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Review Article

The high-altitude peatland carbon cycle: A review of the impacts of climate change, human disturbance and management

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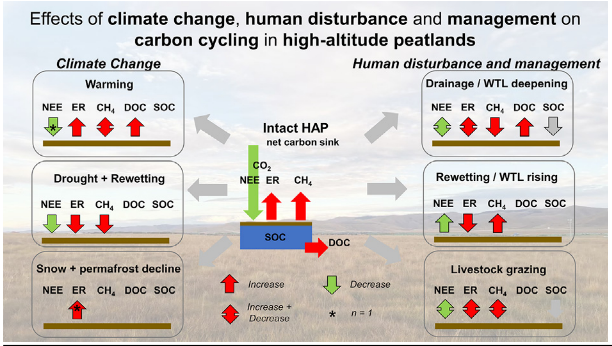
HIGHLIGHTS

- High-altitude peatlands (HAPs) are important C sinks, similar to low-altitude analogues.
- Warming increased HAP C emissions but impacts on vegetation C uptake were less clear.
- Drainage of HAPs clearly increased C losses, which restoration may help recover.
- Peak C uptake in intact HAPs may occur with shallow below-surface water tables.
- The interaction between climate and human management on HAP C cycling is a major knowledge gap.

GRAPHICAL ABSTRACT



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ABSTRACT

High-altitude peatlands (HAPs; defined as > 1,500 m) provide important ecosystem services including soil carbon (C) storage. However, temperatures in high-altitude regions have been rising rapidly in recent decades, while HAPs are increasingly affected by human activities such as intensive drainage and grazing. Collectively, climate change and land management may strongly affect the HAP C cycle. Here, we synthesise current global progress on the HAP C cycle, focussing on the impacts of climate change and land management. Warming increased both ecosystem respiration (ER) and methane (CH_4) emissions (26 %–86 %), while impacts on net ecosystem exchange (NEE) of CO_2 were still unclear. However, short-term drought decreased ER and CH_4 emissions (7 %–96 %), along with NEE (12 %–52 %). Snow, permafrost, and glacier decline may also impact the C cycle in HAPs, although a limited number of studies have been conducted. Grazing and vegetation degradation impacts on HAP C cycling were related to grazing and degradation intensity, while generally decreasing soil organic C stocks (3 %–51 %).

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Moving from shallower to deeper WTLs stimulated ER (9 %–812 %), while reducing CH_4 emissions (13 %–100 %), with variable effects on NEE (-53 %–700 %). Restoration by rewetting began to reverse the trend of drainage. We highlight several knowledge gaps, including limited understanding of climate change and land-management effects on gross primary productivity and dissolved organic carbon, while there is still limited knowledge of regional differences in HAP C cycling. Future research should focus on the interaction of land-use and climate change in HAPs, including HAP restoration, which may help future conservation of these valuable ecosystems.

1. Introduction

Peatlands are major providers of ecosystem services, located across tropical, temperate and boreal zones where waterlogging impedes the decomposition of organic matter. This results in the accumulation of peat, often defined as ≥30 cm soil with ≥30 % organic matter content (Rydin and Jeglum, 2013). A near-surface water table means that peatlands are a type of wetland providing habitat for a wide array of specialist biodiversity, while regulating the discharge and water quality of many rivers (Bonn et al., 2016). Peatlands have a carbon (C)-rich composition, such that they are a dense soil C store, estimated to store around ∼600 Gt C (∼25 % of the world's soil C) (Yu et al., 2010), despite covering only 2.84 % of the global land area (Xu et al., 2018). Peatlands, thus have a climate regulating effect on a global scale (Leifeld et al., 2019). However, climate change, human disturbance and land management are major pressures on peatlands, causing degradation and loss of ecosystem services (including stored C), thereby threatening their long-term sustainability (Dorrepaal et al., 2009; Hopple et al., 2020).

In high-altitude regions, peat accumulation occurs within a narrow climatic window due to temperature induced vegetation zonation, making high-altitude peatlands (HAPs) extremely sensitive to environmental change (Benavides, 2014a; Planas-Clarke et al., 2020). In addition, HAPs typically form from a combination of extreme humidity and cool conditions, leading to peat formation on slopes and substrates that would otherwise be unsuitable at lower altitudes (Gorham, 1957). Despite their widespread prevalence, the global HAP area and distribution remains uncertain (UNEP, 2022). Recent studies have reported significant declines in the intact HAP area in the Zoigê region of the Qinghai-Xizang Plateau (QXP), where drainage, grazing, and climate change have collectively degraded HAPs into meadow and grassland states (Luan et al., 2014; Li et al., 2015). Similarly, many HAPs in the Andes have also been exposed to a greater pressure from grazing, leading to degradation, as the mix and numbers of livestock increase. In some areas, the risk of fire has increased due to drying, while others have received increased glacial meltwater inputs (Benavides et al., 2013; Hribljan et al., 2016). Collectively, the impacts of recent climate change, human disturbance and land management on HAPs are significantly affecting both soil C stocks and recent C accumulation rates across different regions, including the QXP and Andes (Benavides, 2014a; Li et al., 2018; Planas-Clarke et al., 2020). In addition, pressure from future climate change to HAP functioning may be exacerbated, as high-altitude environments are experiencing more rapid climate warming than elsewhere, doubling the global average over the past 40–50 years (Wang et al., 2016; Hock et al., 2019). However, very few studies have postulated if HAPs are at greater risk from climate change than other peatlands, while none have answered this question. Recent research has suggested that future warming may decrease the C sinks in some HAP areas, mainly through increased carbon dioxide (CO_2) emissions (Volkova et al., 2021; Wu et al., 2022). However, many uncertainties remain across the wide range of geographical regions and local environmental conditions encompassed by HAPs (section 3.1).

The effects of climate change and human disturbance and management on HAP are thus significant, yet our understanding of how these valuable ecosystems may be affected by future change remains very limited. To date, few studies have addressed the effects of climate change, human disturbance and management on the HAP C cycle at regional or broader scales (Benavides et al., 2013; Gaffney et al., 2023), as most studies have focused on individual sites. Our review aims to address this knowledge gap by conducting a global-scale analysis of both contemporary and long-term HAP C cycling, which has not been previously attempted (section 2). Critically, we also assess current knowledge of the effects of climate change and human disturbance and management on the HAP C cycle, highlighting key findings, shortcomings and knowledge gaps (sections 3–4). Our analysis indicates future research priorities including key C cycle components, climate change phenomena and land management practices where knowledge is lacking in HAPs. While previous studies of global peatlands evaluated latitudinal and climatic zone effects, those of altitude were not considered. Here, we consider potential altitude effects by comparing C cycling in intact HAPs with other (low-altitude) peatlands, to contextualise this important function in HAPs (section 5). Finally, we discuss possible future trends on the HAP C cycle. Throughout the review, we also discuss regional differences in HAP C cycling in relation to HAP characteristics and local climate, which is important for future management and policy development.

With current and predicted future rates of climate warming in high-altitude regions outpacing the global average (IPCC, 2018), there is an urgent need to understand the effects on the HAP C cycle. In gaining a deeper understanding, progress towards future conservation actions for HAPs can be made, along with protection of their critical ecosystem services.

2. High-altitude peatland characteristics

Following a systematic literature search (Appendix 1 in Supplementary materials 1), we identified 145 studies of C cycling in HAPs, 75 of which were directly included in our analyses (Table S1 in Supplementary materials 1, Fig. 1).

We define HAPs as peatlands located at elevation above 1,500 m. This operational definition considered both the effects of elevation dependent warming and global peatland distribution (see Appendix 1, section A1.1). The HAPs included in our analyses of C cycling spanned a large latitudinal range (47° N to 34 °S), including tropical, subtropical and temperate regions (Fig. 1). Elevation ranges varied across regions: from 1,500 m to 2,500 m (NE China, Japan, Australia, Italy, Austria, Switzerland and California) to 2,500–3,500 m (QXP / Zoigê Plateau and Rocky Mountains), and up to 3,300–4,800 m (Andes). Mean annual temperature (MAT) varied between different HAP studies from -2.0 °C to 13.5 °C (strongly influenced by latitude and elevation), while mean annual precipitation (MAP) varied between 270 mm and 1,816 mm, showing that HAPs can exist through a wide precipitation range, although in many areas, water inputs from glacier meltwater (Andes countries, European Alps, Austria) and permafrost (NE China, Argentina) aid moisture supply (Table 1).

The peat type was mostly poor to rich fen peat (based on pH values) (Rydin and Jeglum, 2013), showing some degree of runoff/groundwater influence (often from upper mountain slopes), although two HAP studies were from ombrotrophic bogs (Australia, Switzerland). Vegetation was mostly dominated by sedges (Zoigê, QXP, Rocky Mountains; often *Carex* spp.), *Sphagnum* mosses (Subtropical China, Japan, Australia, Switzerland), a mixture of the two (NE China, Italy, Austria, Sierra Nevada) or cushion plants, mainly the *Distichia* and *Plantago* genus (Andean HAP). Although cushion plants were the dominant vegetation across Andean HAPs, we also note that both *Sphagnum* and sedges were present in some studies (Table 1).

Table 1

High-altitude peatland (HAP) characteristics across different regions, where studies of HAP C cycling were conducted. Data compiled from the final 75 C cycling studies, identified during the literature search (Table S1 and Appendix A1.8 in Supplementary materials 1). Abbreviations are water table level (WTL), mean annual precipitation (MAP) and mean annual temperature (MAT), while column P/G represents the presence of permafrost or glaciers, respectively. Mean values are presented in bold text, while the range of values for each characteristic is reported in brackets (where available).

