Groundwater Microbial Communities in Times of Climate Change

Alice Retter, Clemens Karwautz and Christian Griebler*

University of Vienna, Department of Functional & Evolutionary Ecology, Althanstrasse 14, 1090 Vienna, Austria; * corresponding author

Email: alice.retter@univie.ac.at, clemens.karwautz@univie.ac.at, christian.griebler@univie.ac.at

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Abstract

Climate change has a massive impact on the global water cycle. Subsurface ecosystems, the earth largest reservoir of liquid freshwater, currently experience a significant increase in temperature and serious consequences from extreme hydrological events. Extended droughts as well as heavy rains and floods have measurable impacts on groundwater quality and availability. In addition, the growing water demand puts increasing pressure on the already vulnerable groundwater ecosystems. Global change induces undesired dynamics in the typically nutrient and energy poor aquifers that are home to a diverse and specialized microbiome and fauna. Current and future changes in subsurface environmental conditions, without doubt, alter the composition of communities, as well as important ecosystem functions, for instance the cycling of elements such as carbon and nitrogen. A key role is played by the microbes. Understanding the interplay of biotic and abiotic drivers in subterranean ecosystems is required to anticipate future effects of climate change on groundwater resources and habitats. This review summarizes potential threats to groundwater ecosystems with emphasis on climate change and the microbial world down below our feet in the water saturated subsurface.

Introduction

Groundwater ecosystems contain 97 % of the non-frozen freshwater resources and as such provide an important water supply for irrigation of agricultural land, industrial use (e.g. cooling agent), as well as for production of potable water. Worth mentioning, in Europe, around 50 – 70 % of all drinking water stems from groundwater (Zektser and Everett, 2004). Groundwater constitutes a major component of the hydrological cycle and sustains streams, lakes, and wetlands, many of which would not be perennial without the direct connection to an aquifer. Groundwater ecosystems are typically covered by vegetated soil and vadose sediment layers of varying thickness. Where the protective layers are thin and perforated (e.g. in mountainous areas and karstic rock) or even absent, and where groundwater reaches land surface (e.g. wetlands and springs), the down below systems are highly vulnerable to disturbance from above. Moreover, due to the comparably long residence time of groundwater in the subsurface (Danielopol et al., 2003), its response time to external impacts can be delayed and sometimes masked by complex hydrologically patterns (Alley et al., 2002; Kløve et al., 2014). The subsurface is a naturally light deprived and nutrient limited environment, hence the energy required for sustaining groundwater ecosystems is largely derived from the surface. In fact, the groundwater ecosystems balance is susceptible to several external influences. It is on one hand largely dependent on energy import from the surface, but on the other hand responding sensitively to increased input of organics and nutrients as well as various types of contaminants including heavy metals and heat. While in the past, groundwater pollution mainly resulted from source contaminations with deposited or spilled petroleum hydrocarbons and halogenated solvents as well as leaking landfills, modern impacts to groundwater ecosystems are numerous. A major threat still (and ongoing) comes from intensive land use in terms of agriculture and urbanization (Saccò et al., 2019a). Application of fertilizers and pesticides to agricultural land is a major issue besides surface sealing, down below infrastructure and geothermal energy use in big cities. Accelerated import of organic matter, nutrients and chemicals cause eutrophication as well as acute and chronic toxicological effects. In urban areas, a groundwater warming constitutes a typical phenomenon.

Related to wastewater discharge, a long list of emerging pollutants including pharmaceuticals, anticorrosion agents, artificial sweeteners, drugs, or sanitary products comprise a future challenge not only for groundwater. Finally, the application of manure to arable land and the infiltration of wastewater influenced surface water occasionally lead to groundwater contamination with biological agents such as human pathogenic germs and viruses (Krauss and Griebler, 2011). Not

