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Environmental Significance Statement

Ecosystem nutrient subsidies are the transfer of nutrients across ecosystem boundaries. Subsidies can occur between the terrestrial environment, cryosphere, atmosphere, and aquatic systems. The topic of cross-ecosystem subsidies has gained increased attention over the past two decades. Cross-ecosystem nutrient subsidies are important to lake ecosystems because they influence ecological community structure and ecosystem functioning, such as the rate of nutrient or carbon cycling. This review synthesizes recent freshwater ecosystem subsidy research, identifies knowledge gaps, and identifies remote lakes as ideal target systems for future subsidy research. Environmental changes continue to affect the amount, quality, and timing of nutrient subsidy transfers to lakes. Thus, understanding how nutrient subsidies affect ecosystems will improve our ability to predict lake ecosystem impacts.

Cross-ecosystem nutrient subsidies in Arctic and alpine lakes: implications of global change for remote lakes

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Abstract

Environmental change is continuing to affect the flow of nutrients, material and organisms across ecosystem boundaries. These cross-system flows are termed ecosystem subsidies. Here, we synthesize current knowledge of cross-ecosystem nutrient subsidies between remote lakes and their surrounding terrain, cryosphere, and atmosphere. Remote Arctic and alpine lakes are ideal systems to study the effects of cross ecosystem subsidies because a.) they are positioned in locations experiencing rapid environmental changes, b.) they are ecologically sensitive to even small subsidy changes, c.) they have easily defined ecosystem boundaries, and d.) a variety of standard methods exist that allow for quantification of lake subsidies and their impacts on ecological communities and ecosystem functions. We highlight similarities and differences between Arctic and alpine systems and identify current knowledge gaps to be addressed with future work. It is important to understand the dynamics of nutrient and material flows between lakes and their environments in order to improve our ability to predict ecosystem responses to continued environmental change.

Introduction

Ecosystem subsidies, defined as cross-boundary material fluxes between ecosystems[1], are important because they enrich communities with nutrients, materials, and energy that might otherwise be scarce or unavailable. Commonly discussed nutrients in freshwater ecology research (as well as this review) include the elements nitrogen, phosphorus, silica, iron, and carbon (N, P, Si, Fe, and C, respectively), their inorganic forms (such as dissolved inorganic N, or DIN) and organic forms (such as polyunsaturated fatty acids, or PUFAs) that are present in the environment as resources for organisms. In aquatic environments, nutrient subsidies can support algal communities dominated by few high-nutrient species[2,3], change ecosystem function and food web dynamics[2,4-6], sustain species abundance, increase community turnover[7-9], and influence biological richness of animals, plants, and microbiota[10,11], but effects will vary depending on environmental nutrient limitation. In this review, we address the need for a synthesis of the growing body of research investigating subsidies to freshwater ecosystems. Due to their sensitivity and location within rapidly changing environments, we focus primarily on Arctic and alpine lake ecosystems. We highlight the common themes, differences, and emerging challenges and opportunities for subsidy research within Arctic and alpine lakes and confirm these remote systems as important locales for continued subsidy research.

The study of cross-ecosystem subsidies emerged as ecologists assessed processes occurring over multiple spatial and temporal scales.[12] Growing from this recognition of complex and multiscale ecosystem processes, the two subdisciplines of landscape ecology and meta-ecosystems emerged. Landscape ecology recognized the importance of considering broad geographic scales and heterogeneous patterning of landscapes in shaping ecosystems and ecological communities.[13] Importantly, two of its main foci include “the interactions and exchanges across heterogeneous landscapes,” (172) and “the ways in which fluxes are controlled within heterogeneous matrices” (331).[14] Within the schema of landscape ecology, ecosystem subsidies are exchanges between heterogeneous environments nested within a broader landscape. Further, the heterogeneity of a landscape (for instance, the variable vegetation cover of lake catchments moving up an elevation gradient) affects the quantity and quality of transported materials. Thus, ecosystem subsidies are centrally important in landscape ecology.

To explain how ecological processes operate over multiple spatial scales, Loreau et al[15] described the meta-ecosystem concept. A meta-ecosystem is a group of ecosystems that are connected through fluxes of material, species, and energy. This differs from the landscape ecology perspective in that connected ecosystems need not be spatially continuous or defined at a particular spatial scale (i.e. the landscape scale). Thus, ecosystem subsidies that originate remotely from the site where they are transported (such as agricultural fertilizers that are atmospherically deposited on distant alpine ecosystems) are included within this conceptual framework.

The singular topic of cross-ecosystem subsidies, which move across heterogeneous landscapes and enrich receiving ecosystems with nutrients or energy, was explicitly addressed by Polis et al.[1] In particular, Polis et al reviewed the effect of ecosystem subsidies on food web dynamics and described the connectedness of habitats via fluxes of material, nutrients, or organisms. Following Polis et al[1], much of ecosystem subsidy research has remained focused on food web and community effects (e.g. refs. 16-26).

At present, new challenges are evident in ecosystem subsidy research. For instance, over the past 20 years studies note that peak productivities and transfers between aquatic/terrestrial habitats can be asynchronous and seasonal (e.g. refs 4,27). In other words, fluxes can vary temporally.[28] In the past decade research has demonstrated that subsidies of matter and organisms can be bidirectional, or reciprocal, across coupled ecosystems.[29] Further, ecosystems are experiencing rapid climate change, a driver that exercises both direct and indirect effects upon the timing, direction, quality, and quantity of ecosystem subsidies. Leavitt et al[30] demonstrated that in lakes experiencing climate warming, lake inputs can be divided into two categories, energy (E) and mass (M). While lakes will tend to respond coherently through time to changes in E inputs (for instance, increased PAR irradiance), lake responses to M inputs will likely be much more variable depending on a host of catchment and lake properties and processes. Cross-ecosystem subsidies can be categorized as M inputs. The topic of ecosystem subsidies is therefore complex: ecologists are not only concerned with structural ecosystem responses to unidirectional subsidies (e.g. ref. 31), they are concerned with effects of climate change upon the direction, timing, and magnitude of subsidies themselves. There is a hierarchy of factors and responses involved (Figure 1), and many are interactive, making it difficult to focus on any single pair of response/control variables.

In the face of this challenge, systems that exhibit naturally well-defined ecosystem boundaries, measurable fluxes of material or organisms, and measurable ecosystem responses to subsidies will lend themselves to ecosystem subsidy research. Lake ecosystems are therefore exemplary for such studies. While lakes are open systems, their physical boundaries are distinct, and they are relatively self-contained depending on water residency time. Following Strayer et al[32], we consider lake ecosystem boundaries in this review in terms of our investigative goals, relevant scale, and processes of interest. The ecosystem boundary of lakes in this review are therefore delineated by the basin and body of lake water, because we are focused on whole-lake ecological responses to ecosystem subsidies. However, we recognize lakes are part of their larger watershed (meta-ecosystem), and the lake subsidies we consider can be categorized as within-basin (e.g. benthic to pelagic transfers such as sediment P release), within-watershed (e.g. groundwater inputs of DOM), and extra-watershed transfers (e.g. atmospheric N deposition).