Region	Country	Sites	#	Lat-long	Elevation (m)	MAT (°C)	MAP (mm)	Peat type	pH	Peat depth (m)	WTL (cm)	Vegetation	Land use	Snow (cm)	P/G
Zoigê Basin (E QXP)	China	Hongyuan/ Rueorgai counties	43	31°51′ N–34°16′ N, 101°30 E’–103°40′ E	3,430–3,510	**1.4** (0.6–3.6)	**709** (560–860)	fen	**6.8** (6.6–7.0)	**2.6** (0.7–4.4)	**-17.4** (-28.0– -2.0)	Sedge (*Carex* spp. / *Kobresia* spp.)	Drainage, intensive yak, horse, sheep grazing	20	-
NE QXP	China	Luanhaizi, Qinghai, NE QXP	1	37° 35′ N, 101° 20′ E	3,250	**-1.1**	**490**	fen	**-**	**-**	**-**	Sedge (*Carex* spp. / *Kobresia* spp.)	-	-	-
NE China	China	NE Fenghuang mountain, Heilongjiang	2	42°11′ N–44°06′ N, 120°39′ W–128°19′ W	1,541–1,730	**-0.8** (-2.7–2.2)	**620** (391–780)	bog and fen	**-**	**1.8**	**-18.0**	*Sphagnum* spp., Sedge	-	-	P
Subtropical China	China	Dajiuhu, Shennongjia Forestry District, Hubei	2	27°46′ N–31°28′ N, 99°54′ W–110°00′ W	1,760	**6.4** (5.4–7.4)	**1,089** (618–1560)	fen	**5.3** (5.0–5.5)	**3.5**	**-12.5** (-21.0– -4.0)	*Sphagnum* spp.	National park	-	-
Nikko National Park	Japan	Ozegahara Mire, Naka-tashiro	1	36°55′ N, 139°12′ E	1,500	**-**	**-**	fen	**5.3** (4.5–6.0)	**-**	**5.0** (-10.0– 20.0)	*Sphagnum* spp.	Sika deer grazing	-	-
New South Wales Australian Alps	Australian	Kosciuszko National Park	2	34°26′ S, 148°20′ E	1,511–1,801	**9.1**	**1,816**	bog	**-**	**0.6**	**-**	*Sphagnum* spp.	Feral horse grazing	-	-
European Alps	Austria	Otzal Range, Rotmoos valley	3	46°50′ N, 11°03′ E	2,250	**-1.3**	**820**	fen	**-**	**1.7** (0.5–2.9)	**-**	Sedge (*Carex* spp.)	Moderate sheep, horse grazing	235	G
European Alps	Italy	Trento	3	46°01′ N–46°21′ N, 10°49′ E–11°44′ E	1,563-1,800	**4.2** (3.0–5.4)	**1,145** (100–1,290)	fen	**-**	**2.6** (0.8–4.3)	**-27.6**	*Sphagnum* spp., Sedge	Cattle grazing	100	-
European Alps	Switzerland	Hochrajen	1	46°36′ N, 7°58′ E	1,885	**3.5**	**1,620**	bog	**-**	**-**	**-**	*Sphagnum fallax*	-	-	-
Rocky Mountains	USA	Niwot Ridge, Front Range and San Juan Colorado, Medicine Bow Wyoming	4	37°38 N’–41°20′ N, 105°35′ W–107°50′ W	2,600–3,590	**-1.0**	**1,006**	fen	**6.0** (5.0–7.0)	**1.7** (1.0–2.4)	**-12.8** (-45.0– -3.8)	Sedge (*Carex* spp.)	-	37	-
Sierra Nevada	USA	Yosemite National Park, California	1	37°46′ N, 119°44 W	2070–2500	**11.4**	**1065**	fen	**-**	**-**	**-**	*Sphagnum* spp., Sedge	-	-	-
Andes	Colombia	Cordillera Central and Eastern, Nevados and Chingaza National Parks	8	4°50′ N–6°40′ N, 72°16′ W–75°40′ W	4076–4462	**7.7**	**1381** (869–1990)	fen (cushion)	**5.3** (4.7–6.3)	**4.0** (1.2–5.0)	**-11.5** (-20.6– 7.0)	Cushion plants (*Distichia*), *Sphagnum* spp., Sedge	Drainage, grazing, runoff from cropland	-	G
Andes	Equador	Cayambe-Coca National Park, Antisana Ecological Reserve	5	0°18′ S–0°48′ S, 78°08′ W–78°48′ W	3,900–4,800	**6.8** (5.2–10.0)	**1172** (781–1,500)	fen (cushion)	**6.0** (5.2–7.6)	**4.4** (2.9–9.4)	**-15.0** (-24.2– -5.8)	Cushion plants (*Plantago*), herbs, graminoids	Cattle Grazing	-	G
Andes	Peru	Huascaran National Park	2	9°28 S’–9°41′ S, 77°14′ W–77°22′ W	4,200	**13.5**	**698** (632–764)	fen (cushion)	**5.9**	**-**	**-6.1** (-7.6– -4.6)	Cushion plants, herbs, graminoids	Drainage, grazing	-	G
Andes	Bolivia	Manasya, Tuni	3	16°13′ S–18°04′ S, 68°13′ W–69°02′ W	4,615	**4.6**	**554** (321-700)	fen (cushion)	**5.8** (5.0–6.5)	**5.3** (2.0–10.0)	**-16.7** (-20.0– -15.0)	Cushion plants (*Distichia*)	Llama and alpaca grazing	-	G
Andes	Argentina	Parque Provincial Cordon del Plata, Cordillera Frontal, Mendoza	1	32°57′ S, 69°24′ W	3,300–4,800	**-2.0**	**270**	-	**-**	**1.0**	**-**	Sedge	Wild guanaco grazing	2	P, G

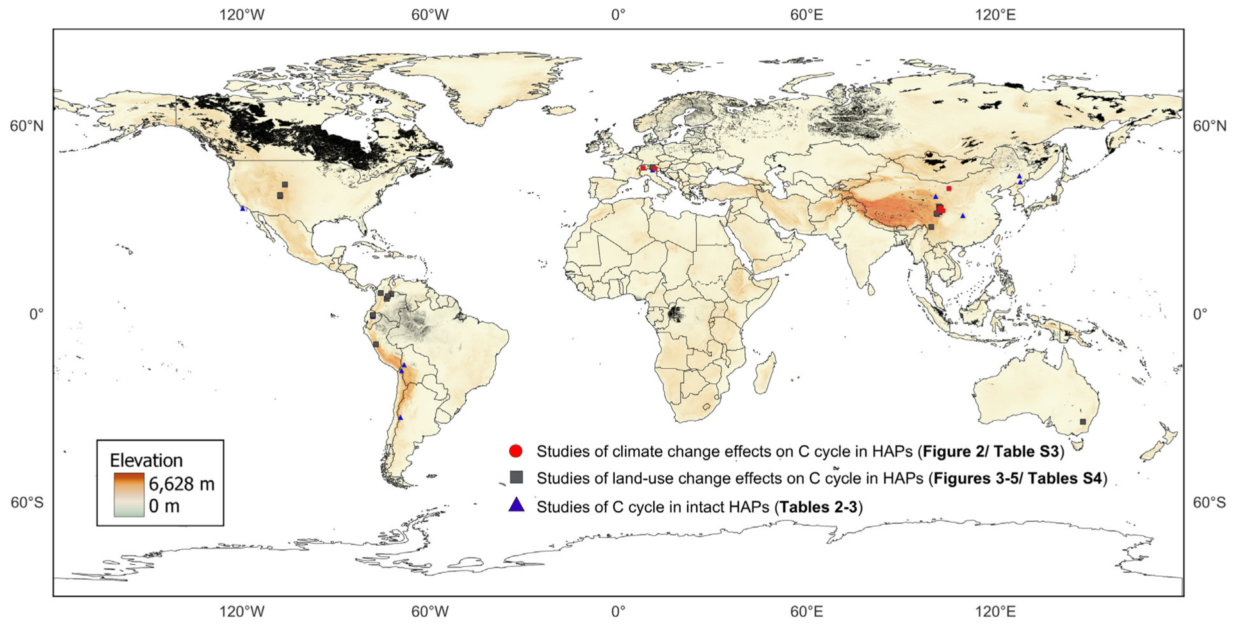

Fig. 1. Global digital elevation model (DEM) with locations of studies of HAP C cycling included in our analyses (Tables 2–3, S3–S6 and Figs. 2–6). Global peat distribution is shown for reference in grey-black shading, with darker shading indicating higher percentages of peatland cover (data provided by PEATMAP; Xu et al., 2018).

Mean peat depth (where recorded) was also generally similar between regions, except in the Andes where reported mean peat depths were deeper (excluding Argentina). Across all studied HAPs (in intact condition), mean WTLs were similar and near surface (as is required for peat accumulation). Some studies recorded snow depths, with significant winter accumulations noted in the European Alps.

2.1. High-altitude peatland carbon cycle

The peatland C cycle is a balance between inputs of CO_2 (gross primary productivity; GPP) and outputs of gaseous and aquatic forms of C, mainly comprising CO_2 (ecosystem respiration, ER), methane (CH_4) and dissolved organic carbon (DOC) (Gaffney et al., 2023; Liu et al., 2024).

It can be represented over various timescales, including the contemporary C cycle, termed net ecosystem carbon balance (NECB), which represents the current C cycle. Historical C accumulation rates (CAR) can be measured over the medium (e.g., tens-hundreds of years) and long-term (e.g., thousands of years) timescales termed recent relative C accumulation (RERCA) and long-term relative C accumulation (LORCA) rates, respectively (Turunen et al., 2002; Yu et al., 2010). The C accumulated and stored as peat is termed soil organic carbon (SOC).

2.2. Carbon accumulation rates

In general, a range in mean LORCA rates have been measured in HAPs, ranging from 11 g C m^2 yr^{-1} to 47 g C m^2 yr^{-1}, although some studies have reported a wider range of CAR between 2 g C m^2 yr^{-1} and 88.4 g C m^2 yr^{-1} from peat cores of different ages (1–11 Ka BP) (Table 2). Most C accumulation studies in HAPs were from China (QXP) and South America (Andes), with similar LORCA rates measured between both regions, although large differences in core ages (signifying the peatland ages) were reported. For future research, it is recommended to explore CAR across a wider geographical range, e.g., including areas such as the European and Australian Alps, and the Rocky Mountains, to better understand variations in C accumulation and peatland initiation across global HAPs.

Meanwhile, in the Andes, current knowledge suggests that many Andean HAPs initiated less than 4 ka BP (Table 2), which may have been related to a combination of human and climatic factors (Domic et al., 2018; Huaman et al., 2020). Over the last 2000 years Andean pastoralists may have played a role in HAP development and expansion, by diverting water to grazing areas (Domic et al., 2018; Yager et al., 2021). In earlier times, the Mid-Holocene Climatic Anomaly from around 3.06 ka BP to 3.34 ka BP, may have reduced Andean peat (and C) accumulation due to a drier climate and deeper water tables (Huaman et al., 2020). More recently (1.4 ka BP) increased moisture levels in the South American Antiplano may have aided an expansion in peat formation, on what were previously largely grassland areas (Domic et al., 2018). In contrast, peatlands on the QXP in China are significantly older. Here, peatland initiation began around 17 ka BP with an expansion in peatland initiation and formation occurring 10–11.5 ka BP related to climatic factors, including strong climatic seasonality, increased solar insolation and changes in moisture related to monsoon activity (Chen et al., 2014; Zhao et al., 2014). Although similar LORCA rates were found between QXP and Andean peatlands, differences in peat bulk density, peat accumulation rates and C content were found, which may help explain how similar depths of peat accumulated over different timescales (Table 2).

Recent C accumulation (RERCA) has been investigated in HAPs from China (QXP and North East China), South America (Andes) and the USA (California), ranging from 43 g C m^2 yr^{-1} to 4,000 g C m^2 yr^{-1} (Table 2). The Andes HAP generally had the largest RERCA values, followed by QXP, NE China and Californian HAP. In Andean HAP, C accumulation rates are among the highest for high-altitude ecosystems on earth, due to the fast growth rates of *Distichia muscoides* cushion plants, which can result in peat accumulation rates of 10–30 mm yr^{-1} (Benavides et al., 2013; Cooper et al., 2015). Indeed, RERCA from *Distichia* peat (e.g., 184–4,000 g C m^2 yr^{-1}; Cooper et al., 2015; Benfield et al., 2021) was considerably higher than RERCA rates from non-*Distichia* Andean HAP, dominated by brown moss, herbs and graminoids (43–219 g C m^2 yr^{-1} ; Hribljan et al., 2016; Table 2). Meanwhile, fens dominated by sedges on the QTP showed higher RERCA (279–392 g C m^2 yr^{-1}), than ombrotrophic bogs in NE China dominated by Sphagnum and ericaceous shrubs and sedges (129–204 g C m^2 yr^{-1}), which was generally higher than sedge fens in the Sierra Nevada, California (54–120 g C m^2 yr^{-1}) (Table 2). Thus, while vegetation plays an important role in determin-

Table 2

Carbon accumulation in HAPs measured as long-term relative C accumulation (LORCA) and recent relative C accumulation (RERCA) from a range of studies. Additional data including core ages and depths, carbon content and bulk density are provided where available for additional context. Mean values are presented in bold text, while the range of values for each parameter is reported in brackets (where available). The number of cores, *n*, specifically refers to numbers used in calculation of carbon accumulation rates (CAR). For full reference list, see Appendix 1 (Supplementary materials 1; section A1.8).