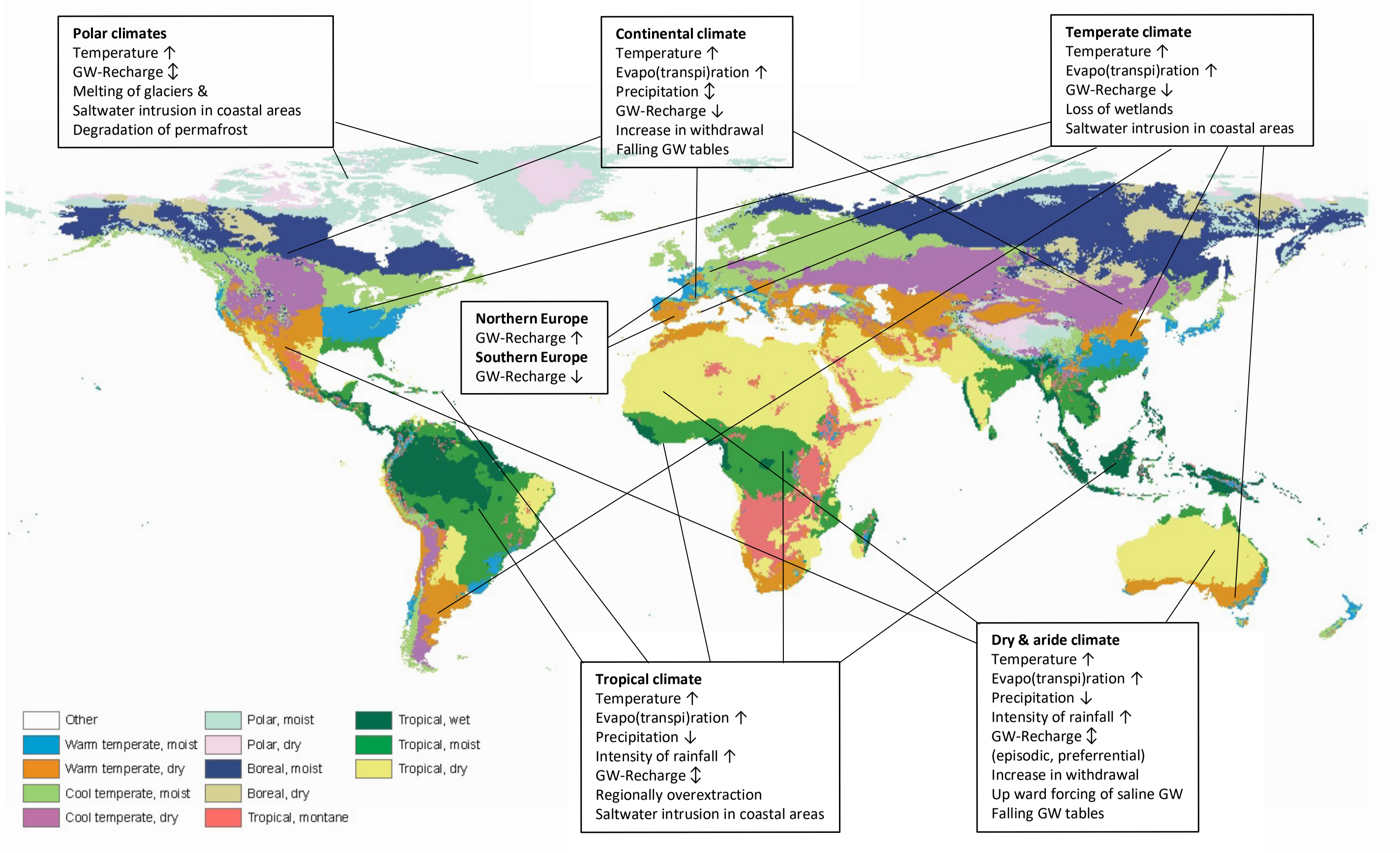

Figure 13.1 Major hydrological and meteorological effects with relation to groundwater quantity and quality caused by climate change. Information compiled mainly from Treidel et al. (2011). Map of world climate zones from https://ec.europa.eu/jrc/en/.

surprisingly, also excessive water withdrawal constitutes a major threat to groundwater ecosystems. In this context, it is timely to evaluate the possible effects of climate change to the groundwater microbiome.

Climate change impacts on groundwater ecosystems

Abiotic effects of global warming

Climate change and its consequences for global warming present one of the biggest environmental and societal challenges of our time. The pace at which it is advancing varies across ecosystems in different parts of the world and is determined to a large extent by geographic location and atmospheric chemistry e.g. greenhouse gas concentrations (Yvon-Durocher et al., 2010). The changes in seawater levels, climate, and environmental conditions alter the recharge, flow direction, storage, and discharge capacities of groundwater (Edmunds and Milne, 2001). Current climate change models predict more extreme weather events in the future that will directly affect the hydrological dynamics of groundwater (Alley at el., 2002). Fig. 13.1 compiles available information on predicted changes in precipitation and groundwater recharge for the world's major climate zones.

Some consequences of climate change already appear globally (e.g. increase in mean air temperature) while others show up geographically distinct or act only on a local scale. Prominent effects include increasing frequency of extreme hydrological events, i.e. droughts and floods, and heavy rainfall, increasing evapo(transpi)ration rates, vertical expanding of the vadose zone, horizontal expanding of dry areas including modified soil properties, decline of groundwater tables, rising sea levels and salt water intrusion, loss of glaciers as water stores, among others (Fig. 13.2) (Bates et al., 2008; Treidel et al., 2011; Richts and Vrba, 2016; Bastin et al., 2017; Betts et al., 2018). And without doubt, global warming also affects groundwater temperatures on a regional to global scale (Fig. 13.3).

