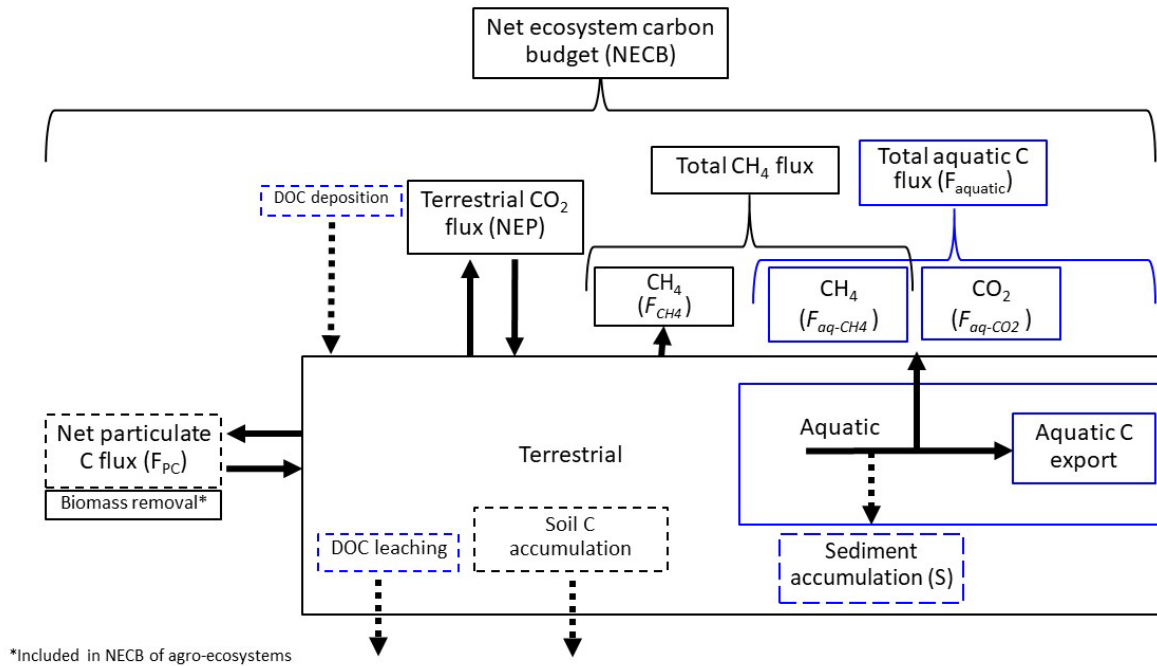
28 Figure 4: Relationship between log₁₀ transformed total aquatic carbon flux (sum of export
29 and evasion, where reported) and terrestrial NEP from individual catchment budgets. Colours
30 represent different ecosystem types and cross symbols reference systems.

31 Figure 5: Linear regression of log₁₀ transformed catchment specific total aquatic carbon flux
32 (A) and catchment specific NEP (B) with annual precipitation.

33 Figure 6: Relative contribution (%) of total aquatic carbon flux ($\text{g C m}^{-2} \text{ yr}^{-1}$) to annual NEP
34 ($\text{g C m}^{-2} \text{ yr}^{-1}$) across a variety of ecosystems. (A) illustrates all studies including negative
35 NEP, and (B) illustrates the linear correlation after \log_{10} transformation of only positive
36 values. Cross symbols represent large scale estimates (Table S2): Global refers to the global
37 estimate; SEpeat refers to disturbed peatlands of South East Asia; Northpeat refers to
38 Northern peatlands; Mangroves refers to the global estimate of mangroves; Sweden refers to
39 the Sweden carbon budget estimate; USA refers to the conterminous United States; and
40 Amazon refers to the regional Amazon estimate. Note that two studies which had aquatic C
41 flux:NEP ratios of 384% and 590% were omitted in 5A due to scale.