Fluxes into and out of lakes are measured or modeled with increasing ease and accuracy (e.g., refs. 33-35). The ease with which ecological responses to cross-system transfers are registered and quantified in lakes also makes them convenient for subsidy research.[36-39] Because of their position at low points in the landscape, lakes behave as integrators and archives of the environmental changes that occur across landscapes and catchment areas.[40] The sedimentation processes that occur within lake basins produce temporally continuous records of ecosystem change. Thus, the effects of subsidies, and the environmental factors that control those subsidies, can be recorded in lake sediment records via quantification of algal pigments[9], diatoms[3], and isotopes.[41]

Finally, lakes are highly sensitive, behaving as sentinels of ecosystem change in response to environmental drivers.[40] Mueller et al[42] summarize why high Arctic lakes located on Ellesmere Island, Canada serve as global sentinel systems of climate warming by drawing on four decades of data collection. Ellesmere Island lake ice-out phenology and mixing regime shifted abruptly in response to changes in air temperature when warming trends changed the lakes from permanently ice-covered systems to seasonally open water. Seasonally open water exposed the lake surface to wind-driven mixing, thus changing the water column structure. Though biological metrics were not explicitly considered by Mueller et al[42], the ecological communities in Ellesmere Island lakes are dependent on water column mixing regime; thus, these lakes were ecologically sensitive to climate forcing and were likely vulnerable to cascading ecological regime shifts in response to the physical lake changes. As Ellesmere Island lake changes occurred synchronously with ice shelf breakup and changes to permafrost, sea ice, and glaciers, the authors demonstrate that lakes serve as robust sentinels of environmental change beyond the regional scale. In summary, ecological sensitivity, physical boundaries, location within the landscape, and a plethora of standard evaluative methods mean lakes are ideal to study how rates of cross-ecosystem fluxes may shift due to anthropogenic pressures such as land use change, nutrient delivery through atmospheric deposition or non-point sources, and climate change.

Dilute, nutrient-poor and cold-water lakes with relatively simple ecological communities are particularly sensitive to cross-ecosystem subsidies. This is due to watershed characteristics of high Arctic and alpine lakes that enhance transport of nutrients to lakes (e.g. refs. 35, 43,44) and because nutrient-poor lake ecosystems respond to lower thresholds of nutrient inputs (for example, alpine lakes in western US respond to lower amounts of atmospherically deposited N compared to other ecoregions).[45-47] Thus, high-elevation mountain and Arctic lakes are very responsive to changes in subsidy patterns.[42,48] Because of Arctic and alpine lake sensitivity, ecosystem responses observed first in these systems provides insight into changes ecologists might expect to eventually observe in lakes situated in warmer climates (i.e. lower latitude and lower elevation climates with higher annual mean air temperature compared to Arctic or high elevation environments) with more complex and diverse ecological communities.[40] For these reasons, Arctic and alpine lakes are exceptional systems in which to conduct nutrient subsidy research.

Arctic and alpine lakes have served as systems to evaluate ecosystem subsidies for several decades. In the 1970s, nutrient fluxes were studied in Arctic ponds of Barrow, Alaska to account for ecosystem nutrient budgets.[49] This study provided early insights into the sources and fates of nutrients within the tundra landscape. Lake eutrophication in the high Canadian Arctic resulting from N and P associated with sewage effluent was evaluated by Schindler et al.[50] Ecological effects of enhanced N delivery to Lake Tahoe (located in the Sierra Nevada Mountains of California) were evaluated by Goldman[51] using a time series dating back to 1968. Eutrophication from land use changes and urbanization decreased lakewater clarity and increased lake primary productivity.

Arctic and alpine lakes are situated in areas that are experiencing accelerated rates of climate warming.[52] The pan-Arctic region includes large areas of North America, Europe, and Asia. Major alpine lake districts are distributed globally, including the North American Rocky Mountains, European Alps, Himalayas and Tibetan Plateau in central and western Asia, and the South American Andes. Climate warming controls many environmental changes that are occurring in Arctic and alpine lake catchments, including glacier recession[53], catchment "greening"[54], permafrost degradation[55-56], increased abundance of waterfowl[57], altered quantity and timing of insect emergence[58], and altered hydrological connectivity.[59] In turn, many of these environmental changes control the magnitude, frequency, timing, and quality of subsidies delivered to lakes from the atmosphere, cryosphere, and terrestrial catchment. Changes of cross-ecosystem subsidies are presently not well accounted for. Large scale environmental drivers such as climate warming will continue to impact ecosystem subsidies into the future, making this area of research timely and urgent. Thus, alpine and Arctic areas are insightful landscapes in which numerous “natural experiments”, or comparative studies, can be conducted to understand how cross-ecosystem subsidies affect lakes. Already, researchers have compared effects of glacial meltwater[60], permafrost slumping[61], insect emergence[62-63], and dissolved organic carbon (DOC) impacts[64] on nearby paired Arctic and alpine lake ecosystems that are differentially influenced by environmental changes. Equally important are the paleoecological insights that lake sediment records provide, whereby pre-Anthropocene algae assemblages or isotope chemistries can be compared to recent ones within the same lake ecosystem.

In this review we will synthesize such studies in order to outline the current state of ecosystem subsidy research in Arctic and alpine lakes. Previous studies have reviewed subsidy effects in remote lakes (Catalan et al 2006; Hobbs et al 2010; Catalan et al 2013).[65-67] However, these papers focused on paleolimnological records[66-67] or were location-specific.[65] Our review surveys cross-ecosystem subsidies to remote lakes drawing on both contemporary ecological as well as paleolimnological research. Because of its central importance to cross-ecosystem subsidies, we will highlight the current and future effects of abrupt climate change. Though we consider community and food web consequences of lake ecosystem subsidies, we emphasize biological and biogeochemical responses and trends in order to situate cross-ecosystem subsidy research as an important facet of Arctic and alpine carbon (C) and nutrient cycling and climate change feedback loops. Conceptual models that illustrate current understanding of the drivers and effects of lake subsidies explore this paradigm. Finally, we will address certain challenges and open questions in lake ecosystem subsidy studies and call for research to address these knowledge gaps.

Arctic lake subsidies

Cryosphere

Across arctic and alpine landscapes alike, perhaps the most visually obvious change is the rapidly changing cryosphere involving the recession of glaciers, permafrost thawing, and diminishing snowpack. Glaciers concentrate and store atmospheric compounds, including anthropogenic pollutants. In this way, glaciers behave as “natural archives” because the combined effects of emission trends and air circulation patterns is recorded within their ice.[68] Thus, glaciers are reservoirs and secondary sources of anthropogenic pollutants[69], because these compounds are present in glacier meltwater and are delivered to downstream ecosystems. Climate warming increases glacial meltwater output and accelerates the release of accumulated pollutants.[70] While glacial pollutant storage is often associated with mountain glaciers that are in closer proximity to source emissions, anthropogenic organic pollutants have been detected in remote Arctic glacial ice and snowpack.[71-73] In addition to pollutants, glacier meltwater contains nutrient solutes as well as minerogenic particulates that are ecologically important. These nutrients and minerals may be sourced from the atmosphere and concentrated in glacier ice to be released upon melt[74], similar to anthropogenic pollutants, or derived from bedrock material that gets weathered by biogeochemical and physical processes and washed out via subglacial flow.[75] Ice sheets and glaciers store a significant amount of labile particulate and dissolved organic matter (DOM)[76,77], N[60], P[78-80], Si[79,81], as well as many other micronutrients (such as Fe)[82]. Thus, Arctic glacier meltwaters represent an important nutrient subsidy for downstream freshwater ecosystems.