Currently, it is difficult to provide quantitative predictions to which extent climate change is modifying the frequency and intensity of these events and how this directly and indirectly feeds back on groundwater quantity and quality, and in consequence on microbial processes and the sequestration and cycling of matter in the subsurface. This leaves huge uncertainties to the full impact of climate change on groundwater ecosystems (Boulton, 2005). In fact, most recent studies indicate an overall deteriorating trend with respect to groundwater quantity and quality, with only few exceptions; i.e. increased groundwater recharge in northern regions of Europe

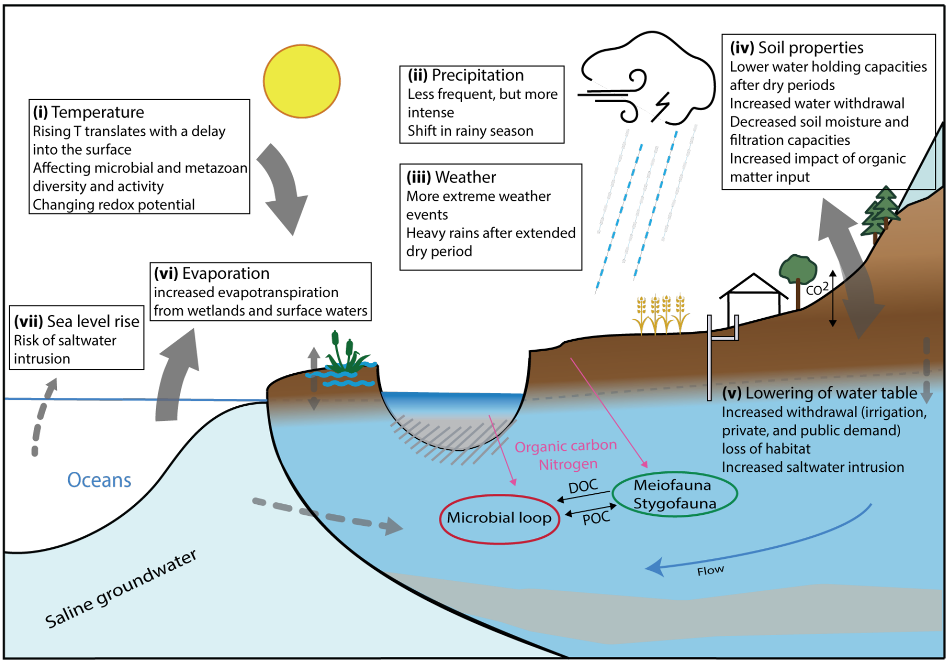

Figure 13.2 Cross-section scheme highlighting impacts of climate change on the hydrological cycle with regards to the groundwater ecosystems, water tables, physicochemical states, as well as groundwater communities and food webs.

and partly in regions where ice stocks and permafrost is melting (e.g. polar regions) or some dry and arid regions that may receive intensified rain falls (Fig. 13.1; Treidel et al., 2011).

Groundwater aquifers, as well as connected surface ecosystems (i.e. groundwater associated aquatic ecosystems [GWAAES] and groundwater dependent terrestrial ecosystems [GWDTES]) are believed to be highly vulnerable to consequences of climate change and related pressures (Nathan and Evans, 2011; Barthel and Banzhaf, 2016; Jasperson et al., 2018). With the GWAAES and the GWDTES it is mainly quantitative issues, i.e. the temporal disconnection to groundwater that matters besides consequences from altered groundwater quality that may affect the connected surface ecosystems. The vulnerability of groundwater ecosystems is related to various basic conditions. First, their low productivity goes hand in hand with a low resilience to disturbance. Second, any negative impact that traced into an aquifer stays there for long, because water residence times in the subsurface may be orders of magnitude higher than in surface waters (Danielopol et al. 2003). Third, groundwater ecosystems are typically characterized by stable environmental conditions (e.g. temperature, water chemistry, oligotrophy) all year round. In such systems, minor disturbances can have major effects on the well-adapted communities therein and the processes they mediate.

Global warming is influencing the various subterranean habitats at different spatial and temporal scales. Depending on groundwater depth, changes in the annual mean air temperature will translate into the subsurface with a time lag of years to decades compared to surface habitats, and daily or yearly fluctuations are usually attenuated (Fig. 13.3) (Menberg et al., 2014; Mammola, 2019 and citations therein). Accordingly, shallow groundwater aquifers are most exposed to external impacts and