Study	Location	GPS	Elevation	Core ages (ka BP)	Depth Cores (cm)	Carbon Stocks (kg C m^{-2})	Carbon Content %	SOC storage/ density (kg/ m^3)	Bulk Density (g / cm^3)	Peat accum. rate (mm yr^{-1})	LORCA (g C m^2 yr^{-1})	RERCA (g C m^2 yr^{-1})
Sun et al., 2001	Hongyuan, Zoigê, China	32°46′ N, 102°30′ E	3,500	115,00						(0.3–0.6)		
Large et al., 2009	Hongyuan, Zoigê, China	32°46′ N, 102°30′ E	3,500	9,600	620		**38.4** (22.5–54.7)	(1–231)	**0.09** (0.00–0.83)		**11.0**	
Zhao et al., 2011	Zoigê, China	32°27′ N, 102°39′ E	3,467	10,304	650				**0.10**		**30.6**	
Wang et al., 2014	QTP China	32°20′ N, 101°30′ E	3,467	1,000–15,500							**32.3** (20.7–52.3)	
Chen et al., 2014	QTP China	32°20′ N, 101°30′ E	3,467	1,635–14,095	20–600		(9.9–38.9)	(11–174)	(0.05–0.09)	(0.1–0.9)	**20.4** (5–48)	
Zeng et al., 2017	Hongyuan, Zoigê, China	32°46′ N, 102°30′ E	3,509	14,057	450				**0.35** (0.20-1.40)	**0.4** (0.2–0.5)	**34.0** (17.5–52.3)	
Zhao et al., 2014	Zoigê Basin, China	32°20′ N, 101°30′ E	3,467	60–11,500	35–870		**35.3**		**0.16**	(0.1–1.7)	**31.1** (2.0–88.4[*])	
Liu et al., 2018	Zoigê Plateau (modelling)	32°10′ N, 101°45 E	3,350–3,450	0–12,000	460–599					**0.5** (0.4–0.5)	**26.0** (23–29)	
Yang et al., 2023	NE China	42°11′ N, 128°19′ E	1,730	1,160–8,414								
Benfield et al., 2021	Columbia	6°20′ N, 72°19′ W	4,076–4,462	1,463–10,932	30–320	**0.5** (0.4–0.6)					**19.6** (6.2–43.8)	
Hribljan et al., 2024	Colombia (average, *n* = 8)	5°13′ N, 74°00′ W	3,640	11,810	491	**175.2** (67.6–423.0)	**31.6** (15.9–47.3)	**52.6** (29.3–90.4)	**0.20** (0.06–0.34)		**23.8** (7.7–105.3)	
Hribljan et al., 2016	NE, Ecuador	0°30′ S, 78°14′W	3,900-4,800	3,412–8,036	294–605	**89.8** (59.8–134.7)	**21.2** (19.1–23.9)		**0.22** (0.17–0.27)	**0.8** (0.5–1.4)	**16.3** (9–30)	
Chimner and Karberg, 2008	Ecuador	0°48′ S, 78°48′W	3,968	3,122	395	**133**	**20.7** (8.0–37.0)		**0.40** (0.17–0.62)	**1.3**	**46.0**	
Hribljan et al., 2017[**]	Ecuador	0°48′ S, 78°08′W	>3,500	MODELLED	350–940	(135.8–285.8)	(14.0–16.0)	(28.2–34.2)	(0.28–0.43)			
Hribljan et al., 2024	Equador (average, *n* = 8)	0°30′ S, 78°17′ W	4,135	5,368	392	**81.7** (24.5–132.6)	**15.4** (10.3–30.0)	**47.6** (37.5–65.4)	**0.40** (0.14–0.55)		**30.9** (13.3–53.9)	
Hribljan et al., 2024	Peru (average, *n* = 7)	9°28′ S, 77°22′ W	4,201	8,127	514	**155.0** (43.1–403.1)	**25.4** (8.1–33.5)	**52.8** (38.4–70.6)	**0.30** (0.12–0.76)		**26.6** (6.4–45.7)	
Hribljan et al., 2015	Bolivia, Manasya	18°04′ S, 69°02′ W	4,496	3,675	500	**104.0**	**24**	**35.8**	**0.17**	**1.4**	**47**	
Hribljan et al., 2015	Bolivia, Tuni	16°13′ S, 68°13′ W	4,615	2,563	550	**57.2**	**47.8**	**21.5**	**0.05**	**2.2**	**37**	
Hribljan et al., 2024	Bolivia (average, *n* = 2)	16°13′ S, 68°13′ W	4,358	7,332	478	**137.4** (107.5–1673.0)	**36.0** (24.1–47.8)	**31.2** (22.5–40.0)	**0.20** (0.05–0.17)		**46.8** (41.9–51.6)	
Li et al., 2018	Huahu Lake, Zoigê, China	33°55′ N, 102°46 E	3,430	180	13–20		**45.9** (37.3–56.1)		**0.45** (0.43–0.53)	**1.4** (1.3–1.7)		**316** (279–392)
Ma et al., 2016	Hongyuan, Zoigê, China	31°51′ N, 101°51 E	>3,000		30			**69.5**				
Bao et al., 2015	NE China (Great Hinggan, Changbai, Fenghuang mountains)	44°06′ N, 128°02 E	1,541–1,690	188–212	29–78	**31.0** (27–52)	(17.9–38.1)		(0.08–0.37)			**158** (129–204)
Drexler et al., 2015	California, USA	33°46′ N, 119°44 W	2,070–2,500	50	30		(32.2–43.6)	(26–65)	(0.06–0.18)	(1.6–3.2)		(63–120)
Drexler et al., 2015	California, USA	33°46′ N, 119°44 W	2,070–2,500	100						(1.3–2.3)		(54–100)
Benavides, 2014b	Colombia	5°41′ N, 73°25′ W	3,563–3,831	110	35	(7.5–15.0)						**150**[****]
Benfield et al., 2021	Colombia	6°20′ N, 72°19′ W	4,076–4,462	14–131	23–161	**0.5** (0.3–0.7)						**449** (184–850)
Benavides et al., 2013	Colombia	6°28′ N, 72°16′ W	4,300–4,700	50						(3.6–6.4)		(200–300)
Benavides et al., 2013	Colombia	6°28′ N, 72°16′ W	4,300–4,700	10								**1,400**
Hribljan et al., 2016	NE, Ecuador	0°30′ S, 78°14′W	3,900–4,800	118–490	70–100	**18.7** (12.8–24.5)	**30.0** (29.9–30.0)		**0.15** (0.14–0.16)	**4.7** (1.3–8.1)		**131** (43–219)
Cooper et al., 2015	Bolivia	16°13′ S, 68°13′ W	>4,450	1.5	30[***]				**0.08** (0.04–0.14)	(9.6–53.7)		(1,500–4,000)
Kuhry et al., 2022	Argentina	32°57′ S, 69°24′ W	3,300–4,800		30	**11.3**						
Kuhry et al., 2022	Argentina	32°57′ S, 69°24′ W	3,300–4,800	335	100	**23.1**						

[*] full range modelled using mean bulk density and C content,

[**] remote sensing estimates + modelling,

[***] crank wires method estimates of C accumulation (not coring),

[****] calculated from data presented in paper (approximate)

ing RERCA rates in HAPs, climate and other local factors also exert a strong influence, which could be further explored in future research to gain a better understanding of controlling factors.

2.3. Net ecosystem carbon balance (NECB)

Several studies ($n = 13$) have reported components of NECB for intact HAPs. Between 2008 and 2017, HAPs, on average, accumulated 125 $\mathrm{g\,C\,m^2\,yr^{-1}}$ as CO_2, while emitting 22 $\mathrm{g\,C\,m^2\,yr^{-1}}$ as CH_4 (Table 3). However, these estimates carry substantial uncertainty (particularly for CO_2, SD = 117). To allow estimation of NECB for HAPs, we included the mean DOC export reported in the literature for other peatlands (< 1,500 m), as there were no reports of annual DOC export from HAPs (and in general a lack of information on DOC in HAPs; see Appendix 1, section A.1.4.1 in the Supplementary materials 1). On average, we estimate HAPs were a C sink accumulating 88 ± 118 $\mathrm{g\,C\,m^2\,yr^{-1}}$. The large standard deviation around this mean estimate suggests that HAP can range from a large C sink to a small C source. We also estimated the greenhouse gas (GHG) balance of HAPs (CO_2 and CH_4 only), using a 100-year global warming potential (IPCC, 2022). On average, over a 100-year period, we estimate that HAPs on average are a net GHG source 334 ± 726 g CO_2 $\mathrm{m^2\ yr^{-1}}$ (Table S2 in Supplementary materials 2). However, the GHG balance was influenced by the relatively large annual CH_4 emissions measured from Zoigê HAPs (of which there were several measurements conducted), while limited measurements were undertaken in other HAPs (which had lower CH_4 emissions). Therefore, more data are needed to refine GHG balance estimates in HAPs.

In terms of net ecosystem exchange (NEE) of CO_2 and CH_4 emissions, results were mostly derived from eddy covariance (continuous, landscape scale) measurements ($n = 10$), while some annual estimates ($n = 3$) were derived from year-round flux chamber measurements (Table 3). Although all measurements were conducted intact, i.e. relatively pristine HAP, some ($n = 2$) were found to be net CO_2 sources (located in the northeast QXP and Italian Alps, respectively). These sites had a short CO_2 uptake period and high respiration rates, tipping the CO_2 balance to a net C source (Pullens et al., 2016; Song et al., 2021). However, most HAPs ($n = 8$) were found to be net CO_2 sinks of varying magnitudes on an annual timescale (Table 3), with considerable interannual variation within sites due to differences in local climatic and hydrological conditions (Hao et al., 2011; Yao et al., 2022). Some variation in NECB components was also observed between sites; a subtropical HAP (China), dominated by Sphagnum (and with high MAP and MAT; 1,560 mm and 7.4 °C), showed the highest NEE (CO_2 uptake). In contrast, sedge fens in Zoigê (China) and the Austrian Alps exhibited a lower NEE (although similar to each other; Table 3). Although substantial progress has been made in understanding annual NECB in HAPs, there have been no reports from areas such as the Andes, Rocky Mountains or Australian Alps. Continuous annual measurements (such as Eddy Covariance towers) in these areas would vastly help improve understanding of variation in NECB across global HAPs. Current estimates are also limited by a lack of DOC export measures from any intact HAPs, which should be a future research priority.

Annual CH_4 emissions from minerotrophic (fen) HAPs on the QXP were generally similar (ranging from 32 $\mathrm{g\,C\,m^2\,yr^{-1}}$ to 45 $\mathrm{g\,C\,m^2\,yr^{-1}}$), while considerably higher than from a subtropical Sphagnum HAP (China; 4–8 $\mathrm{g\,C\,m^2\,yr^{-1}}$), which was more similar to that of a nutrient-poor sedge fen (Italy; 2 $\mathrm{g\,C\,m^2\,yr^{-1}}$; Table 3). Differences in CH_4 emissions were likely related to HAP nutrient status, vegetation type, and peat composition (Chen et al., 2011; Cheema et al., 2015; Villa et al., 2019). For example, CH_4 emissions from *Carex* dominated fens (QXP) may be higher than that of *Sphagnum* bogs or forested fens, because they may be wetter or contain more vascular plants which contribute to CH_4 production, transport and emission (Franchini et al., 2015; Chen et al., 2021).