In southwest Greenland, Bhatia et al[82] and Hawkings et al[81] demonstrated significant amounts of P, N, Si, and Fe are contained in meltwater discharged from the Greenland Ice Sheet. Ice sheet meltwater total P (TP) and DIN were important determinants of distinct algal communities and higher algal biomass in Greenland glacially-fed lakes compared to nearby snow and groundwater-fed lakes.[80] Similarly, a lake sediment record from northeast Greenland (Bunny Lake, fed by the Renland Ice Cap) show diatom community changes that likely coincided with glacier meltwater inputs starting a thousand years ago.[3] Glacially-fed lakes in Svalbard and northern Sweden also exhibited elevated TP concentrations.[78] Together, these studies show the widespread potential for glacier meltwater being an important source of nutrient subsidies in the Arctic and highlight the potential importance of glacially-fed lakes along the ice sheet behaving as hotspots of C and nutrient cycling as a result of these glacial meltwater additions. Fluxes of particulate and solute nutrients are greater in years of higher melt[81]; thus, future climate warming may increase nutrient delivery to freshwater systems. These trends and interactions will likely have important implications for Arctic C and nutrient cycling.[83]

While significant work has been completed on glacier nutrient subsidies in streams and rivers (e.g. refs. 25,84,85), glacier fed Arctic lakes represent potential hotspots of nutrient cycling[86] and should be more thoroughly investigated. Compared to alpine regions, little research has been conducted on Arctic lakes to understand how glacial meltwater affects their ecology. Given that meltwater delivery to Arctic lakes will increase due to climate warming, as well as a projected increase in the abundance of glacially-fed Arctic lakes due to glacier recession[87], the ecological responses of these systems should be a research priority.

Permafrost is sensitive to changes in air and ground temperatures[88-90] as well as rainfall.[91] Similar to glaciers, permafrost thaw in Arctic areas is therefore predicted to significantly increase in response to climate warming.[55,56,92,93] Permafrost thaw is an important source of lake nutrient subsidies. Thaw events can be episodic, representing pulse disturbances to lakes, or they can be gradual and persistent, representing press disturbances.[94] Moreover, permafrost thaw contributes to lake nutrient subsidies directly and indirectly (Figure 2). The active layer of soil that sits above the permafrost controls the tundra landscape's hydrology and biogeochemistry.[89,95-98] As such, changes to the active layer depth affect groundwater and nutrient delivery to freshwater ecosystems.[89,99,100] However, a deepening of the active layer may have variable results; DOM inputs to freshwaters may increase (e.g. refs. 101-104) or decrease due to mineral sorption[105] or groundwater flow paths becoming deeper.[106-109] The quality of DOM transported to lakes may change to more biolabile pools.[110] Research in Alaska and the Canadian high Arctic suggested that DIN and TP flux to freshwaters will increase with continued warming.[98,99,111-113] Permafrost thaw that results in altered lake catchment biogeochemical and hydrological processes is an indirect control of nutrient subsidies. In contrast to trends in current literature suggesting Arctic lakes may represent hotspots of nutrient and C cycling, a recent study in Alaska revealed that the transfer and within-lake respiration of terrestrial organic C was minimal.[114] This study was located in an arid area of interior Alaska that may be broadly representative of arid Arctic landscapes. Instead of allochthonous DOC mineralization, periods of lake heterotrophy consisted of autotrophically produced organic C mineralization. Together, these studies suggest that permafrost thaw will have spatially variable lake subsidy outcomes depending on thaw patterns, active layer depth, soil type, biolability of C and nutrient pools, and local hydrology.

Other thermokarst processes, such as permafrost slumping, involve a direct physical transfer of particulate sediments and solutes from terrestrial environments into Arctic lakes. While thermokarst events can form lakes that occupy tundra depressions where permafrost degraded, established lakes within the Arctic landscape (originated from other processes, such as glacial scouring) can be influenced by thermokarst processes within their watersheds. This is a common occurrence in the Canadian and Russian Arctic. For instance, one in ten lakes in certain areas of the Canadian uplands were affected by permafrost slumping.[115] In this study, ionic concentrations were higher in lakes affected by permafrost slumping compared to undisturbed lakes. Higher ionic concentrations in affected lakes were due to the exposure of hitherto frozen watershed sediments to weathering processes, and subsequent transfer of soluble materials to lakes by surface runoff. Permafrost thermokarst events in northern Alaska increased DOC and DIN concentrations in feature outflows, with potential ecological consequences for downstream freshwaters.[116] In contrast, sedimentation of organic material associated with slump sediments lowered lake nutrient concentrations (total dissolved N and TP) and increased water clarity, with more recently slump-affected basins exhibiting greater clarity.[115,117-119] Increased water clarity following slumping may have driven increased macrophyte production in affected lakes[61] as well as diatom species turnover with increased prevalence and diversity of periphytic diatoms.[119] In the Canadian uplands, lakes disturbed by permafrost slumping events exhibited doubled macroinvertebrate abundance.[120] However, increasing water clarity may expose pelagic organisms to harmful UV radiation.[117] Accelerating rates of thermokarst activity in the Arctic in response to climate warming[121,122], coupled with lake responses to such disturbance events described above, suggests that permafrost slumping will be an important modulator of lake nutrient subsidies.

Climate warming across the Northern Hemisphere pan-Arctic region is driving a general reduction in snow accumulation since 1979, though there is much regional variability associated with this trend.[123] Snow accumulation is an important driver of ecological patterns, such as plant, lichen, and moss species distributions[124], plant phenology, peak plant greenness[125], and maximum plant greenness.[126] As such, changing snow accumulation patterns are an important impact on lake catchment processes. Accumulated snow converts to meltwater during spring thaw[127], contributing nutrients, minerals, and particulates into lake ecosystems which may increase the relative abundance of littoral epilithic algae[128] or phytoplankton communities of Arctic lakes.[129]

Shortened lake iced-over periods and earlier spring ice-out is a general trend across the Pan-Arctic in response to climate warming[130], and ice-out phenology has important implications for Arctic lake stratification (whereby the top epilmnion and bottom hypolimnion physically separate due to temperature-based water density gradients). Increased intensity and stability of lake thermal stratification is an anticipated response to climate warming[87,131,132], though this may be modulated by changing ice-out phenology.[133] Increased stratification is important for within-lake benthic-to-pelagic subsidies, because hypolimnetic oxygen can become depleted (anoxic) when lake thermal stratification inhibits the diffusion of oxygen from the epilimnion.[134] Hypolimnetic anoxia increases the chemical reduction potential and favors the release of P from lake sediments that is otherwise associated with Fe and aluminum (Al) during oxygenated conditions.[135-136] In low elevation temperate lakes, sediment P release is related to algae blooms.[137-139] Benthic to pelagic P subsidies may be an important Arctic lake response to climate warming, but there has been little research of anoxic sediment P release conducted in Arctic lakes. Determining the mechanisms that control Arctic lake sediment P release should therefore be a research priority, so that we may better predict Arctic lake responses to increased climate warming and seasonal variability.