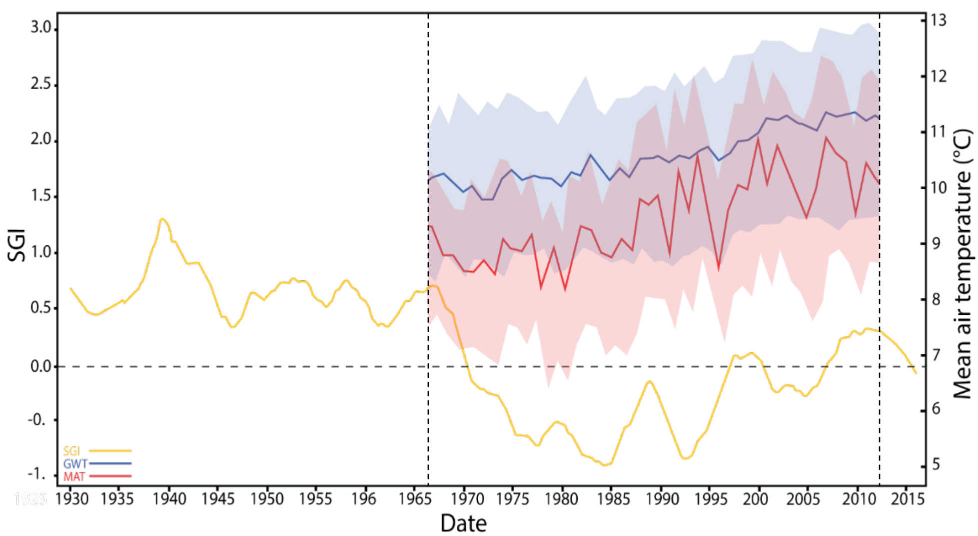

Figure 13.3 An exemplary time series from Austrian depicting trends in mean surface air temperature (MAT) and mean groundwater temperatures (GWT) (modified from Benz et al., 2018), as well as the trend of the standardized groundwater index (SGI) for Austrian groundwater (modified from Haas and Birk, 2019), showing the deviation from long-term average water levels, where negative values (<0.0) indicate declining groundwater levels; so called groundwater droughts (Uddameri et al., 2019). The general deviation between MAT and GWT relates to temperature measurements mainly in very shallow groundwater (see Benz et al., 2018).

are expected to respond more rapidly to changing temperatures than deeper aquifers. Especially in highly urbanized and agricultural areas and areas of low vegetation cover, shallow groundwater temperatures can be expected to rise even within a relatively short period of time (Henriksen and Kirkhusmo, 2000; Menberg et al., 2014; Kurylyk et al., 2015). Elevated subsurface temperatures directly alter the physical- and chemical properties of the groundwater, by lowering the solubility of gases (e.g. dissolved oxygen), as well as leading to a higher variation in dissolved organic carbon (DOC) concentrations and increased mineralization rates (Bonte et al., 2013). Additionally, a change in temperature can alter the organic matter (OM) composition and quantity of above-ground OM sources (e.g., surface flow-paths, the riparian zone, soils) that subsequently enter the groundwater via seepage water (Griebler et al., 2016; Stegen et al., 2016; Moldovan et al., 2018).

Indeed, climate change may affect the composition and quantity of OM ultimately reaching the groundwater table. As depicted in Figs. 13.1 and 13.2, changes in spatiotemporal precipitation dynamics, soil properties and groundwater recharge initiate shifts in the vadose zone thickness, which in turn influences the passage of OM, nutrients, but also contaminants into the aquifer (Ward et al., 2017). Thus, the OM from the surface dynamically entering during recharge events potentially alters the composition and activity of groundwater microbial communities on different temporal scales (Hofmann and Griebler, 2018; Benk et al., 2019). The same applies to allochthonous microorganisms introduced into the subsurface during recharge, possibly invading and re-assembling indigenous microbial communities, or even acting as a source for the groundwater microbiome (Fillinger et al., 2019; Yan et al., 2020).

The soil layer acts as a natural filter reducing or even impeding the seepage of contaminants from the surface into shallow groundwater. Extreme rainfall events have been linked to impaired groundwater quality and waterborne diseases (Ebi et al., 2017). Environmental factors such as the geographical region, land use or season do modify these effects (Guzman Herrador et al., 2015; Sonthiphand et al., 2019). Rain events can mobilize antibiotic resistant microbes from soils increasing their levels in riverine microbial communities and potentially groundwater (Di Cesare et al., 2017).

The groundwater is intricately linked to other components of the hydrological cycle through refined flow- and recharge dynamics (Havril et al., 2018). Climate change related modifications in hydrological settings thus will in some areas lead to less, but more intense carbon, nutrient, as well as contaminant inputs into the groundwater (Kaushal et al., 2014). At the same time, an associated change in groundwater table depth cause the deterioration of groundwater and linked freshwater ecosystems. This is already leading to altered carbon source, sink, and carbon cycle feedback behavior in some parts of the world (Mander et al., 2015; Dhillon et al., 2019). Besides the fast disappearance of wetlands that has been going on for centuries, hydrological dynamics of GWDTEs are dramatically changing, affecting their size and permanence. For instance, there is an ongoing trend of peatland desiccation (Swindles et al., 2019), as well as an increase of surface water areas elsewhere, for example high altitude lakes (Moore and Knowles, 1989; Zhang et al., 2017; Davidson et al., 2019), partly a leftover from disappearing glaciers.