3. Effects of climate change on the high-altitude peatland carbon cycle

3.1. Climate change in high-altitude peatland regions

High-altitude areas have experienced higher rates of warming than elsewhere in recent decades, thus they are particularly vulnerable to climate change (Wang et al., 2016; Wang et al., 2018). For example, mountain surface air temperatures from Western North America, the European Alps and High Mountain Asia have seen increases of 0.3 °C $\mathrm{decade^{-1}}$ (Hock et al., 2019), higher than the global warming rate of 0.2 °C $\mathrm{decade^{-1}}$ (IPCC, 2018), although at the local and regional scale elevation dependent warming patterns are more heterogeneous and variable (Wang et al., 2018; Hock et al., 2019). Data (ERA 5) extracted from all the HAP study regions included in our analyses, showed that mean air temperatures (1980–2015) have increased between 0.1 °C $\mathrm{decade^{-1}}$ and 0.8 °C $\mathrm{decade^{-1}}$ (average 0.4 °C $\mathrm{decade^{-1}}$), while 56 % (of study regions) showed significant warming trends, greater than the global average (Table S3 in the Suppmentary mateirals). Of these regions, the European Alps exhibited the greatest significant warming trend (0.4–0.8 °C $\mathrm{decade^{-1}}$), while the New South Wales Australian Alps showed the lowest significant rate of warming (0.1 °C $\mathrm{decade^{-1}}$). At the regional scale, warming patterns have led to differing changes in growing and non-growing season mean temperatures in HAPs (Li et al., 2015), with some regions (e.g., European Alps) experiencing enhanced warming in summer, while others show greater warming during winter (QXP) (IPCC, 2018; Liu et al., 2022).

Changes in annual precipitation patterns in high-altitude areas in recent decades are less apparent, with no clear trends in recent decades across mountain regions (Hock et al., 2019). We also found that most of the HAP study regions in our analyses showed non-significant changes in total annual precipitation, while NE China, subtropical China, the Rocky Mountains and Colombia showed significant decreases of 0.1–0.2 mm $\mathrm{day^{-1}}$ $\mathrm{decade^{-1}}$ from 1980 to 2015 (Table S3). Future projections for the 21st century include 5 %–20 % precipitation increases in some areas (Asia, European Alps) while decreases in others (Southern Andes) (Hock et al., 2019). Data from CMIP 6 suggest similar patterns between these regions, albeit of a smaller magnitude (Table S3).

Rising temperatures also suggest that snowfall (and snow cover) will continue to decrease in coming decades due to warming, along with shrinking of permafrost (Hock et al., 2019; Hu et al., 2022). For example, on the QXP (much of which is permafrost covered), permafrost cover has shrunk in recent decades and the lower limit has increased by 100–200 m altitude on the north-eastern side (Wang et al., 2017). The thermal insulation effects of overlying HAP may help slow the permafrost temperature increase somewhat (Yang et al., 2015; Wang et al., 2017). Similarly, most high-mountain glaciers have also shown recession and mass loss in recent decades, which was primarily driven by atmospheric warming (Zemp et al., 2015; Hock et al., 2019). In some HAPs, glacier melting has increased water supply with impacts on C cycling (Benavides et al., 2013).

3.2. Warming temperatures

Increasing temperatures have resulted in significant changes to NECB components in HAPs (Fig. 2 and Table S4). In general, warming of between 1.5 °C and 5 °C resulted in an increase between 26 % and 86 % in CO_2 emissions (ER) (Fig. 2c), from a small range of studies including the Zoigê Plateau (sedge fens, China) and the European Alps (ombrotrophic bogs, Switzerland). Notably, warming studies with and without precipitation manipulation showed similar effects on ER (Table S4), while their effects on DOC (concentrations) were more variable (-7 % to 22 %; Fig. 2j).

Increased ER and DOC concentrations in HAPs have been mainly attributed to increased heterotrophic respiration (Lou et al., 2014; Bragazza et al., 2016; Yang et al., 2017b), e.g., from increased organic

Table 3

Net ecosystem carbon balance (NECB) of HAPs, estimated from studies measuring NECB components using eddy covariance (EC) and flux chamber methods. The final mean NECB is derived for mean NEE, CH$_4$ and DOC components. Abbreviations are water table level (WTL), mean annual precipitation (MAP) and mean annual temperature (MAT). All EC studies include continuous year-round measurements, while flux chamber studies include measurements in all seasons. For full reference list, see Appendix 1 (Supplementary materials 1; section A1.8).

Study	Location		GPS	elevation (m)	type	WTL (cm)	MAP (mm)	MAT (°C)	vegetation	years	method	Annual NECB (g C m^{-2} yr^{-1})				
												NEE	CO_2 GPP	ER	CH4	DOC
Hao et al., 2011	China	Zoigê National Wetland Natural Reserve	33° 56′ N, 102° 52′ E	3430	ombrotrophic bog		650	1.1	*Carex muliensis* and *Eleocharis valleculosa* (aquatic area), *Kobresia tibetica*, *Cremanthodium pleurocaule*, *Potentilla bifurca*, and *Pedicularis* sp. (hummocks)	2008	EC	-47.0	-89.8	542.7		
										2009		-79.0	-672.1	592.4		
Song et al., 2021	China	Luanhaizi peatland	37° 35′ N, 101° 20′ E	3250	fen	+20 (GS)	490	-1.1	*Kobresia tibetica*, *Carex pamirensis*, *C. alrofusca*, *Blysmus sinocompressus*, *Hippuris vulgaris*, and *Triglochin palustre*	2018/19	EC	41.5	-631.5	673.0		
Yao et al., 2022	China	Hongyuan County	32° 46′ N, 102° 30′ E	3510	fen	-	746	1.8	*Carex muliensis* and *Kobresia tibetica*	2014	EC	-226.0	-898.0	671.4		
										2015		-185.0	-776.8	591.5		
Peng et al., 2015	China	Hongyuan County	32° 46′ N, 102° 30′ E	3510	-	-2 – -28	560–860	0.6–1.2	*Carex muliensis* and *Kobresia tibetica*	2013/14	chamber			600.0		
Liu et al., 2019	China	Riganqiao peatland, Hongyuan County	33°06′ N, 102°39′ E	3400	-	-	720	1.5	-	2013	EC	-187.0				
										2014		-133.0				
										2015		-199.0				
										2016		-284.0				
										2017		-53.0				
Wu et al., 2018	China	Ruoergai, Hongyuan County	32° 46′ N, 102° 30′ E	3510	-	-	746	1.8	*Carex muliensis* and *Kobresia tibetica*	2015		-80.0				
Peng et al., 2021	China	Hongyuan County	32°46′ N, 102°30′ E	3510	-	-	746	1.8	*Carex mulieensis* and *Kobresia tibetica*, *Caltha palustris*, *Gentiana formosa*, and *Trollius farreri*	2014	EC	-91.0			37.0	
										2015		-44.0			33.0	
Peng et al., 2019	China	Ruoergai, Hongyuan County	32° 46′ N, 102° 30′ E	3510	-	-	746	1.8	*Carex muliensis* and *Kobresia tibetica*	2008	EC				35.1	
Chen et al., 2021	China	Riganqiao peatland, Hongyuan County	33°06′ N, 102°39′ E	3460	fen (pH 6.6-7)	-22.3	748	3	*Carex muliensis* and *Scirpus triqueter*	2013	EC				33.0	
										2014					44.8	
										2015					38.9	
										2017					32.3	
Liu et al., 2024	China	Dajiuhu peatland, Hubei province	31°28′ N, 110°00′ E	1760	-	-4 – -21	1560	7.4	*Sphagnum palustre*, *Carex argyi*, *Juncus effusus*, *Festuca rubra* and *Sanguisorba officinalis*	2016	EC	-233.9			4.0	
										2017		-320.1			5.8	
										2018		-342.3			8.0	
										2019		-192.3			6.6	
										2020		-285.9			6.5	
Koch et al., 2008	Austria	Otzal Range, Rotmoos valley	46°50′ N, 11°03′ E	2250	wet fen	near surface	820	-1.3	*Carex Nigra* (30 % cover)	2003	chamber	-58.0				
										2004		-53.0				
Koch et al., 2008	Austria	Otzal Range, Rotmoos valley	46°50′ N, 11°03′ E	2250	fen	-	820	-1.3	*Carici echinatae*, *Trichophoretum caespitosi* (100 % cover)	2003	chamber	-134.0				
										2004		-96.0				
Pullens et al., 2016	Italy	Trento, Italy	46°01′ N, 11°02′ E	1563	fen, nutirent poor	-27.6±18	1290	5.4	*Carex rostrata, Valeriana dioica, Scorpidium cossonii* and *scattered Sphagnum* spp., *C. nigra*, *Trichophorum alpinum* and *Drosera rotundifolia*, *Molinia caerula*, *Eriophorum vaginatum*, *Calluna vulgaris*	2012	EC	28.2	-272.6	300.8	2.4	
										2013		71.7	-309.3	381.0		
										2014		47.9	-340.6	388.5		
Estimated DOC*										-						15.4*
Mean												-125.4			22.1	15.4
SD												117.2			16.3	5.1
NECB												**-87.8**				
SD												**118.4**				

* Estimated DOC compiled from other intact peatland studies (not HAPs) - see table S6/ Appendix 1.

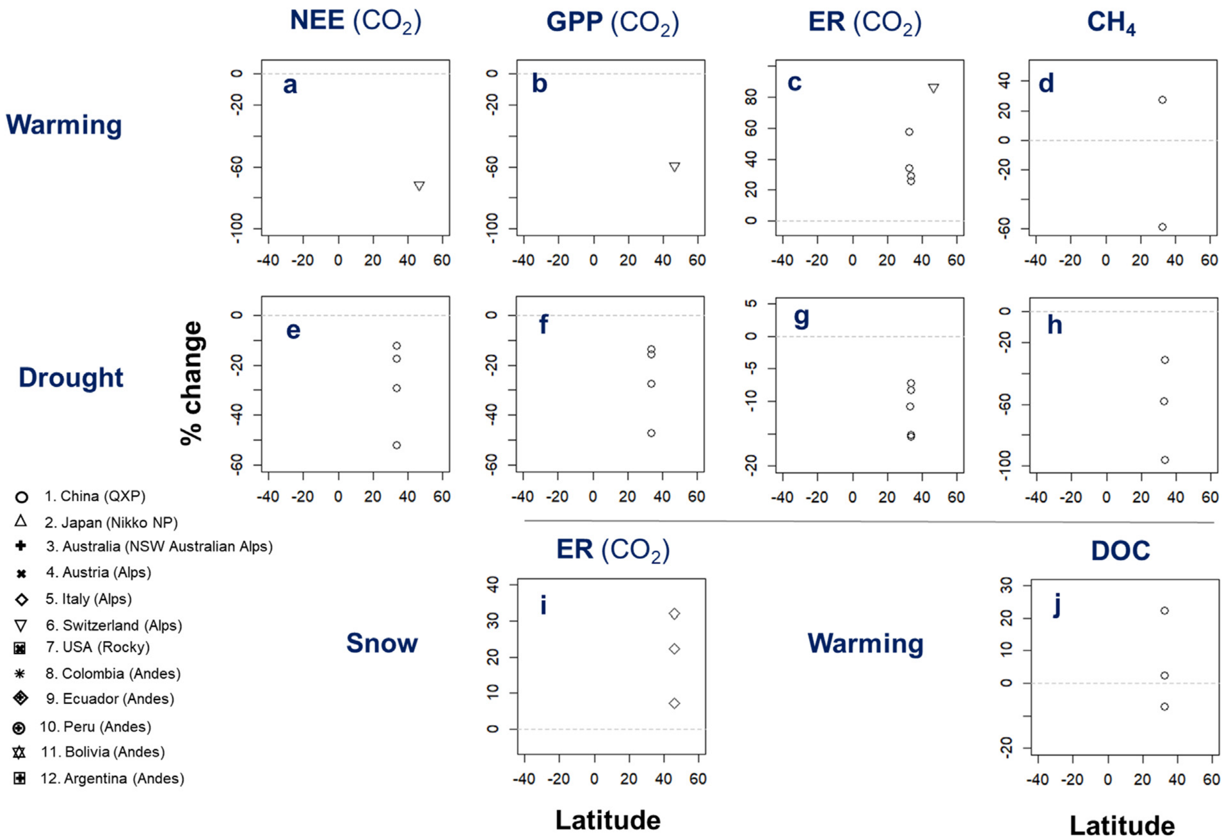

Fig. 2. The effects of climate change manipulations on NECB components, including warming (a–d, j), drought (e–h) and snowmelt timing manipulation (i). Data presented are percentage changes (*y*-axis) in net ecosystem exchange (NEE), gross primary productivity (GPP), ecosystem respiration (ER), methane (CH_4) emissions and dissolved organic carbon (DOC), in treatments relative to controls (unimpacted reference) in manipulative studies across global HAPs, represented by latitude (*x*-axis). Symbols correspond to HAPs in different countries, where HAP C cycling studies were found. For raw data and further details of each study (data point), see Table S4 in Supplementary materials 2.

matter decomposition by soil microbes. In support of this theory, recent work also showed that warming increased soil fungi vertical distribution (Wang et al., 2022). Additionally, decomposition may also be in part, stimulated by root exudates from increased vascular plant below-ground biomass (Bragazza et al., 2016).