Reduced river ice jamming in the McKenzie River Delta is a cryosphere change driven by Arctic warming trends that decreases the duration of hydrological connectivity between rivers and lakes at higher elevations within the Delta (5.2 m above sea level).[140] In contrast, the duration of river-to-lake connection during peak water levels has increased in lower elevation areas (2.4 m above sea level) within the Delta, due to sea level rise. It is likely that these trends will have ecological effects because McKenzie River Delta lakes with frequent river-to-lake connectivity were associated with enhanced colored DOM, P concentrations, and light attenuation rates but lower ammonium and non-colored DOM concentrations averaged over the open-water season.[141] Patterns of lake nutrient and light availability were likely responsible for higher abundance and production rates of bacterioplankton within less-frequently flooded lakes. These studies demonstrate that even small environmental gradients (i.e. a change from 2.4 to 5.2 m elevation) can alter the directional trends in lake subsidies and the environmental factors that influence them.

Many factors determine the nature, direction, and magnitude of ecological impacts in aquatic systems from cryosphere-derived subsidies. For instance, glacier meltwater effects will depend on magnitude of meltwater delivery, glacier bedrock material, and quality of nutrients. Permafrost effects will depend on soil quality, depth and biogeochemical activity of the active layer, water flow paths, and slumping events. Lastly, recent snow pack trends are highly variable throughout the Arctic, which will affect photosynthetically active radiation (PAR) and spring snowmelt nutrient additions. Parsing out this variability will be critical to understand why certain trends are occurring in some areas of the Arctic but not others, or why opposite responses follow seemingly identical disturbance events in different areas (e.g. DOC concentrations following permafrost degradation, or nutrient concentrations following slumping events).

Atmospheric deposition

N deposition is considered to be more important to lakes in mid-latitude areas that have experienced higher anthropogenic development, compared to high-latitude Arctic areas which are more remote and typically have lower rates of N deposition (Figure 3a; refs. 66, 142). For example, Hobbs et al[66] suggested that changes observed in diatom beta diversity over the 20th century in the Greenland Arctic are driven by rapid climate warming, versus that observed in western US alpine lakes, driven by high rates of atmospheric reactive N (N_r) deposition. However, Holmgren et al[143] observed that recent changes in preserved Arctic lake sediment diatom assemblages on Svalbard are coincident with enhanced sediment N derived from anthropogenic sources, suggesting a causal link between lake ecological change and N deposition. Diatom sediment records demonstrated that anthropogenic N deposition in the Canadian Arctic, along with climate warming, had driven lake conditions and diatom communities to no-analogue states in two nearby lakes.[144] Community changes include increased abundances of *Aulacoseira distans*, *Brachysira vitrea*, *Fragilaria* spp., *Cyclotella rossii*, and *Discostella stelligera*, which indicated nutrient enrichment. Similarly, Holmgren et al[143] demonstrated that four Svalbard lakes exhibited diatom community changes over the past 30 years coherent with increased rates of N deposition. A study conducted in sub-Arctic Sweden demonstrated that lakes shifted from N to P limitation as a result of N deposition.[145] As the study lakes were remote, high latitude, dilute and unproductive, they serve as good analogues for Arctic systems. Climate warming cannot be ruled out as a synergistic driver of these ecological changes because of the coherence of warming, N deposition, and diatom responses.[144,146] Taken together, however, these studies suggest a causal link between sensitive Arctic lake ecosystem change and high latitude N deposition.

Though Greenland is remote, it is downwind of North American industrial emission sources and is thus vulnerable to modifications of the Northern Hemisphere atmosphere.[147] Several ice cores demonstrated recent increases in NO_3^- concentrations in Greenland,[147-149] Svalbard[150,151] and the Canadian Arctic.[152,153] Averaged across sites, these records showed a 30% increase of NO_3^- flux since preindustrial times (from 2.5 to 3.2 $\mu g\ cm^{-2}\ yr^{-1}$),[154] with more than a doubling in some locations such as Greenland.[147] N isotope analysis ($\delta^{15}N$) indicated that NO_3^- in Greenland ice is derived from increasing anthropogenic N emissions since 1850.[155] Matching these cryosphere records, the presence of anthropogenic N deposition has coherently increased in lake sediment cores across high latitudes of the Northern Hemisphere since the beginning of the 20th century.[156] An outstanding question, however, is whether N deposition rates in the Arctic are high enough to be ecologically important.

N deposition in the Arctic is typically low (0.2 - 0.5 kg NO_3^- ha^{-1} yr^{-1})[144] but Arctic freshwaters are sensitive to small inputs of nutrients. Though rates of N deposition have not been as high in Arctic areas compared to mid-latitude ones, there is a clearly increasing trend that could be ecologically important. Anderson et al[41] used lake sediment cores to demonstrate that coastal Greenland lakes have received increased amounts of anthropogenically sourced Nr since 1860, despite relatively low deposition rates in this area (0.4 kg ha^{-1} yr^{-1}). This trend was not recorded in inland lakes possibly because lower deposition rates (0.2 kg ha^{-1} yr^{-1}), and higher in-lake TN pools and microbial cycling rates could further confound the signal of external anthropogenic inputs. Arens et al[157] demonstrated by nutrient addition experiments that small amounts of N deposition (0.5 g m^{-1} yr^{-1}) have nonlinear impacts on terrestrial Arctic ecosystem structure and function, increasing vegetation cover, photosynthesis, and CO_2 exchange. Similarly, Gordon et al[158] observed that their lowest N addition treatment (10 kg ha^{-1} yr^{-1}) increased physiologically active bryophyte shoots in Arctic heath, indicating the minimum ecologically important rate of atmospheric N deposition is likely below this value. These results suggest even small increases in rates of atmospheric deposition will be ecologically important.

The vulnerability of Arctic lakes to environmental change is due to spatially variable acid neutralizing capacity (ANC),[144,159,160] sparse catchment vegetation, short growing seasons, shallow active soil layers,[161] and low in-lake nutrient concentrations and productivity. Evidence for Arctic freshwater sensitivity comes from ecological and paleoecological studies. For instance, Benstead et al[162] enriched a small Arctic stream on Alaska’s north slope with NH_4-N and soluble reactive P (SRP) to 6.4 µM and 0.45 µM, respectively. This addition increased algal biomass (measured as Chlorophyll *a*; Chl *a*), fungal biomass, rates of litter breakdown, and macroinvertebrate abundance and biomass.[162] In a long-term, whole-lake manipulation experiment in Arctic northern Alaska, half of Lake N-2 was subsidized with 131 mmol N m^{-2} yr^{-1} and 10.4 mmol P m^{-2} yr^{-1}, approximately five times the normal loading rates of nearby Toolik Lake, while the other half was partitioned off as a control.[163] Ecological responses included increased phytoplankton biomass and productivity, lower water clarity, and eventual hypolimnetic anoxia coupled with sediment P release.