Drought periods are expected to increase. Extended dry periods lead to desiccated surface soils which entail two main effects in terms of groundwater recharge. On one hand, dry soils have a decreased capacity to take up and hold water. In case of heavy precipitation, a large proportion of rainwater is thus directly lost from recharge by surface run-off. Simultaneously, dry cracks in desiccated soil allow some of the freshly precipitated water together with material collected at the surface to infiltrate fast via preferential flow paths, missing the natural attenuation during slow sediment passage. Thus, the decreased water retention capacity of soils and by that associated formation of cracks could lead to stronger seepage water pulses which were shown to be an important driver in cell transport and microbial community assembly in groundwater (Yan et al., 2020).

A temperature related rise in sea-level, while mostly unrecognized, will lead to increasing groundwater levels in coastal regions with devastating effects (Colombani et al., 2016). The impact of groundwater salinization can be two-fold. First, with a rise in sea-level, saline groundwater will ingress into subterranean freshwater aquifers, and secondly due to an extended demand and a resulting increase in groundwater withdrawal, a decreasing groundwater table is pulling saline groundwater inland (Treidel et al., 2011). This is of particular concern when it comes to small islands, where fresh groundwater habitats are especially vulnerable due to their confinement by the sea. The groundwater ecosystems therein especially in proximity to shorelines could thus be threatened, and anchialine habitats will probably shift inland or disappear completely (Rotzoll and Fletcher, 2012; Moritsch et al., 2014; Rogers et al., 2019).

Warming of permafrost and associated ground ice melting, as well as englacial temperatures have increased within the last decades (Ding et al., 2019). The melting of arctic permafrost leads to elevated emissions of carbon dioxide and other greenhouse gases that until now have been stored within the arctic soil. Conversely, a study of Voigt et al. (2019) showed that dry permafrost peatlands store methane rather than emitting it under warming scenarios. Without doubt, discontinuous permafrost and melting of glaciers alter the hydrology, chemistry and biology of the underlying groundwater bodies, which may experience a change from confined to unconfined aquifers. The latter will introduce the risk of groundwater pollution in case of existing above ground contaminant sources. Groundwater below glaciers and surface water ecosystems fed by them are influenced by several factors, such as thermal regimes (Ravier and Buoncristiani, 2017), the production of meltwater, and groundwater recharge, which changes when glacier size decreases (Haldorsen et al., 2010). The overall extent of climate change on aquatic habitats in polar regions can so far only be roughly estimated. They seem to harbour a distinct microbiome (Wurzbacher et al., 2017), but further research on biodiversity as well as climate change induced dynamics of carbon- and nutrient in these remote regions is urgently needed.

The groundwater food web

Groundwater ecosystems provide habitats with constant darkness and stable temperatures, narrow space, as well as low carbon, nutrient, and energy levels. In fact, the subterranean biosphere is inhabited by a diverse selection of well adapted organisms, including microbes and metazoan. Because groundwater ecosystems are among the least-studied habitats on earth (Devitt et al., 2019), the majority of the members in subterranean communities, estimated at 50,000 to 100,000 obligate subterranean metazoan species and millions of microbial taxa, still await formal description (Culver and Holsinger, 1992; Griebler and Lueders, 2009). In light of the ongoing trend of global species extinction, there is a great risk of losing species even before their discovery.

Most dominant in groundwater food webs are microbes such as bacteria, archaea, fungi and protozoa - most of them sharing a heterotrophic lifestyle. However, as already stated, groundwater also harbours micro-, meio-, and macrofauna, including a multitude of crustaceans (i.e. copepods, isopods, amphipods, ostracods), worms (oligochaetes, polychaetes, nematodes, platyhelminths), gastropods and mites. In cave waters even salamander or fish are home. Metazoans depend on microbes as food source, although opportunistic predation within their own trophic levels occurs as well (Saccò et al., 2019b). Groundwater fauna often displays highest diversity and abundance at the upper boundaries of aquatic subterranean habitats where they take advantage of increased food availability (Fišer et al., 2014). Groundwater fauna in general is highly adapted to a narrow temperature range. There are exceptions with some taxa that have a relatively broad temperature tolerance, however, always with a much better survival under temperature conditions resembling those of their natural habitats (Eme et al., 2014).

With the absence of major primary producers (i.e. photoautotrophs), groundwater food webs are typically truncated (Gibert and Deharveng, 2002). Trophic interactions appear to be bottom-up regulated, driven by the import of dissolved organic carbon, being important electron donor for microbial redox processes in groundwater (Hofbauer and Griebler, 2018; Saccò et al., 2019b). In situ microbial OM production in the light-deprived subsurface by chemolithoautotrophs is currently not considered a major contribution to the global carbon cycle. However, chemolithoautotrophic bacteria have been shown to account for a large proportion of expressed functional genes in shallow alluvial groundwater and may share functionally redundant metabolic pathways (Jewell et al., 2016). Several studies (Sarbu et al., 1996; Hutchins et al., 2016; Lau et al., 2016; Galassi et al., 2017) underline that locally, i.e. in caves and deep groundwater systems, chemolithoautotrophic production is playing a substantial role in driving trophic complexity and species abundances over long timescales. In any case, due to its huge dimensions, groundwater ecosystems represent a significant storage of global organic carbon, for example, in form of microbial biomass (Whitman et al., 1998; Magnabosco et al., 2018).