Increasing temperatures in HAPs have often resulted in vegetation changes, in both the Zoigê and European Alps regions (Bragazza et al., 2013; Yang et al., 2015), and may also act to lengthen the plant growing season (Yao et al., 2022). Experimental warming on the QXP reduced species richness and diversity in HAPs, while increasing vegetation cover, above- and below-ground biomass (Yang et al., 2015). Similarly, in the European Alps, increased summer HAP temperatures were found to decrease *Sphagnum* mosses and increase vascular plants (Gerdol et al., 2008), while other studies have shown increases in ericaceous shrub abundance following a warming gradient (Bragazza et al., 2013). Such changes may both increase vegetation C uptake (GPP), while potentially priming heterotrophic respiration and peat decomposition through release of labile C substrates (Bragazza et al., 2016). However, very few studies have considered warming effects on GPP (Table S4), which future research should address. Current knowledge is mainly limited to warming effects on ER during the growing season.

Experimental warming (+ 1.9 °C) in Zoigê HAP, was also found to increase CH_4 emissions (+27 %; Fig. 2d), (Yang et al., 2014), while methanogenic community composition was not affected by warming (Cui et al., 2015). In contrast, the combination of warmer (+ 2 °C) and drier conditions (20 % precipitation reduction) was found to decrease CH_4 emissions (-59 %; Table S4) in Zoigê HAP compared to ambient conditions. Decreased CH_4 emissions may be partly due to reduced peat temperature sensitivity, production of other substrates from organic matter decomposition and increased CH_4 oxidation, all of which can occur under lower moisture conditions (Yang et al., 2014; Wu et al., 2020).

3.3. Permafrost, freeze-thaw and snow

Many HAPs are located in permafrost zones, which are affected by increasing temperatures, thus changes to freezing and thawing cycles may also impact upon the HAP C cycle in regions such as the QXP and Altai-Sayan Mountains (which border China, Mongolia, Russia and Kazakstan) (Rao et al., 2020; Volkova et al., 2021; Yang et al., 2022). Specifically, research from the Xinjiang (China) Altai mountains suggested that permafrost thaw at high elevations (e.g., ~4,000 m) could increase water supply at lower elevations (e.g., ~1,700 m), where HAP were located (Rao et al., 2020). Similarly, shrinkage of glaciers in the Xinjiang region has increased meltwater runoff by approximately 10 % in the past three decades (Xu et al., 2010). In the Andes, increased glacier meltwater, has enhanced growth of *Distichia muscoides* peatlands (Colombia) over the past 10 years, favouring increased peat and C accumulation (Benavides et al., 2013). *Distichia* peat occurs at key points in time, often associated with mineral inputs washed in from melting glaciers (Benfield et al., 2021). Rapid C accumulation, following a temporary increase in mineral inputs, particularly phosphorus, is a phenomenon recorded across many different peatland types (Hughes et al., 2013; Kylander et al., 2018). In relation to deglaciation, this feedback is poorly understood but could potentially cause a large impact on HAP C accumulation. Future research should therefore explore deglaciation effects on the HAP C cycle in more detail, as they are relevant to many HAP areas (Cooper et al., 2015; Zhang et al., 2020).

In addition, other recent research (from Zoigê HAP) demonstrated that the thawing period in HAPs (when soil temperatures were continuously > 0 °C) was the largest contributor to the annual CH_4 budget (69 %–83 % annual emissions), compared to frozen, frozen-thawing, and thawing-freezing periods (Chen et al., 2021). Thus, if increasing temperatures in permafrost zones increase the length of the thawing period, CH_4 production and emissions may potentially increase (Yang et al., 2015; Chen et al., 2021). Furthermore, as the active soil layer expands due to permafrost warming, plants may exploit deeper water and nutrient resources, increasing deep root biomass (Yang et al., 2015), impacting on C cycling and decomposition processes in these deeper layers (Volkova et al., 2021).

Changes to snow cover may also potentially affect HAP C cycling due to effects on soil moisture, soil nutrients and microbial biomass (Bombonato and Gerdol, 2012). HAP snow cover manipulation experiments from the European Alps (Italy) found that either late or early snowmelt slightly increased mean ER (7 %–32 %; Fig. 2i; Table S4). The limited impact of snow manipulation suggested that summer ER was dominated by autotrophic respiration (and decoupled from microbial biomass and heterotrophic respiration by soil microorganisms; Bombonato and Gerdol, 2012).

3.4. *Drought*

Drought is an increasingly likely future scenario under warmer, drier conditions (Jia et al., 2019). In HAPs, drought periods caused a reduction in ER, CH_4 emissions and GPP (Fig. 2e–h), shown by a range of studies from Zoigê HAPs (Table S4), leading to an overall decrease in NEE (i.e., reduced C uptake). Reductions in ER under short- term droughts (defined here as 32 days without precipitation) were relatively small (7 %–15 %; Fig. 2g) and often not statistically significant, while NEE decreases were greater (12 %–52 %; Fig. 2e), showing that GPP (plant uptake of CO_2) was significantly reduced by drought (Table S4 and Fig. 2f). During drought periods, soil temperature continued to regulate maximum CO_2 uptake and release (Kang et al., 2018) and despite a reduction in NEE, the peatlands studied remained net C sinks for CO_2 during the growing season (Table S4). Notably, we found no reports of longer-term drought impacts on HAP C cycling, while current studies were all from the China in the QXP.

In HAPs, drought induced decreases in GPP may be due to water stress potentially reducing C fixation through photosynthesis (Yan et al., 2021). Similar responses have been observed in other peatlands, which were found to optimise water use efficiency over long periods of time, showing reductions in C uptake during times of drought (Kettridge et al., 2016). The observed reductions in ER were likely due to reduced plant root and microbial respiration (Kang et al., 2018). Reduced C fixation under drought may have reduced labile C substrate availability, while microbial activity was likely also limited by water stress (Kang et al., 2018; Yan et al., 2021). Similarly, in response to drought, activities of the enzymes responsible for labile C turnover (hydrolases) increased, while activities of enzymes responsible for decomposition of more recalcitrant C (oxidases) decreased. This suggests a potential drought induced change in HAP organic matter composition (Yan et al., 2020), which may also likely impact soluble decomposition products and DOC concentrations (Fenner and Freeman, 2011). However, we did not find any reports of drought induced changes on DOC in HAPs.

Similarly, drought significantly reduced CH_4 emissions, with the relative decrease in CH_4 emissions due to drought was larger than that for ER (31 %–96 %; Fig. 2h; Table S4). One study showed a change from functioning as a CH_4 source to a CH_4 sink in response to summer drought, which may be caused by an increased thickness of the aerobic soil layer, where CH_4 is oxidised rather than emitted to the atmosphere (Kang et al., 2018). In general, drought periods with no precipitation, can represent a transition from anaerobic to aerobic conditions in HAPs, decreasing CH_4 generation and enhancing CH_4 oxidation, overall acting to decrease CH_4 emissions (Wu et al., 2020).

3.5. *Fire*

Drought conditions may be followed by fires, which are also a risk to HAP ecosystems (Hock et al., 2019), although we found limited reports of HAP wildfire incidences. However, in HAPs of Peru, fires are widespread, particularly in the adjacent drier grasslands which then spread to peatlands (Román-Cuesta et al., 2011). In these montane forested peatlands (just below the alpine grasslands) fire which occurred during a severe drought (in 2005) was found to reduce SOC stocks (in the top 40 cm) by up to 89 % (Román-Cuesta et al., 2011). Due to climate change (warming) the incidence of peatland fires may increase (Jia et al., 2019), risking further loss of peat SOC (through combustion) (Román-Cuesta et al., 2011).

4. Effects of human disturbance and management on the high-altitude peatland carbon cycle

4.1. *Human disturbance and management in high-altitude peatland regions*

High-altitude peatlands are commonly utilised by humans living in the surrounding areas (Zhang et al., 2014; Yager et al., 2021). Land-use is limited by near surface water tables and harsh climatic conditions, meaning only specialist vegetation species can thrive there (Shang et al., 2013; Benavides, 2014b). Livestock grazing is widely practiced by local people, and is the main land-use, as other forms of agriculture are often infeasible (Xiang et al., 2009; Zhang et al., 2011). Generally, drainage of HAP is required to lower water tables and encourage growth of more suitable grazing vegetation (Li et al., 2015; Cao et al., 2018), which may include networks of ditches around one metre deep and several metres wide, connected to natural drainage streams (Zhang et al., 2014).

Grazing has been practiced in Andean HAPs by pastoralists over the last 2,000 years, when camelid grazing was the main economic activity (Domic et al., 2018). Currently livestock numbers are high, with a greater mix of animals and grazing has damaged peatland vegetation and function (Salvador et al., 2015; Hribljan et al., 2016; Planas-Clarke et al., 2020). Andean HAPs are important water and food sources for livestock and are commonly managed for grazing alpaca and lama along with non-native animals such as sheep, cattle, horses and goats, which may be more damaging to HAPs due to different grazing methods and increased trampling (Benavides, 2014a; Fonkén, 2015; Domic et al., 2018).

Similarly, on the QXP peatlands, grazing of yak and cattle is commonly practiced, as the main form of agriculture here (Xiang et al., 2009; Yang et al., 2017a), while grazing numbers have also increased significantly since the 1950s (Zhang et al., 2011). Reports of overgrazing by horses, cattle and sheep in HAPs in the Altai Mountains, has also led to degradation and loss of peat accumulating ecosystems (Volkova et al., 2021). In the European Alps, grazing of HAP by sheep and horses has been reported as a traditional land-use (Koch et al., 2007). Yet, there are fewer reports of human impacts on HAPs here, perhaps as many of the peatlands are smaller areas, less utilised by humans (Franchini et al., 2015). However, in general for HAPs, where grazing density is not regulated, overstocking can result in negative impacts. More sustainable practices are thus needed to protect HAPs from grazing damage (Yager et al., 2021).