Wind can distribute fine particulate matter, including pollen, bacteria, diatoms, and dust, long distances to Arctic and alpine areas.[39,164-168] Dust production, emission, and deposition rates can be high in glacierized Arctic landscapes, such as Canada, Alaska, Greenland, and Iceland (see Bullard et al[169]), comparable to rates of lower latitude regions such as New South Wales, Australia[170] or Nevada and California, USA.[171] Glacier dust production occurs when glacial flour (fine mineral particulates resulting from subglacial bedrock erosion) is transported to floodplains by subglacial meltwater. Winds then deflate the glacier flour, and can transport it across tundra, lakes, rivers, and ocean. Key controls of dust production include subglacial substrate erodibility, drainage system size and structure, ice mass size, and meltwater runoff rates.[169] The amount of high-latitude dust contributions to the earth’s dust budget is currently estimated to be ~5% and is expected to increase with climate warming.[172] The magnitude of dust events in southwestern Greenland, for example, has increased since the 1990s (calculated using the Dust Storm Index).[173] Most of the dust produced in high latitude areas remains in these regions. In western Greenland for example, dust transport from the Ice Sheet margin was mostly confined to the local landscape, with a small percentage reaching the North Atlantic Ocean, and very little being transported back onto the ice sheet itself.[173] This was due to the consistent direction of the katabatic winds blowing west from the ice sheet,[174] as well as a lack of thermal uplift in the Arctic that is required for long-distance transport of dust-containing stable air parcels.[175,176] Conversely, dust plumes derived from glaciofluvial deposits along the Gulf of Alaska (GoA) coastal region can be deposited into the ocean several hundred kilometers beyond the continental shelf, serving as an Fe subsidy for Fe-limited marine systems.[177] It is unknown to what extent glaciofluvial-derived dust is deposited into lake ecosystems in this region, but glacially-sourced dust accumulates in nearby terrestrial systems.[178] A sediment core from an interior western Alaska lake isolated from glacial processes suggested dust deposition is related to aridity, lack of catchment vegetation, and windiness as opposed to glacial processes.[179]

The ecological effects of dust deposition on Arctic lakes are not well understood.[173] Because dust production and deflation in Greenland occurs throughout the entire year including the winter months,[173] accumulated dust on and within lake ice and snow can cause a pulse disturbance to lake ecosystems during snowmelt and ice off periods in spring, in contrast to a more consistent press disturbance of dust addition to lakes throughout the summer months.[180] Glacier flour in southwest Greenland is P and Fe-rich,[79,82] properties which carry over into deflated dust from this area,[181] and coastal Alaska.[177,178] Fowler et al[181] proposed DOM adsorption to Fe-rich dust as a mechanism for recent decadal DOC concentration declines observed in a number of Greenland lakes, though microcosm incubation experiments did not support this hypothesis. To the extent that the P content of glacially derived dust is bioavailable,[80] dust addition to lakes could stimulate lake bacterial production and metabolism,[182,183] or in-lake sediment P cycling.

More evidence is needed to assess the ecological effects of atmospheric N and P deposition in Arctic lakes. This mode of ecosystem subsidization has not been paid due attention in the Arctic, likely because of the relatively low absolute values of N deposition rates compared to low elevation temperate regions. However, studies which attribute recent changes of algal communities in Arctic lake sediment records to climate warming alone[184] may be missing the important contributions of anthropogenically sourced atmospheric deposition. High latitude dust production was only recently assessed as a significant contributor to the global dust budget (see Bullard et al[169]), positioning Arctic dust deposition as an intriguing topic of research for terrestrial and aquatic ecologists and biogeochemists. Further, climate warming will likely influence N_r and dust deposition alike. Greenland ice core NO_3^-, a proxy for atmospheric N_r deposition, was correlated with the North Atlantic Oscillation, suggesting greater deposition of anthropogenic N_r occurs when the NAO is in its positive phase.[154] A climate change impact model on atmospheric N deposition suggested that increased precipitation will enhance N deposition rates in northern Europe.[185] Though changes in N deposition will be gradual in most areas, certain areas, including western Norway, may experience a 40% increase in N deposition by 2100 due to projected increases in precipitation. Warming could also release previously deposited and accumulated N_r from perennial snow packs and glaciers in the form of meltwater. Lastly, warming will likely increase dust production in high latitude areas because increased meltwater will deposit greater amounts of glacier flour into floodplain areas.[169]

Animal vectors

Animals are important vectors for nutrient transfer between ecosystem types, and this mode of transfer between aquatic and terrestrial systems has received increased attention over the past decade. Unlike other transfers that have been discussed thus far, animals represent a bi-directional flow of energy and nutrients, whereby inputs of terrestrial C and nutrients to lakes are cycled back to terrestrial environments by boundary-crossing organisms.[24] The C that is delivered to terrestrial systems from emerging mosquitos, for instance, is a mix of terrestrial and aquatic material, and the terrestrial:aquatic C ratio depends on the magnitude of terrestrial inputs into the aquatic ecosystem, as well as light intensity.[186] Vander Zanden and Gratton[187] highlighted that insect emergence and subsidies to terrestrial systems increased as a function of lake size, while rates of terrestrial inputs of particulate organic C to lakes decreased as a function of their size. Thus, reciprocal transfers between lakes and terrestrial habitats are modified by environmental variables. A detailed understanding of variables that influence reciprocal transfers between lakes and watersheds is an important research priority, because it will allow for better assessment of how reciprocal subsidies will be affected by different environmental changes.

In the Arctic, aquatic-terrestrial transfers often take place as abrupt seasonal pulses, and can be limited by distance from the lake, with an exponential decrease of insect infall with distance from lake.[188,189] However, observed transfer distance was greater from lakes (150 m) than from streams (50 m).[190,191] For instance, midges (Diptera: Chironomidae) are an important nutrient subsidy from lakes to terrestrial systems. In Iceland, annual midge inputs from lakes were as high as 1200-2500 kg ha^{-1} yr^{-1}, though these inputs decreased logarithmically from shore.[188] Peak rates of midge infall occured in August and can reach rates over 1500 kg ha^{-1} d^{-1} at a distance of 5 m from shore (median rate 290 kg ha^{-1} d^{-1}).[192] Midge N content is 9.2%, and so this seasonal transfer was nutrient-rich, as high as 230 kg N ha^{-1} yr^{-1}.[188] $\delta^{13}C$ and $\delta^{15}N$ isotope analysis demonstrated this subsidy is important for terrestrial arthropods (e.g. spiders), which consume midges directly or indirectly as a food source. Aquatic insects are a high-quality food source, in part because of their polyunsaturated fatty acid content. Martin-Creuzburg et al[193] demonstrated that the terrestrial subsidies of polyunsaturated fatty acids from aquatic insect emergence was significant (mean rate was 150 mg m^{-2} yr^{-1} within 100 m of shore). Thus, in areas with high midge emergence rates, midges maintain higher abundances of terrestrial arthropods compared to areas with low midge emergence rates. In Iceland and northern Sweden, subsidized terrestrial arthropods include detritivore and herbivore species as well as predators.[62,194-196] An Icelandic study demonstrated that willow (*Salix phylicifolia*) located at high-midge emergence lakes contained 8-11% higher N content than those located at low-midge emergence lakes, and herbivorous caterpillars (*Hydriomena furcata*) were 72% heavier at the high-midge emergence sites.[63]

Arctic Chironomid midge emergence is synchronous, with the bulk of the community emerging from a single pond within 4 weeks, and a single species emerging within one week.[197] In response to climate warming, Alaskan midge emergence has advanced by one week since the 1970s.[198] As midge adults only live for a few days, such shifts in aquatic insect phenology may have repercussions for Arctic predators, such as avian consumers. For example, in UK lakes in the South Pennines, climate warming shifted the dates of egg laying by an Arctic wader species (golden plover, *Pluvialis apricaria*) and tipulid (cranefly) emergence earlier, but at different rates.[199] Thus, climate predictions for 2070-2090 suggest that first-laying dates for golden plover will advance 25 days, but tipulid emergence only 12 days. As emerging tipulids are an important prey resource for golden plover chicks, this phenological mismatch may reduce breeding success of this species at this location by 11%. Because Arctic lake midge emergence is synchronous, short in duration, and is an important resource for Arctic terrestrial and avian predators, phenology of Arctic lake midges and their predators require more investigation in order to determine if temporal mismatches will occur, and what ecological impact they will have.