Climate change effects to the groundwater microbiome

Much has been said about the ‘abiotic’ effects of climate change and global warming to groundwater in terms of quantity and physical-chemical quality. But what do these expected and already ongoing changes in salinity, temperature, as well as carbon import to the subsurface mean to groundwater microbial communities? For some of the effects that work on groundwater ecosystems or that will gain importance in the future we have strong evidence, while in other cases we currently can only speculate.

It is well documented that a change in temperature alters microbial metabolic rates and affects microbial community composition. Elevated water temperatures, especially in temperate- and subpolar zones can be expected to influence the generation times and abundance of microorganisms in subsurface- and groundwater ecosystems (Rodó et al., 2013; Karthe, 2015; Shocket et al., 2018). Higher temperatures will speed up microbial mediated processes including the turnover of organic matter and respiration (redox processes). However, key to the expected effects is the magnitude of temperature change and the time scale. A temperature increase by only 1-2°C may not exhibit short-term (acute) changes in metabolic rates at the significance level taking the natural heterogeneity in groundwater systems into account. On a long-term perspective even slightly elevated rates of carbon turnover may exhaust carbon and nutrient pools available to the microbial communities if not replenished in time. There are complex scenarios to be considered, including as examples (1) elevated microbial activities along with decreasing pools of energy or (2) slightly increasing activities along with higher loads of carbon (including contaminants) arriving in pulses. In a field study targeting the influence of groundwater warming on various microbial pattern, it was concluded that in very clean groundwater, i.e. groundwater that lacks labile organic carbon as well as toxic compounds, a rise in temperature does not significantly affect the abundance and growth of prokaryotic cells (Brielmann et al., 2009). When overriding the energy limitation, as has been evaluated in subsequent lab experiments, even moderate temperature changes lead to shifts in microbial growth, biomass and respiration (Brielmann et al., 2011; Griebler et al., 2016). The limitation by an essential nutrient (e.g. phosphorus) may have similar effects. Bacterial cells that have enough bioavailable organic carbon but lack an element to build new biomass continue respiring OM without growth (Hofmann and Griebler, 2018). In consequence, OM is turned over without the production of prokaryotic biomass needed by other members of the (microbial) food web such as protozoa or meiofauna. Indeed, predator - prey interactions have shown to be temperature dependent, and the degree of dependency changes according to taxonomic affiliation, as well as species- and food web traits (Hutchins et al., 2016; Archer et al., 2019). Not to forget, the solubility of gases is also temperature dependent. Even small temperature changes may turn groundwater with already low concentrations of dissolved oxygen into hypoxic or even anoxic habitats. There is ample evidence from lab experiments and small scale field studies that the switch from oxic to anoxic conditions in groundwater triggers a cascade of effects including (1) the onset of anaerobic processes, (2) the accumulation of unwanted solutes in the water (ferrous iron, hydrogen sulfide, methane), and (3) a dramatic shift in community composition. In summary, already small changes in groundwater thermal regimes may lead to a decoupling of balanced food web interactions with consequences to the cycling of elements and the composition and structure of communities. In addition to the direct effects of a changing climate, human activities intended to counteract climate change, such as the sequestration of CO_2 in deep geological layers and the use of geothermal energy as sustainable alternative, pose threats to groundwater communities and ecosystems (Bonte et al., 2013; Griebler et al., 2016; Lawter et al., 2017; Westphal et al., 2017; Oelkers et al., 2019).

As already mentioned briefly, changes in the availability of organic matter will modulate microbial activities and processes. Groundwater microorganisms drive carbon- and nutrient cycling, catalyse the breakdown of contaminants, and modulate soil fertility and consequently global food webs (Cavicchioli et al., 2019). According to the scenario of irregular and more frequent extreme hydrological events, we may assume organic matter import into the subsurface on one hand to pause during extended periods of droughts and, on the other hand, to rapidly increase during times of heavy rain and floods. In the latter case, DOM may enter the subsurface in short-term pulses that cannot be processes spontaneously but are subject to a delayed microbial degradation (Foulquier et al., 2011; Reiss and Schmid-Araya, 2011; Saccò et al., 2019b). New degradation products will cause a reorganization of microbial communities in a compositional and functional manner. For instance, microbial communities in alkaline groundwaters were found to strongly relate to environmental factors such as pH, carbon monoxide, and methane concentrations (Twing et al., 2017). This will also impact the groundwater carbon cycle feedback to global warming (Allison and Martiny, 2009; He et al., 2010). Still, it is largely unclear to what extent groundwater habitats will experience a shift in the carbon sink-to-source ratio, and where to position groundwater within the global carbon cycle (Chapelle et al., 2016). Without doubt, changes in subsurface organic matter turnover will translate into changes in greenhouse gas emissions from the aquifers, a subject that so far received hardly any attention.