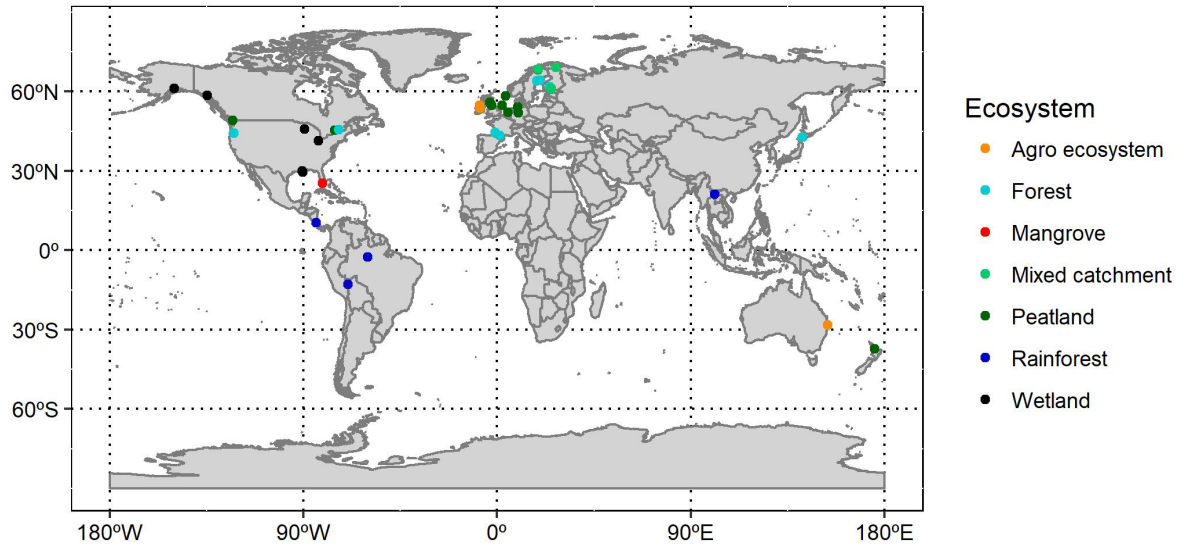
42 Figure 7: Bar plot illustrating the percentage of studies reporting carbon flux components
43 included in the NECB for each ecosystem; Agro-ecosystem ($n = 3$), forest (10), Mangrove (n
44 = 12), mixed catchment ($n = 7$), peatland ($n = 21$), rainforest ($n = 7$), wetland ($n = 7$).