With climate warming and other anthropogenic environmental changes, waterfowl habitat range and population sizes are increasing. Global goose population, for example, nearly doubled from 1996 (12.5 million)[200] to 2006 (21.4 million).[201] Dense nesting colonies of waterfowl have the potential to transfer significant amounts of terrestrially derived nutrients (N and P) into Arctic lake ecosystems in the form of feces.[202,203] In Svalbard, goose guano has caused lake and pond eutrophication, increasing P concentrations four-fold since the 1960s.[204] A small-scale incubation experiment demonstrated that algal biomass increases from goose guano-derived nutrients.[205] Sediment cores from Canadian Arctic ponds demonstrated strong relationships between algal biomass and chironomid heads in response to N derived from seabird guano.[206,207] Paleolimnological records demonstrated an increasing colony population enriches lake sediment $\delta^{15}N$, indicating a marine to lake linkage. Thus, coastal Arctic lake ecosystems may experience subsidies from different sources compared to inland lakes.

Particular areas of the Arctic, such as Iceland, have received attention regarding lake-to-land transfers of nutrients in the form of emerging aquatic insects, but there is a lack of research in other Arctic areas where lake-to-land nutrient transfers would be seemingly important. For instance, some Greenland lakes experience high densities of emerging chironomid adults during peak summer, which have not been characterized in terms of nutrient quality and quantity. Further, with high rates of climate warming in western Greenland, outbreaks of moth larvae (*Eurois occulta* and *Gynaephora groenlandica*) have become more common.[208] These larvae commonly fall into lakes and streams (personal observation). Though larval outbreaks in western Greenland have been linked to terrestrial defoliation[209] and changes in C-burial rates,[208] the effect on aquatic ecosystems is unknown.

Alpine lake subsidies

Cryosphere

Alpine areas in North America have numerous glaciers and rock glaciers. 1500 glacier and 10000 rock glacier features have been identified in the western US alone.[210] Because of their abundance and location within the continental US and Europe, studies published to date that investigate the effects of nutrient-rich glacial meltwater on lake ecological structure and function have largely focused on alpine rather than Arctic lakes (e.g., refs. 2, 60, 210, 211). Climate warming has increased glacier melt to mountain surface waters in the Pacific Northwest region of the US over the past 70 years.[212] Enhanced glacial melting has also increased glacial lake abundance and area across the Central and Patagonian Andes.[213] Glacier recession is widespread and accelerating throughout the Tibetan Plateau[214,215], and is cited as one of the factors leading to increased lake levels across the region.[216-218] In addition to warming trends, climate-mediated dust deposition can alter glacier snow and ice albedo leading to greater glaciofluvial transport of glacier meltwater to high elevation lakes in southwestern Tibet.[219] Glacier meltwater subsidizes systems with essential elements such as Ca, K, Mg, nutrients such as Si, Fe, N and DOM, and organisms such as microbes, though the characteristics of these subsidies differ among mountain ranges and between glacier types (rock glaciers vs glaciers).[161,219] In contrast to Arctic glacier meltwater, which typically has high P but low to medium N content, alpine glacier meltwater can have elevated NO_3^-, with subsidized lakes containing concentrations as high as 236 µg NO_3^{-1}-N L^{-1}.[60] Thus, NO_3^--N enriched glacially-fed lakes in the Beartooth Mountains of Wyoming and Montana exhibit lower diatom species richness[60] and higher phytoplankton primary productivity rates and biomass compared to nearby snow and groundwater-fed lakes.[2] Although glacially-fed lakes in both Arctic and alpine areas are often turbid with suspended glacial flour, the target glacially-fed lakes from the Beartooth Mountains in these studies were clear due to either minimal subglacial weathering or upstream entrapment.[60] These studies are useful because the clarity of the glacially-fed lakes makes them similar to snow and groundwater-fed lakes. Thus, the ecological effects of these particular glacially-sourced N subsidies could provide insights into remote cold, oligotrophic lakes receiving other types of N subsidies (such as atmospheric deposition, or increased goose guano).

As in Arctic lakes[80], glacial transport of suspended mineral particulates that constitute milky-colored glacial flour can alter the transparency and light penetration of alpine lakes, giving them a characteristic grey to turquoise hue.[220] Turbidity can reach high levels in alpine lakes (644 NTU recorded in the Swiss Alps;[221] unit conversion by Sommaruga and Kandolf[220]).

Sediment transport is increased during glacial recession as a function of meltwater flux and is therefore affected by climate warming.[222,223] Because of their small size (<32 μm)[224] and sharp edges, glacial flour particulates can have direct negative impacts on interception- or filter-feeding aquatic organisms (such as *Daphnia*, and heterotrophic nanoflagellates), that may ingest them.[220,225] Other physical consequences of suspended glacial flour in alpine lakes includes density underflows (also a function of cold meltwater temperature),[226] a reduced euphotic zone and high UV light attenuation, both of which have consequences for ecosystem primary production rates,[227] phytoplankton and zooplankton stoichiometry,[228,229] and plankton survival.[227] Further, surface temperature of glacially-fed alpine lakes can be surprisingly warm (late August mean surface temperature from 3 glacially fed lakes was 16.0 °C, calculated from Peter and Sommaruga[230]), similar to that of a nearby snow and groundwater-fed, clear lake (15.3 °C).[230] Though mean lake water temperatures can be cooler in glacially-fed lakes compared to snow and groundwater-fed ones (a 1.1 °C difference was demonstrated in Alaska, for example; Koenings et al[225]), the warming of the surface by attenuated solar radiation leads to discontinuous polymictic thermal stratification, a situation where thermal stratification of these lakes can undergo fast and abrupt mixing throughout the summer, caused by cold night-time temperatures or precipitation events.[230]

While Arctic glacier meltwater contains P that is associated with weathered minerogenic subglacial flour[80] the source of NO_3^- that is concentrated in alpine glacier meltwater is unclear.[211] Determining the extent to which meltwater NO_3^- is derived from anthropogenic sources, minerogenic material, or subglacial microbial processing of organic material may inform conservation or management decisions. Further, alpine glaciers are projected to disappear in the American Rocky Mountains by 2030,[231] and certain areas of the European Alps by 2050.[232] It is currently an outstanding question what the ecological effects of glacier disappearance will be on glacially-fed lakes, and whether legacy effects of previously glaciated catchments will persist following deglaciation. For instance, given the abundance of glaciers in the western United States,[210] it will be important to determine how C and nutrient cycling may change as a lake goes from turbid and glacially-fed to clear and fed by groundwater sources.