4.2. *Grazing and agriculture effects on carbon cycling*

Grazing in HAPs has been found to both increase and decrease NEE, ER and CH_4 emissions in comparison to non-grazed control sites (Fig. 3a–b,d). NEE has been found to increase and decrease by similar amounts (+81 % to -118 %) from studies in both Andean (Ecuador) and

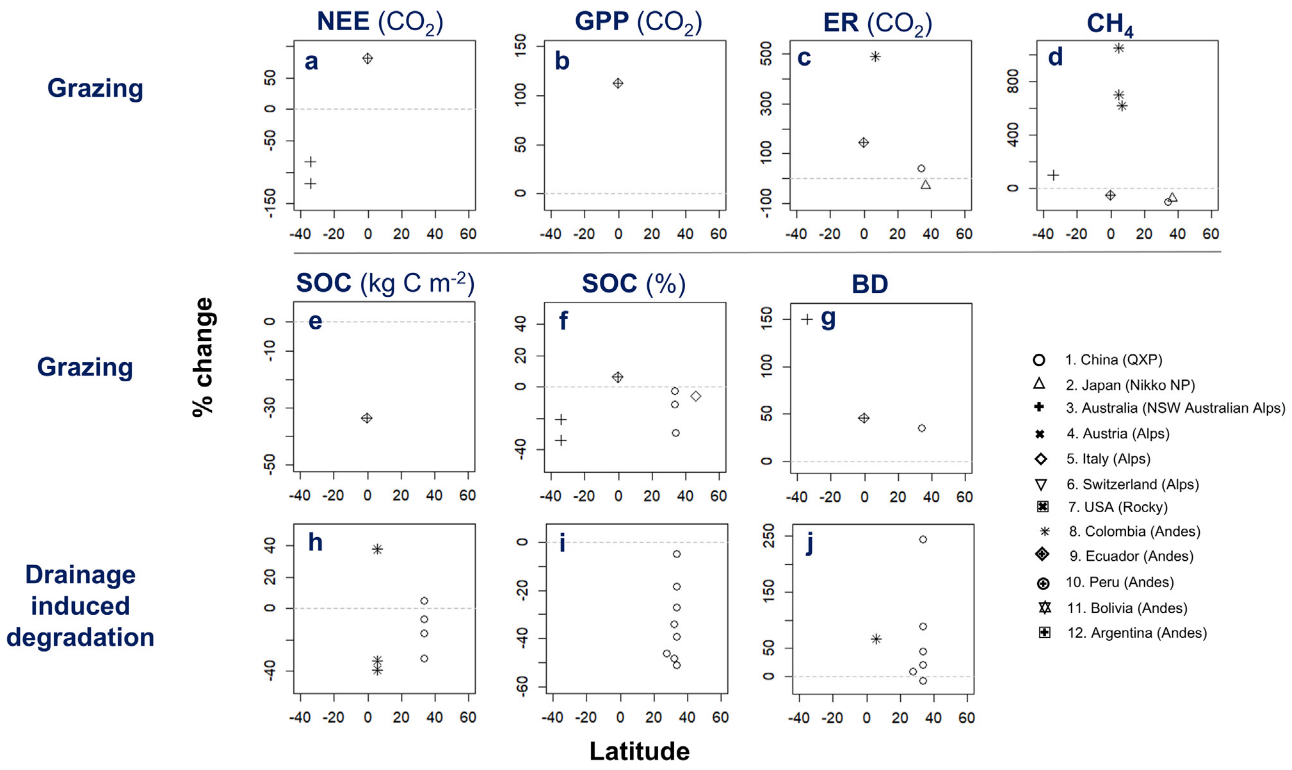

Fig. 3. The effects of human disturbance and management on net ecosystem carbon balance (NEBC; a–d) and soil organic carbon (SOC; e–j) in HAPs, including effects of grazing/ animal impacts (a–g) and drainage induced degradation (h–j). Data presented are percentage changes (*y*-axis) in net ecosystem exchange (NEE), gross primary productivity (GPP), ecosystem respiration (ER) and methane (CH_4) emissions (a–d), and SOC stocks (e, h), % carbon (f, i) and bulk density (BD; g, j) in treatments relative to controls (unimpacted reference) in field studies across global HAPs, represented by latitude (*x*-axis). Symbols correspond to HAPs in different countries, where HAP C cycling studies were found. For raw data and further details of each study (data point), see Tables S5 (NECB) and S6 (SOC). For effects of drainage on NECB, see Fig. 4.

Australian HAPs, respectively (Fig. 3a; Table S5 in Supplementary materials 2). Increased NEE was likely due to an increased density of vascular plants which can result from moderate grazing, thus accumulating more C through plant productivity (GPP) (Sánchez et al., 2017). However, few studies have actually measured grazing impacts on GPP to support this theory (Table S5). On the other hand, in Australian HAPs grazed by feral horses, loss of *Sphagnum*, the dominant vegetation, reduced vegetation C uptake and correspondingly NEE was decreased (Treby and Grover, 2023). Therefore, the dominant vegetation may play an important role in determining grazing impacts; *Sphagnum* bogs may be more vulnerable than sedge peatlands.

Most studies found that grazed sites had higher ER (42 %–490 %; Fig. 3c; Table S5). Trampling by grazing animals and vegetation consumption can reduce plant height and biomass, increasing bare ground, peat temperature and oxygen exposure. Cumulatively, this can cumulatively increase heterotrophic respiration (by soil microbes) and therefore ER (Sánchez et al., 2017; Ma et al., 2020a). In contrast, grazing can also increase species richness, as the natural peatland vegetation community undergoes succession (Bergamini et al., 2001). Vegetation changes may also partly explain why one HAP study found that sites grazed by deer had lower ER than non-grazed sites (Nakayama et al., 2022). However, intensively grazed and trampled sites with patches of bare ground are likely net C sources, thus the grazing intensity strongly influences the impacts on C cycling (Sánchez et al., 2017; Treby and Grover, 2023). Current research has therefore highlighted the negative impacts of intensive grazing on C cycling in HAPs.

Grazing had huge impacts on CH_4 emissions, with increases and decreases observed in HAPs globally (+1,050 % to -97 %; Table S5). The fertilisation effect of animal manure may increase CH_4 production potential (Veber et al., 2018), while an elevated supply of root exudates in some grazed sites may also increase substrate available for CH_4 production (and emissions) (Sánchez et al., 2017). Notably, grazing effects on CH_4 emissions also differed between vegetation communities. For example, sedge communities experienced greater emissions and a greater increase under grazing disturbance than cushion plants (Benavides et al., 2023). Conversely, decreases in CH_4 emissions under grazing may have been due to a dominant control of a deeper WTL and lower soil moisture between grazed and non-grazed sites, limiting CH_4 production and promoting its oxidation to CO_2 (Ma et al., 2020a; Nakayama et al., 2022).

Grazing can also significantly affect SOC stocks and content in HAPs (Fig. 3e–g), with most studies showing a decrease in both in response to grazing (-3 %– -34 %; Table S6 in Supplementary materials 2). As this effect was common between both Zoigê (China; sedge dominated), Australian (Sphagnum dominated) and Andean (Ecuador; cushion plant) HAPs, it suggests that a negative impact of grazing on SOC may be generally common across different peatland types. Impacts may also be influenced by mechanical disturbance by different grazing animals browsing and digging soil during grazing. Likewise, animal excreta can influence soil pH, microbial communities and enzyme activity, collectively increasing SOC decomposition (Liu et al., 2019; Nakayama et al., 2022). In addition, trampling/compaction from grazing animals, has also been found to increase peat bulk density (36 %–150 %; Table S6) (Ma et al., 2020b; Treby and Grover, 2023).

4.3. *Drainage and water table effects on carbon cycling*

In general, we found that WTL was a strong control on C cycling in HAPs, and the collated data (incorporating mesocosm studies and field studies from intact vs drained sites and sites with naturally different WTLs) show strong differences in all NECB components in relation to WTL differences (5–128 cm) within studies (Fig. 4; Table S5). More specifically, the effects of artificial drainage, which is widely im-

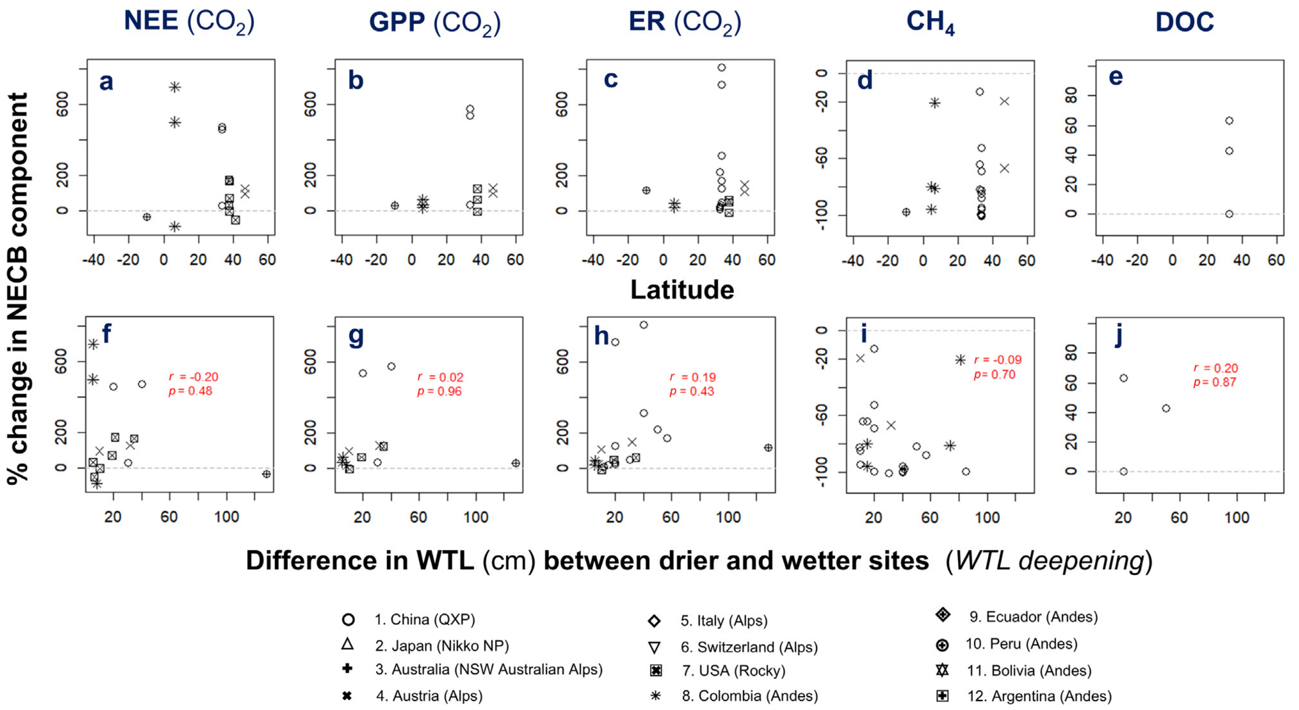

Fig. 4. The effects of drainage and water table level (WTL) drawdown on NECB components. Data presented are percentage changes (*y*-axis) in net ecosystem exchange (NEE), gross primary productivity (GPP), ecosystem respiration (ER), methane (CH_4) emissions and dissolved organic carbon (DOC), in treatments relative to controls (unimpacted reference). Data are collated from field and mesocosm studies across global HAPs, represented by latitude (*x*-axis; a–e). NECB data are also plotted against the difference in WTL (i.e., the magnitude of lowering) between treatments (drier) and controls (wetter) (f–j). Symbols correspond to HAPs in different countries, where HAP C cycling studies were found. For raw data and further details of each study (data point), see Table S5.

plemented across global HAPs, are also described separately (section A2.1; Appendix 2).