45 **Figure 1**



47 **Figure 2**

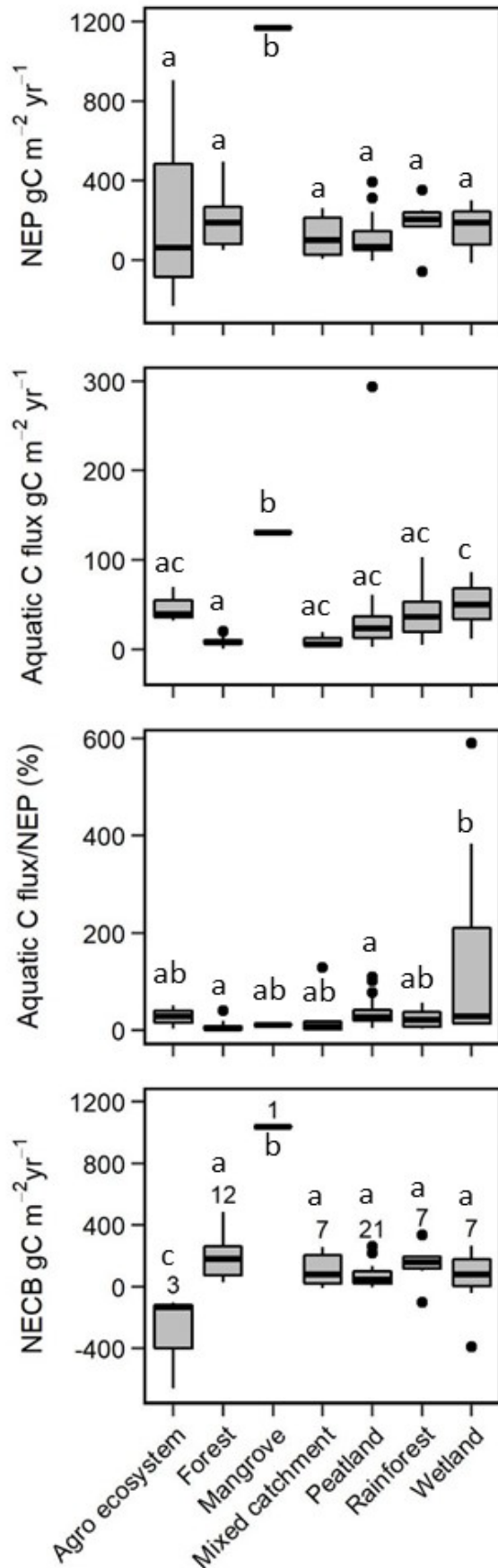
48



49

50 **Figure 3**

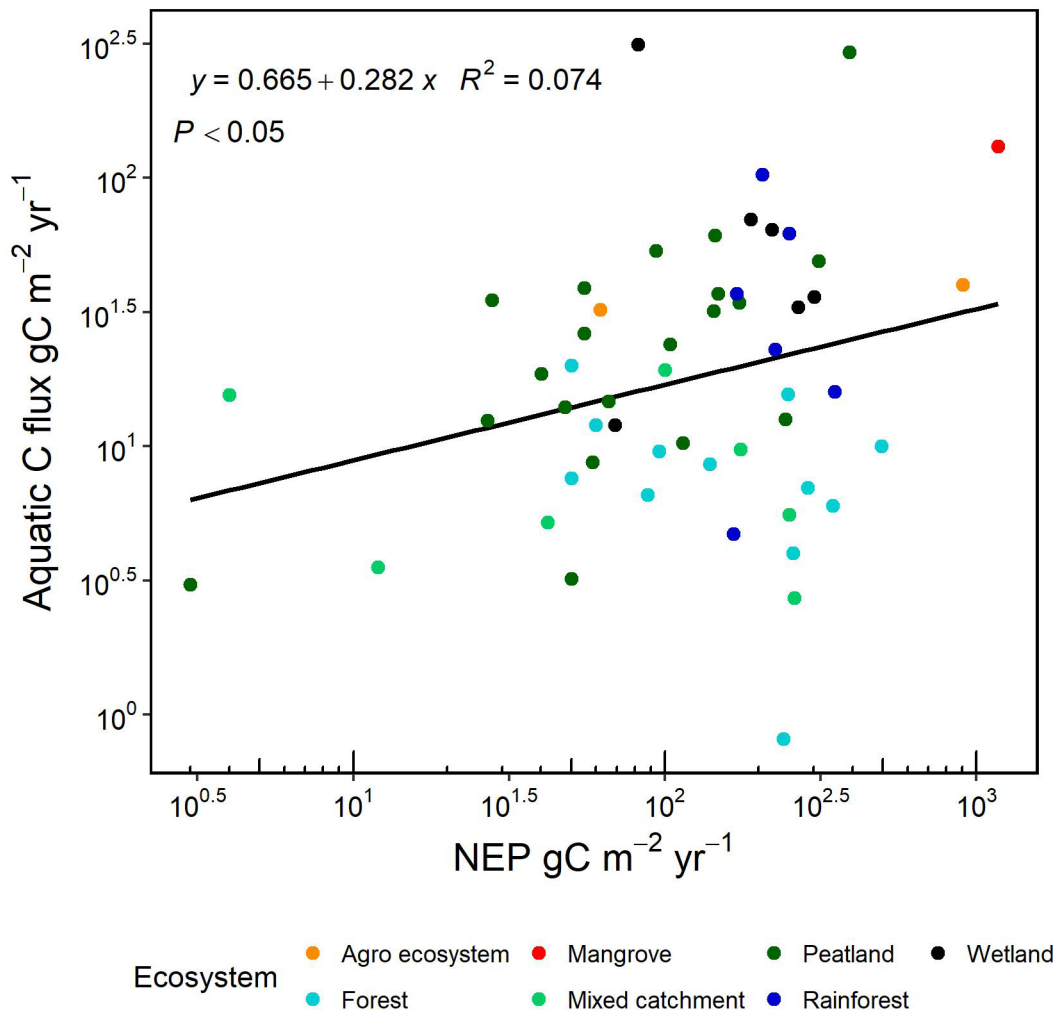