Changes in environmental conditions, i.e. temperature, salinity, carbon availability, all have in common that they directly or indirectly influence the composition of microbial communities. Microbial community composition in response to altered environmental conditions is linked to changes in ecosystem functioning. *Vice versa*, increased, or decreased process rates affect microbial diversity (Jesußek et al., 2013, Stegen et al., 2016). It is a paradigm that ecosystems rich in microbial species diversity exhibit a higher stability and resilience when facing disturbances due to a high functional redundancy. Species richness and biodiversity, on the other hand, are somehow connected to the energy available. There is conclusive evidence from several studies conducted in different aquatic environments that changes in organic matter supply in terms of quantity and quality steers shifts in microbial community composition (Shi et al., 1999; Baker et al., 2000; Findlay et al., 2003; Carlson et al., 2004; Judd et al., 2006; Kritzberg et al., 2006; Li et al., 2012; Wu et al., 2018). In particular, if the altered DOM supply lasts for longer than just a couple of hours or days (Herzyk et al., 2014; 2017; Grösbacher et al., 2016). However, we are only beginning to understand whether and how energy–diversity relationships known from macroecology apply to complex natural microbial communities. Diversity–productivity patterns from dozens of natural systems were found either negative (35%), positive (28%) or humped (23%) (Smith, 2007). From experimental studies that supplied sediment microbial communities with DOM, a change in community composition was reported, i.e. an increase in relative abundance of Betaproteobacteria with higher biodegradable dissolved organic carbon (BDOC) concentrations (Li et al., 2012). A lower BDOC was accompanied by a higher relative abundance of Firmicutes, Planctomycetes, and Actinobacteria, a pattern that mirrored our own findings. Overall, a decrease of microbial diversity in terms of richness and Shannon-Wiener diversity with higher feed concentrations was observed (Li et al., 2012; Li et al., 2013). In contrary, a positive relationship between bacterial richness and bioavailable organic matter was observed in Arctic deep-sea sediments, hinting at a positive energy–diversity relationship in oligotrophic environments (Bienhold et al., 2012). In fact, we can be sure that altered dynamics of organic matter input to groundwater systems will affect microbial community composition and mediated processes. The same holds true for nutrients (e.g. from fertilization) and in particular for contaminants. Undisturbed groundwater ecosystems are typically energy poor; they have a comparably low microbial biomass, activity and diversity (Griebler and Lueders, 2009) and, in consequence, are assumed to be less resilient to impacts. In other words, groundwater ecosystems and their communities are highly vulnerable.

Climate change will, without doubt, force us to adapt land use and agricultural practices. Several studies indicate that vegetation, land use and irrigation are important driver of the community composition and activity in shallow groundwater (Stein et al., 2010; Korbel et al., 2013; Iepure et al., 2016). The causality behind these effects is often not fully clear but the stressor ‘land use’ may be dissected into (1) fertilization and the application of pesticides that lead to an altered import of carbon, nutrients and contaminants, (2) deforestation and clearance of vegetation that alter conditions for groundwater recharge in terms of quantity and quality, (3) irrigation that changes the structure, moisture and water holding capacity of top soil layers and may lead to the accumulation of salts in case groundwater from deep aquifers is used as water source. Moreover, the application of manure to arable land constitutes a source of pathogenic microbes and viruses which with seepage water may enter shallow aquifers. With the serious changes in hydrological conditions and a higher frequency of extreme weather events such as heavy rainfall, there is an increasing risk of a hygienic contamination (Krauss and Griebler, 2011).

There are significant differences in the composition of microbial communities in saltwater and freshwater habitats. While there are individual studies targeting wetland biodiversity in regard to sea-level rise, little research has been directed to groundwater systems so far. In general, freshwater microbial communities and communities in low-salinity habitats are prone to a loss in diversity in case of saltwater intrusion. As shown for wetlands, microbial community shift went along with changes in the carbon biogeochemistry (Franklin et al., 2017; Dang et al., 2019). In tidal wetlands, for example, the altered carbon cycling directly affected nitrogen turnover. A loss in the ability to remove excess nitrogen leads to an excess of nutrients and increased greenhouse gas emissions in these habitats. Even under reversed climate scenarios, it may take years to decades for these ecosystems to rebalance (Franklin et al., 2017; Dang et al., 2019). A shift in soil and sediment salt content was shown to lead to an altered microbial community functioning, which in turn is depending on the duration and frequency of the salinity exposure (Liu et al., 2017; Rath et al., 2019). A study of Edmonds et al. (2009) underline the different time scales associated with changes in microbial community pattern. While a fast change in the functional component of the community with increased salinity was observed, taxonomic composition and metabolic potential on DNA level remain unchanged in response to salt stress. In summary, saltwater intrusion to fresh groundwater reservoirs poses complex changes that can be long lasting in zones with increasing salinity. Although only little is known for groundwater environments, similar effects as observed in other aquatic habitats can be expected to the groundwater biome.