Most studies (n = 12) found an increase (28 %–700 %) in NEE (whereby the peatland sequestered more CO_2) under deeper WTLs (of 5–35 cm), while a few studies (n = 4) found that NEE decreased (-4 % to -90 %), resulting in lesser CO_2 uptake (6–128 cm deeper). The change in NEE showed a weak negative relationship with the amount by which WTL lowered, and in some cases the largest effects on NEE were found under relatively small WTL differences (Fig. 4f). We did not observe any patterns in NEE changes with specific regions or peat types, with the largest changes found in studies from Colombia (Andes) and China (Zoigê; Fig. 4a). Overall, the collated data implied that in some HAPs, slightly deeper WTLs (e.g., between 20 cm and 35 cm below surface) may enhance C uptake (Table S5). However, in the case of HAP artificial drainage, NEE decreased (n = 1; Table S5; section A2.1, Appendix 2 in Supplementary materials 2), in line with that from other peatlands (Liu et al., 2024). Clearly more studies of drainage on NEE and GPP are still needed to better understand effects on the HAP C cycle.

Under modestly deeper WTLs where NEE increased (i.e., C uptake increased), this may be attributed to vegetation differences (e.g., succession; Koch et al., 2008). For example, the expansion of certain groups such as ericoid shrubs, which typically inhabit drier parts of pristine peatlands and can increase photosynthetic capacity (Martin and Adamson, 2001), while potentially supressing heterotrophic respiration (Ward et al., 2015). In line with this, we generally observed concurrent GPP increases, where NEE increased (Fig. 4b and Table S5). On the other hand, decreases in NEE may be related to poor growth of peatland vegetation under drier conditions (Millar et al., 2017; Planas-Clarke et al., 2020) or the well described disturbance effect where peatland vegetation remains adapted to the previous water table regime (Laiho, 2006).

Almost all HAP studies showed ER increases (9 %–812 %) under deeper WTLs (5–128 cm; Table S5). Little regional variation in ER changes under a deepening WTL were found (Fig. 4c), except that the largest changes in ER were all mesocosm studies (Zoigê peatland, China; Table S5). Field studies mostly showed more modest ER increases (9 %–172 %), under a wide range of WTL differences (deepening between 12 cm and 128 cm). In general, deeper WTLs increase aerobic decomposition and heterotrophic respiration in HAPs, thus ER increases (Cao et al., 2018; Zhou et al., 2021). Overall, we observed a weak positive relationship between WTL difference and change in ER in HAPs, although the largest ER increases found were under moderate WTL differences (Fig. 4h).

Our data collated on the NEE and ER response to WTL lowering in HAPs is consistent with how peatlands behave elsewhere. Typically plant production, and thus also autotrophic respiration, is limited at both shallow and deep water tables (Belyea and Clymo, 2001; Laitinen et al., 2008; Ratcliffe et al., 2019). Optimal C accumulation tends to occur in a mid-range of WTLs that supresses heterotrophic respiration while being non-limiting to plant production (Belyea and Clymo, 2001; Ratcliffe et al., 2019). Current studies of WTL effects in HAPs, thus demonstrate that WTL controls on CO_2 exchange align with general peatland norms.

Methane emissions consistently decreased (13 %–100 %) under a lowered WTL by between 9 cm and 85 cm (Table S5). Observed changes were similar across all regions, while there was no clear relationship with WTL differences (Fig. 4d, i). Under a lowered WTL, increased aeration of surface peat can decrease CH_4 production by methanogens (Zhou et al., 2017), while enhancing methanotroph biomass (microorganisms oxidising CH_4 to CO_2) (Cao et al., 2018).

Few studies investigated the effects of WTL on DOC concentrations and export in HAP. Two Zoigê mesocosm studies showed that DOC concentrations increased between 0 % and 64 % as WTL lowered between 20 cm and 50 cm (Table S5; Fig. 4e), likely due to increased aerobic decomposition (heterotrophic respiration) (Lou et al., 2014), which has also been well documented in other peatlands around the world (Liu et al., 2024). However, limited data are available on DOC in HAPs

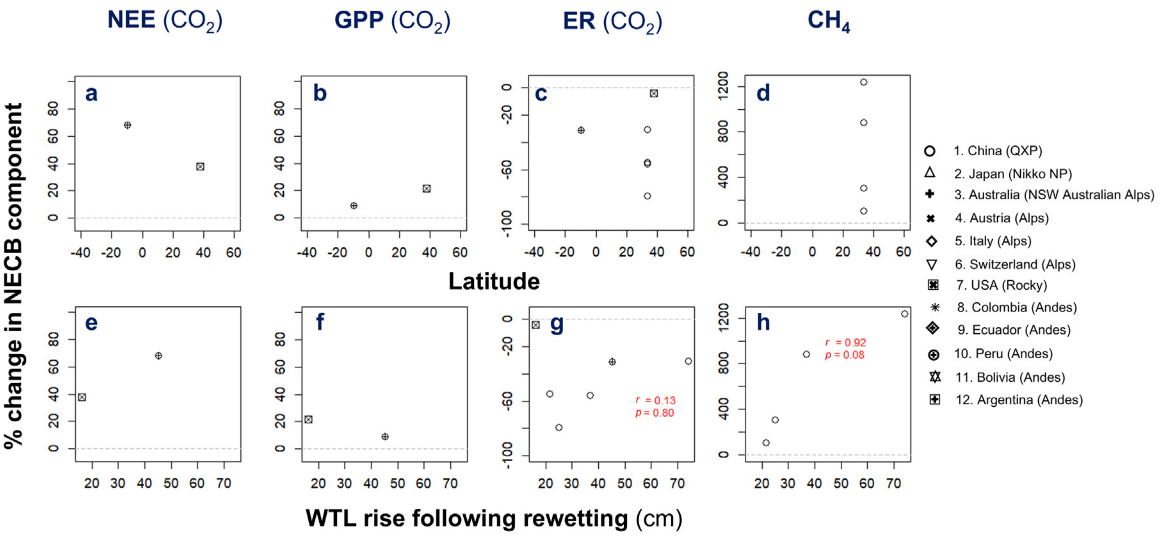

Fig. 5. The effects of restoration by rewetting on NECB components. Data presented are percentage changes (*y*-axis) in net ecosystem exchange (NEE), gross primary productivity (GPP), ecosystem respiration (ER) and methane (CH_4) emissions between post- and pre-rewetting in restoration sites from field studies across global HAPs, represented by latitude (*x*-axis; a–d). NECB data are also plotted against the WTL rise (in cm) following rewetting (e–h). Symbols correspond to HAPs in different countries, where HAP C cycling studies were found. For raw data and further details of each study (data point), see Table S5.

in general, therefore it is important for future work to consider effects on DOC in relation to all aspects of human disturbance and management, including WTL changes.

4.4. Restoration and rewetting in high-altitude peatlands

Peatland restoration aims to improve ecosystem services from peatlands which are degraded and in sub-optimal condition, often due to artificial drainage (Andersen et al., 2016). Peatland restoration generally requires rewetting and hydrological restoration of a near-surface water table, followed by native vegetation and biogeochemical function (Gaffney et al., 2018; Hancock et al., 2018). Most commonly, restoration is carried out on drained peatlands by damming of drainage ditches to raise the water table level (Gaffney et al., 2020). In HAPs, similar restoration practices have been undertaken (Table S5). Indeed, following restoration by ditch blocking (which raised WTL between 17 cm and 25 cm), two studies measured increased NEE (C uptake; 38 %–68 %) within one-year post-restoration (Fig. 5a). In one case (Rocky Mountain sedge fens), C uptake at the restoration site exceeded that of the intact reference sites (Schimelpfenig et al., 2014). However, in the other (a cushion plant dominated minerotrophic peatland), a similar NEE increase was observed in both restoration and unimpacted reference sites, as all experienced a water table rise during the study (Table S5) (Planas-Clarke et al., 2020). Therefore, results from these limited studies are not consistent in showing an effect of ditch blocking on NEE.

Restoration of HAP by rewetting has also been shown to decrease ER (4 %–79 %) and increase CH_4 emissions (104 %–1,238 %) in response to a WTL rise of between 17 cm and 74 cm, in the first one-two years following restoration (Fig. 5c–d, Table S5). Thus, in the short-term, restoration appeared to reverse the trend of drainage and water table lowering, in minerotrophic HAPs from Zoigê (China), Rocky Mountains (USA) and Andes (Peru), with differing dominant vegetation species. These results are in agreement with a recent meta-analysis of global peatland rewetting (Liu et al., 2024). However, from the data collated, no clear relationship was found between the magnitude of change in WTL and ER (weakly positive; Fig. 5g). In contrast, there appeared to be a positive relationship between the rise in WTL and change in CH_4 emissions from Zoigê peatlands (Fig. 5h; $n = 4$). Studies from other (possibly more disturbed) peatlands have shown recovery of C sink function over time following restoration, gradually trending towards intact conditions (~15 years) (Hambley et al., 2019). Although early restoration results from HAP suggest that C cycling may respond very quickly (Table S5), long-term results are yet to be reported.

Future policy in HAPs should seek to reverse effects of drainage, through ecohydrological restoration measures, such as drain blocking to improve function in degraded areas. However, it is important to continue research in this area to understand the longer-term trends in C cycling following restoration and times for recovery of other functions, to inform policy developments. Additionally, it is important for decision makers to understand, the specific restoration measures which are most successful in HAPs and how different drained and degraded areas, respond to different restoration techniques (Gaffney et al., 2022). Therefore, pilot restoration schemes, may be appropriate in the first instance, with sufficient monitoring of their success, which can then be implemented at larger scale. However, due to local population grazing needs it is also important to balance conservation with the need for maintaining livelihoods. Research has shown that light grazing can be beneficial to the C cycle in some HAPs, therefore prioritising managed grazing in key areas is important to ensure that the local population can maintain grazing income (perhaps at more regulated grazing densities). In other more degraded areas, restoration can be prioritised, perhaps in areas designated as nature reserves, where conservation is the main management goal.

5. Contextualising high-altitude peatland C cycling, future trends and research needs

In our data synthesis, we found that the C cycle of HAPs was similar to that of other peatlands both in long term (LORCA) and contemporary accumulation rates (NECB), providing comparable C storage services in high-altitude areas across the globe (Fig. 6). For example, we estimated a NECB of -88 ± 118 $g\,C\,m^2\,yr^{-1}$ for intact HAPs, and collated data for other intact peatlands across the globe of -29 ± 43 $g\,C\,m^2\,yr^{-1}$, while we collated LORCA values of 29 ± 11 $g\,C\,m^2\,yr^{-1}$ and 17 ± 3 $g\,C\,m^2\,yr^{-1}$, respectively. Similar effects of climate warming have also been reported in other peatlands (LAPs) with warming causing increases in ER (Dorrepaal et al., 2009) and CH_4 emissions (Hopple et al., 2020), although we have not analysed the response of peatlands at different altitudes to climate warming as part of this study. However, from our synthesis in HAPs, we highlight several knowledge gaps, which future research should address. First, there are very few studies of warming effects on HAP C cycling, especially with regard to NEE (which consid-