Atmospheric deposition

Like Arctic lakes, alpine lakes are ecologically sensitive to atmospheric deposition due to their slow weathering bedrock and spatially variable ANC, absent or poorly developed catchment soils, sparse catchment vegetation cover, and low nutrient water chemistry.[44,233-234] In contrast to Arctic lakes, high elevation exposes alpine lakes to greater rates of atmospheric deposition.[235] In mountain regions of the US, enhanced N deposition results from fossil fuel and agricultural emissions.[142,236,237]

Atmospheric N deposition can change the nutrient limitation status of lake ecosystems. Many North American alpine lakes were historically N-limited.[60,238-240] However, in both North America and Europe, atmospheric N deposition has shifted lake nutrient limitation patterns from N-limitation to N and P co-limitation or P-limitation.[241,242] Ecological responses to N deposition can be rapid, because primary producers with high reproductive rates, such as phytoplankton, are sensitive to nutrient changes.[46,243] Such responses include increased primary productivity,[5,244,245] increased phytoplankton biomass[5,246] decreased lake clarity,[244,245] and directional algal community changes caused by increased dominance by opportunistic diatom species such as *Fragilaria crotonensis*, *Asterionella formosa*, and *Discostella stelligera*,[7,8,211,244,245,247,248] that respond rapidly to nutrient enrichment.[60,249-251]

In addition to N deposition, alpine lakes are ecologically sensitive to P deposition. In mountain areas, N deposition is associated with both wet deposition (DIN associated with precipitation or fog droplets[252,253]) and dry deposition (consisting of nitric acid and particulate ammonium and nitrate[254]). P deposition is associated with dry deposition (associated with particulate matter, or dust).[255] Dust is sourced from anthropogenic activities and biomass burning,[256] and dust deposition can be related to climate. For instance, dust storms and strong winds have increased in frequency in the Tibetan plateau over the past 44 years, observable via grain-size analysis in a high-elevation lake sediment record (Lake Sugan, 3,000 m above sea level).[34] A longer lake sediment record spanning 1,600 years from Kusai Lake in the central Tibetan Plateau suggests that dust deposition is positively related to summer temperature.[257] The link between dust and climate was also demonstrated in the southwest Tibetan Plateau by Conroy et al[219] by comparing western Tibet temperature[258] and Dasuopu Ice Core[259] dust deposition records over the past 1000 years. Dust deposition has increased 400% in some areas of the western US over the past twenty years, with mountainous areas being particularly impacted.[260] Brahney et al[261] compared paleoecological records from two Wind River Range lakes in Wyoming, North and Lonesome, which were compared as dust-affected and control sites, respectively. The authors demonstrated a tripling in sediment P content, a tenfold increase in diatom production, increasing cyanobacteria, and diatom community changes in North Lake. These changes correspond to increasing dust flux starting around 1940. Brahney et al[262] demonstrated that lakes of the Wind River Range were subsidized by dust deposition rates as high as 276 µg P m^2 day^{-1}. The source of this dust was from a local valley, and lakes closer to the source were more affected by P subsidies. Lake ecological effects included enhanced water and sediment P concentrations, greater phytoplankton and zooplankton biomass, and dominance of diatom communities by high-nutrient species, such as *Asterionella formosa*.

Dust may also originate from distant sources. In the Mediterranean region of Europe, for example, dust deposition was dominated by material from the Sahara-Sahel desert region in northern Africa, with maximum inputs occurring during spring and summer.[263] SRP contained in this dust and deposited in the SW Mediterranean stimulated bacterial abundance and decreased phytoplankton species diversity in an alpine lake in the Spanish Sierra Nevada Mountains.[264] Reche et al[265] observed positive effects of dust inputs on bacterial abundance in two alpine lakes of the Sierra Nevada, Spain, though no effect on bacterial community composition was observed. In addition to P, Saharan dust can deliver chromophoric, aromatic, and fluorescent DOM to European alpine lakes.[266] Saharan dust input could therefore be partially responsible for the relatively higher concentrations of DOC and CDOM in lakes of Sierra Nevada versus those of the Pyrenees and Alps that do not receive this input.[267] Saharan dust also transfered viable bacteria (Gammaproteobacteria) that were deposited and grew in alpine lake water in the Austrian Alps.[268] Similarly, Reche et al[265] observed growth of Gammaproteobacteria in dust-inoculated water of the oligotrophic Quéntar Reservoir in Spain. Together, these studies suggest that atmospheric dust deposition can indirectly affect lake microbial community assemblages by influencing environmental selection pressures (such as P availability or DOM quality) or microbial assemblages can be directly affected by the introduction of exogenous species.

Determining what factors determine lake ecological sensitivity will be a critical research priority that will be able to inform lake management schemes. For instance, critical loads of N deposition (thresholds below which effects of deposition cannot be detected)[269] are typically low (1.0-1.5 kg N ha^{-1} yr^{-1}) for high elevation lake systems in the Sierras and Rocky Mountains of western United States.[45,46] However, nutrient deposition rates alone are not a good predictor of lake ecological sensitivity and response to enrichment. For instance, elevation (positive association), talus cover (positive association), unvegetated catchment area (positive association), alluvium (negative association), and riparian areas (negative association) were important factors in determining surface water susceptibility (measured from stream and lake outlets) to nutrient enrichment following atmospheric N deposition in Yosemite National Park, USA.[44] There are other factors, such as lake depth, clarity, and nutrient limitation that may be important in determining lake sensitivity. Analyses that include these factors across multiple spatial scales will be important in explaining the local and regional variation that we observe in lake responses to atmospheric deposition.

Animal vectors

Like Arctic lakes, high-elevation lakes are connected to their terrestrial environments via reciprocal flows of material. While inputs to alpine lake ecosystems are often passive hydrological or atmospheric processes determined by slope gradient and gravity, lake-to-terrestrial solid and liquid subsidies rely on animal vectors. For alpine lake ecosystems, the relative importance of aquatic- or terrestrial-derived subsidies to its neighboring environment can depend on lake elevation. For instance, based on research in the Sierra Nevada and Klamath mountain ranges of the western United States, Piovia-Scott et al[6] hypothesized that terrestrial C inputs were important controls for in-lake processes at lower elevations, and in contrast, in-lake processes were relatively more important for terrestrial consumers at higher elevation. Though lower-elevation lakes had higher absolute rates of lake-to-land C transfer than high-elevation lakes in the form of emergent insects and amphibians, the difference between lake C output vs. lake C input was smaller in low elevation lakes. This is due to the fact that high elevation catchments deliver significantly less terrestrial C to lake ecosystems. Further, because relatively little C was terrestrially derived in high elevation lakes, their ecosystems were dependent on inorganic C fixation, making them net C sinks. Lower elevation lake ecosystems, with greater amounts of terrestrial organic C, were instead CO_2 sources. Although on average lake-to-land animal C transfer decreased with lake elevation across the Klamath mountain landscape, the density of terrestrial insect infall was higher in high-elevation lakes close to shore compared to lower elevation lakes, creating a hotspot of C and nutrient deposition.[6]

Many species of trout have been introduced into naturally fishless alpine lakes for sport fishing.[270-273] The presence of predatory fish can significantly reduce the quantity of lake-to-land animal C and nutrient transfer due to predation on insect and amphibian larvae.[6] For instance, trout have reduced insect emergence in the Sierra Nevada (U.S.), such that fishless lakes can have 20 times more emergent insect biomass.[274] Introduced trout have reduced amphibian abundance in mountain lakes by predation,[275-277] as has the fungal pathogen *Batrachochytrium dendrobatidis*.[278] Greig et al[58] demonstrated that predatory fish reduce not only insect emergence directly by predation, but also reduce decomposition of terrestrial organic detritus indirectly, where increased phytoplankton blooms influenced by pelagic trophic cascades increase sedimentation rates and establish anoxic benthic conditions. Thus, in addition to reducing lake-to-land subsidies, predatory fish may also modulate land-to-lake C transfer by reducing the amount of terrestrial C that is incorporated into aquatic consumer pathways. Such food web interactions that decouple cross-system subsidies can have important effects on reciprocal communities; in Sierra Nevada (U.S.) lakes, introduced trout outcompete Rosey-finches (*Leucosticte tephrocotis dawsoni*) for mayfly larvae, so that Rosey-finches are 6 times more abundant at fishless lakes.[279] Introduced trout also outcompete and consume native frog species (*Rana muscosa*) such that these frog species are 10 times more abundant in fishless lakes of the Sierra Nevada (U.S.).[274]