Conclusions and Outlook

Climate change affects groundwater in many ways. On the one hand, it seriously alters the interplay of all important components of the hydrological cycle. Groundwater, at least the shallow portion, is changing in quantity and quality. On the other hand, climate change triggers a more intensive use of groundwater for the production of potable water, irrigation and cooling purposes. Both aspects have direct and indirect impacts to the groundwater communities in terms of composition and functions. This will have several consequences. Ecosystem functions and services mediated by microbes will change. In particular, this will apply to the subterranean carbon cycle. We may further expect that increasing temperatures impair groundwater food webs and effects to microbes will also translate into higher trophic levels.

While there is a multitude of models that try to predict climate change scenarios and related changes in carbon cycling or the loss of local to global biodiversity, groundwater ecosystems have so far been hardly considered. Although a huge amount of carbon is stored in the terrestrial subsurface, groundwater ecosystems are not yet implemented in global scale carbon models. As a first step we suggest to analyse climate variability and change in relation to hydrological, meteorological and ecological patterns on the long term (50-100 years or more) including groundwater systems to identify drivers within the oceanic-terrestrial-atmospheric coupling to understand and to be able to predict spatiotemporal changes in precipitation, evapotranspiration, recharge, discharge and groundwater storage, biogeochemical processes, and the fate of contaminants, be it abiotic or biotic (Treidel et al., 2011). For numerous sites, long-term data series are available that await targeted analysis. We also need to have an eye on the climate change induced dynamics of the vadose zone that highly determines what ends up in the aquifer in terms of energy and matter. We further need to quantify groundwater recharge and discharge and the individual pools of carbon and other elements on different spatial scales. Moreover, information on carbon turnover rates including the production and emission of greenhouse gases from groundwater systems is urgently needed. Later, these details can be implemented into scale dependent groundwater models and coupled to already existing models on carbon cycling and climate change.

Currently, our knowledge about the effects of climate change on groundwater microbial communities and interlinked food webs and cycling of matter, as well as their response to global warming is still very limited. As mentioned above, many groundwater taxa, including microorganisms such as bacteria, archaea, fungi, and protozoa are still lacking a detailed taxonomic description (Nawaz et al., 2018; Mulec and Engel, 2019; Savio et al., 2019). Only a minute portion of microbes could yet be isolated and physiologically studied. Almost all information on the microbes' physiology and biochemistry comes from genome, transcriptome, proteome, and metabolome data. This situation can be illustrated with some examples. A study by Hug and co-workers (2016) discovered novel, unrelated lineages and phyla of bacteria and archaea active in carbon fixation, as well as ammonia- and sulphur oxidation in sediment cores from the deep subsurface. Another study reported a novel lineage of nitrogen fixing bacteria, sister to Cyanobacteria that is living in anoxic zones in the subsurface (Di Rienzi et al., 2013). Also, a study by Anantharaman et al. (2016) found a large number of undescribed bacterial phyla in groundwater which were affiliated to Proteobacteria and Candidate Phyla Radiation (CPR), taking on many already known biogeochemical processes closely linked to carbon, hydrogen, and sulfur cycling, but also partly unknown metabolic pathways. Compared to other aboveground freshwater ecosystems, the knowledge about fungi in groundwater habitats, even though we have evidence that the groundwater in fact hosts numerous fungal taxa, is limited regarding species interactions, taxonomic composition and abundance, and community ecology (Grossart et al., 2019). Consequently, many known functions of the biogeochemical cycles in groundwater cannot be unambiguously linked to a certain species or group of organisms and process rates are entirely missing. As such, we are far from integrating taxonomic and functional knowledge of the groundwater microbiome into climate change models. However, this is essential to estimate the contribution of microorganisms to carbon and nutrient cycling in time and space (Antwis et al., 2017; Amend et al., 2019; Cavicchioli et al., 2019).

In the future, new bioinformatics approaches will help to refine ecological traits of microorganism and their interplay with climate change (Simonsen et al., 2019). A comprehensive and standardized study and sampling design followed by the evaluation of genomic and metadata is asked for to allow meta-analysis (Field et al., 2008). These methods need to deal with the environmental complexity and interspecies interactions that often interfere with climate-associated patterns which become apparent on the large scale (Simonsen et al., 2019).

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