51



52

53 **Figure 4**

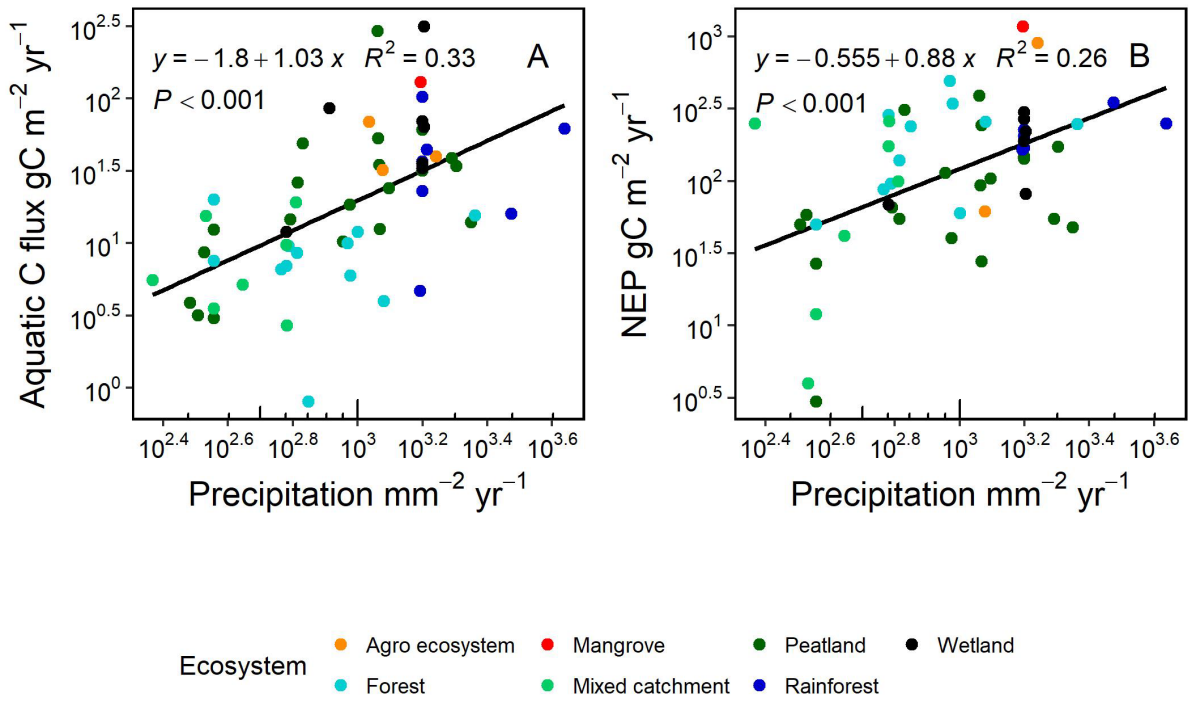
54



55

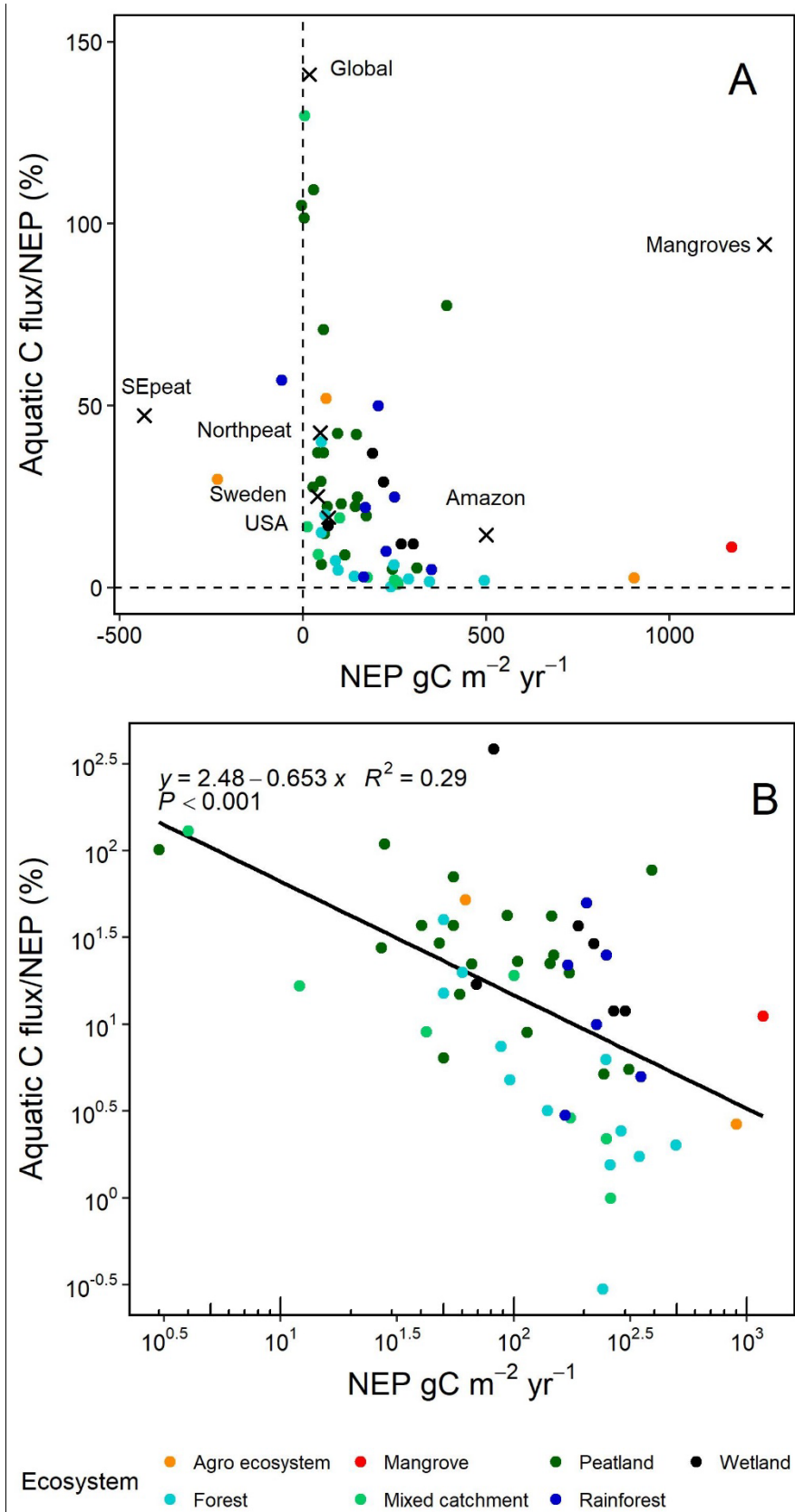
56 **Figure 5**

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59 **Figure 6**



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62 **Figure 7**