Quality of a subsidy and its relative availability in the receiving environment is also an important factor when considering lake-to-land nutrient subsidies.[21,23,280] For instance, long-chain polyunsaturated fatty acids (LC-PUFAs) are critical nutrients for organismal cell membranes, structure, development, function, and signaling.[281-283] LC-PUFAs occur disproportionally in aquatic environments because they are synthesized by algae, but not by terrestrial plants,[281,284,285] and they bioaccumulate rapidly (twice the rate of bulk C) in higher trophic levels because of their nutritional status.[286] Thus, mobile or metamorphic organisms such as frogs, salamanders, aquatic insects, and birds[280,286-290] represent an important terrestrial nutrient subsidy (LC-PUFA) that is disproportionate to the mass bulk of the transferred material.

The ecological effects of climate warming on lake-to-land transfers in alpine areas requires more attention. For instance, it is unknown what effects climate warming will have on the timing, magnitude, species composition, and nutrient quality of lake-to-land transfers across Northern hemisphere alpine areas. Further, the environmental factors that determine average lake respiration vs primary production along an elevation gradient[6] may become less distinct, so that high elevation lakes may become net heterotrophic, and lake-to-land nutrient contributions become relatively less important.

Conclusions and synthesis

The environmental forces acting upon Arctic and alpine lakes are similar: warming rates in the Arctic are greater than the Northern Hemisphere average,[291] and many alpine regions exhibit accelerated warming as well.[292] Atmospheric deposition is subsidizing both areas with N and P,[156,169,241,242,260] though deposition rates and sources of deposition differ between Arctic and alpine areas. Despite high spatial variability, annual precipitation is on average declining in Arctic areas,[123] resulting in reduced annual snowpack and contributing to glacier shrinkage. Though these environmental factors are changing Arctic and alpine lakes nutrient subsidies (both in terms of material inputs and outputs), these changes are not entirely parallel (Figure 4). For instance, both Arctic and alpine landscapes contain an abundance of glacially-fed lakes, but nutrient subsidies delivered into lake ecosystems via glacier meltwater vary regionally depending on bedrock and atmospheric deposition patterns (e.g. refs. 60 and 80).

Ecosystem subsidies across Arctic and alpine landscapes will lead to changes in lake ecosystem C and nutrient cycling depending on a suite of lake, landscape, and climatological variables. For instance, DOC groundwater exports are variable in Arctic landscapes depending on soil and groundwater flow path properties.[106,107] Due to expected trajectories of climatological and environmental changes, Arctic lakes may become greater sources of CO_2 and

CH_4 as respiration and methanogenesis increase from enhanced nutrient and C availability and stronger thermal stratification. Lower-latitude Arctic lakes generally have more vegetated watersheds and developed soils than alpine lakes, thus DOC will likely be important in Arctic lakes compared to alpine ones. DOC is an important factor in determining thermal stratification of Arctic lakes to the extent that it contributes to PAR absorption.[293] Thus, lakes experiencing greater DOC subsidies from their surrounding catchments may exhibit enhanced thermal stratification[129] (Figure 3). In turn, stronger thermal stratification could contribute to hypolimnetic anoxia resulting in greater in-lake P cycling as it is released from the sediments.[294] Further, larger DOC contributions could increase lake respiration, anoxic hypolimnetic methanogenesis, and denitrification rates.[295-298] In contrast, alpine lakes can be expected to increase rates of primary production and C fixation, because declining seasonal snowpack coupled with steep alpine catchments with sparse vegetation means that little DOC is transferred into alpine lake ecosystems.[6] With relatively scarce organic C, increased nutrient loading from glaciers, snowmelt, and atmospheric deposition will likely increase rates of primary production in alpine lakes, establishing them as C sinks.[6]

In the Arctic, increased waterfowl abundance enhances the transfer of terrestrial- and marine-derived nutrients to lakes and ponds, [202,203,206,207] with the potential to cause eutrophication of these remote ecosystems. Lake-to-land transfer of C and nutrients is dominated by insect emergence in both alpine and Arctic lake ecosystems. Increased insect emergence that tracks warming and nutrient availability could lead to altered nutrient cycling in lake catchments. For instance, in lake catchments with high rates of emergent insect infall, nutrient content of plants and size and abundance of herbivorous caterpillars increased.[63]

Similarly, herbivorous, detritivorous, and predatory arthropod abundance increases.[62] Climate warming and increased nutrient loading to Arctic and alpine lakes can be expected to change the timing, magnitude, and species composition of emergence.[6,58] Phenological mismatches may occur in both Arctic and alpine landscapes between emergent insects and their terrestrial and avian predators but more Arctic- and alpine-specific research is needed to confirm and characterize these mismatches, as remote lakes are presently underrepresented in this relatively new research area.

Cross-ecosystem subsidies are mass (M) inputs, and as Leavitt et al[30] describe, lake ecosystem responses to M inputs are variable. This variability comes from differences in lake catchments, ecological communities, physical structure, and water and sediment chemistry that interact with M inputs. Additionally, differences in lake energy budgets between Arctic and alpine areas will likely interact with subsidies in different ways. Many alpine lakes are located at low latitudes with greater annual solar irradiance than those at high latitudes. For instance, among 59 lakes surveyed across the Tibetan Plateau, latitude was positively related to ice cover duration, reflecting lower temperatures and decreased irradiance toward the north.[299] Thus, researchers can expect variation in responses between Arctic and alpine lakes to similar drivers, as well as variation of responses amongst lake groups in either region. From a lake management and conservation standpoint, an important outstanding research priority involves accounting for this variation by assessing what factors determine lake sensitivity and responses to large-scale drivers, such as warming, permafrost thaw, or atmospheric deposition.

In closing, we have summarized cross-ecosystem subsidies to Arctic and alpine lake ecosystems from three major sources: the cryosphere, atmosphere, and animals. Though aquatic-terrestrial links were not addressed with their own explicit category, terrestrial-aquatic interactions were considered across all three types of nutrient subsidy classification. It is clear from this review that there are many questions to be addressed before we have an in-depth understanding of how nutrient subsidies are controlled by environmental factors, and how they in turn control the ecological behavior of cold, dilute, oligotrophic lakes. Research that assesses these factors will be crucial not only for Arctic and alpine ecologists and biogeochemists, but the broader ecological community. This is because ecosystem subsidies provide an important framework to understand and assess the types of environmental and ecosystem changes that will continue to occur in the 21st century. Our goal in this review has been not only to summarize recent ecosystem subsidy research in Arctic and alpine areas, but to promote remote lakes as exemplary systems with much to contribute to ecosystem subsidy research. Remote lakes in rapidly changing areas have much insight to provide concerning the mechanisms, processes, and ecological impacts of cross-ecosystem nutrient subsidies that occur in other ecosystems, such as low-elevation temperate lakes and streams.

Conflicts of interest

There are no conflicts to declare.

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