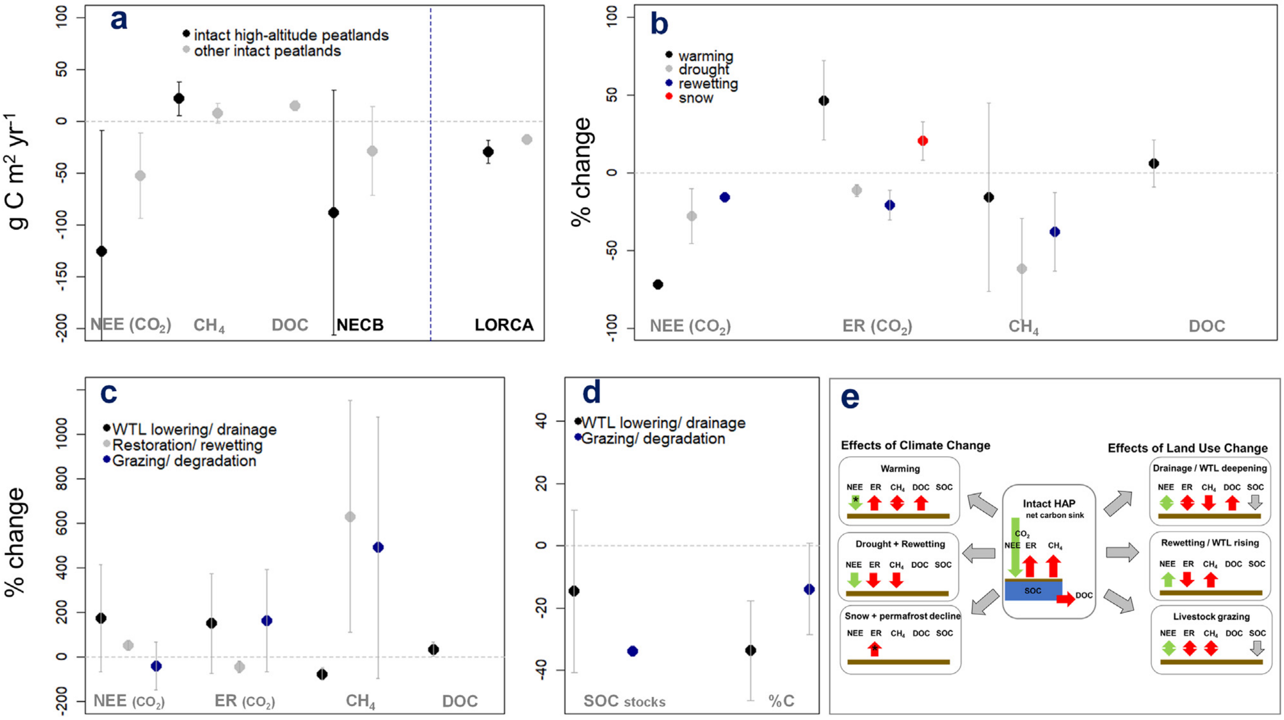

Fig. 6. (a) Comparison of NECB (mean ± SD) and LORCA in HAPs with other intact peatlands around the world. HAP data derived from Tables 2–3. For intact other peatlands, see supplementary material for list of studies and data (Table S7 in Suppmentary materials 2). (b) Summary of effects of climate change manipulations on HAP C cycling. The mean percentage change (± SD) are derived from climate manipulation studies in Table S4. (c and d) Summary of effects of land-use change on HAP C cycling, mean percentage changes (± SD) for NECB components (c) are derived from Table S5, while corresponding changes for SOC components (d) are based on Table S6. For panels (b–d), means with no error bars are derived from only one study, while data gaps are also shown in panel (b) DOC has only been measured in warming studies, other climate treatments did not include impacts on DOC. (e) Graphical summary of the effects of climate change and land-use change on HAP C cycling derived from Tables 2–3 and Figs. 2–5. Arrows represent the general direction of change in response to each scenario, while double arrows show that both increase and decreased were found. (*) indicates based on only one study, while data gaps are shown where no arrows are present. Abbreviations are NEE (net ecosystem exchange), ER (ecosystem respiration, i.e., CO_2 emissions), CH_4 (methane emissions), DOC (dissolved organic carbon), SOC (soil organic carbon).

ers both CO_2 uptake and emissions). Future research should focus on gaining a better understanding of warming effects on GPP, so that ER changes can be contextualised and the net effect on CO_2 exchange can be determined. Similarly, more measurements of warming effects on CH_4 emissions and DOC are also needed, while in general studies of warming should be conducted across more HAP regions. At present, the limited studies of warming effects on HAP C cycling have been conducted only in the QXP and European Alps, while other regions such as the Andes and Rocky Mountains should be considered in future research. Second, the effects of drought on HAP C cycling are also understudied, while most warming and drought studies have been conducted in the QXP, with limited geographical coverage across different HAP types. We suggest that more research on drought effects on all components on NECB be conducted across more HAP regions, including manipulative studies and those utilising real drought periods. Third, climate change impacts on snow, permafrost and glacier effects and their corresponding feedback to HAPs are of ever-increasing importance, but there is still limited knowledge of how HAP C cycling may be affected by such changes. For example, increased glacial meltwater may change NECB across several HAP regions globally, but at present evidence is limited. Future research should investigate increasing (and the eventual far future decreasing) glacial meltwater effects on NEE, CH_4 emissions and DOC. Finally, we note here that other globally important process such as nutrient enrichment, e.g., nitrogen (N) and phosphorus (P) deposition (related to both anthropogenic activities and climate change) (Ackerman et al., 2019) are also rarely studied in HAPs (Luo et al., 2022). Similarly, we found no studies of the effects of elevated atmospheric CO_2 on HAP C cycling, although studies from other peatlands have shown increased GPP and DOC production in response to elevated CO_2 levels (Fenner et al., 2007; Fenner et al., 2021). Nutrient deposition and elevated atmospheric CO_2 levels are both closely coupled with HAP C cycling (Hopple et al., 2020; Niu et al., 2023), and should be also considered in future work, including their synergistic effects in multi-factor studies.

One of the main pressures on HAPs is that they are exposed to higher degrees of climate warming than other ecosystems at low altitudes (Yang et al., 2014; Wang et al., 2018), which is also evident from medium-term future temperature predictions (Table S3). Although the effects of warming and land-use change may be mechanistically similar to that of other peatlands, some studies have suggested that high-altitude ecosystems will be more negatively impacted by future climate change than those at lower altitudes (Wei et al., 2024), due to the larger degree of warming, which has also been hypothesised for HAPs (Benavides, 2014a). However, very few studies have explored this question in depth. A recent global analysis of peat chemistry found that peat from higher elevations may be more easily decomposed under future warming, than peat from lower elevations, due to a higher abundance of carbohydrates to aromatics (Verbeke et al., 2022). In contrast, others argue that mountain peatlands at lower elevations may be more susceptible to climate change than those at higher elevations (Millar et al., 2017). This is because lower elevation mountain peatlands accumulate less snow, which melts earlier and have warmer growing season air temperatures, all of which will be exacerbated under future climate change.

However, many studies predicting the effects of future climate change on HAPs suggest they will continue to be negatively impacted by future climate change (Liu et al., 2022; Wu et al., 2022). For example, in Siberia, climate warming and permafrost decline is most evident in high-altitude areas and has contributed to some HAP vegetation succession towards alpine steppe vegetation, with former hollows (relatively lowlying wet areas) now dominated by grasses (Volkova et al., 2021). As temperatures continue to rise, HAP habitat succession will likely continue to evolve, along with increasing ER (Volkova et al., 2021). Our data synthesis also suggests that HAPs with different dominant vegetation types may respond differently to warming, e.g., sphagnum, which is sensitive to warming may decline, while sedge (graminoid) dominated peatlands may see biomass increases, which will largely regulate their GPP (carbon uptake) and also influence autotrophic respiration and microbial decomposition processes (Gerdol et al., 2008; Yang et al., 2015). Similarly, recent research predicted that the increase in ER in response to future warming on the QXP, is likely to be greater than any warming induced increases in GPP (due to vegetation changes), thus the C sink function of HAP on the QTP may weaken in future decades (Wu et al., 2022). This may be partly explained by recent (and projected future) warming trends that increase non-growing season temperatures more than summer temperatures (Shen et al., 2022), thereby enhancing decomposition rates more than vegetation productivity (Liu et al., 2022), despite this warming trend may also extend the length of the growing and non-frozen seasons (Zhang et al., 2016a).

In depth studies of peat accumulation combined with modelling in Andean HAPs have predicted that sites with high human disturbance will see future net losses of C (and may transition towards rich fens with lower C accumulation rates), while low disturbance HAPs (typically at higher elevations) may become larger C sinks (Benavides, 2014a). Thus, the degree of disturbance from human factors may also play a key role in the future effects of climate change on HAP, while it is at present a critical knowledge gap. To date, very few studies have considered the interaction of land management and warming in HAPs; our collated results of climate change effects on the HAP C cycle, were conducted either in intact HAPs, or using mesocosms (Table S4). Thus, it is relatively unknown how degraded HAPs (or those under restoration) will respond to future climate change, which is a priority for future research. In addition, the local peatland hydrogeological setting is also another important factor (Benavides et al., 2013). Some HAPs in large watersheds may still receive sufficient groundwater inputs to maintain near surface water tables and maintain net C sequestration under future warming (Millar et al., 2017), while in other cases increased glacial meltwater inputs to HAPs, i.e., increased water supply, is promoting increased productivity and C sequestration (Benavides et al., 2013; Benavides, 2014a). However, far future trends, may be influenced by eventual glacier loss (and meltwater supply declines) (Zhang et al., 2016b), which may also have other indirect effects on other peatland functions such as biodiversity (Quenta et al., 2016).

6. Conclusions

High-altitude peatlands (HAPs; > 1,500 m) are on average important C sinks accumulating $88 \pm 118\ \mathrm{g\,C\,m^2\,yr^{-1}}$ (flux derived; NECB) with LORCA rates, derived from cores, on average $29 \pm 11\ \mathrm{g\,C\,m^2\,yr^{-1}}$. Both NECB and LORCA figures from HAPs were similar to other peatlands at low altitudes. The collated results suggest that climate change in HAP may negatively impact upon the C cycle by reducing C uptake (NEE) and increasing ER. In general, warming temperatures increase gaseous and aquatic C emissions, although there is also potential for increased GPP due to vegetation changes and succession. Similarly, drought also decreased HAP productivity, with carry over effects also evident after drought recovery. Further, permafrost and glacier decline and changes to snow cover will likely impact C emissions and accumulation rates.

Drainage or WTL lowering resulted in increased ER and decreased CH_4 emissions across all regions, while effects on NEE were more variable. In some HAPs with naturally lower WTLs, NEE (C uptake) increased, perhaps due to vegetation feedbacks (increased GPP). However, the overall impacts of drainage induced water table lowering and associated degradation on SOC were clear, showing decreased C content and decreased C stocks due to increased peat decomposition. Effects of grazing induced degradation followed a similar trend of decreasing SOC, while effects on NECB were related to grazing intensity; higher grazing intensity resulted greater ER and CH_4 emissions. Short-term (< 2 year) results of restoration (by rewetting) in HAPs suggested that C uptake (NEE) can be increased by raising the water table, along with decreased ER. Future policy should therefore seek to reverse effects of drainage, through ecohydrological restoration measures, such as drain blocking to improve function in degraded areas. However, it is important to balance conservation measures with the grazing needs of local populations perhaps through establishment of designated areas for each.

Few studies of the effects of climate change and land management on HAP C cycling measured all components of NECB; most focussed on ER. Additionally, there was very limited spatial coverage of climate change studies across global HAP regions. Future research should address these gaps, and in particular the interaction of climate warming and land management in different regions. At present the climate sensitivity of degraded HAPs, or those under restoration is unknown. With improved understanding, it may be possible to improve restoration methods to enhance climate resilience and aid future preservation of these valuable ecosystems.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Paul P.J. Gaffney: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Qiuhong Tang:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Jinsong Wang:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Chi Zhang:** Writing – review & editing, Resources. **Ximeng Xu:** Writing – review & editing, Methodology. **Xiangbo Xu:** Writing – review & editing, Resources. **Yuan Li:** Writing – review & editing, Investigation. **Sabolc Pap:** Writing – review & editing, Resources. **Joshua L. Ratcliffe:** Writing – review & editing, Writing – original draft, Investigation. **Quanwen Li:** Writing – review & editing, Software, Investigation. **Shuli Niu:** Writing – review & editing, Resources, Conceptualization.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.geosus.2025.100353.

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