



Whitepaper: Earth – Evolution at the dry limit

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ARTICLE INFO

Keywords:

Atacama
co-evolution
landscape
biology
climate
geographic barrier
isolation
speciation
water limitation
hyper arid

ABSTRACT

At the land surface, the availability of water controls the evolution of life as well as the morphological development. It is currently hardly known how far both evolutionary processes interact in water-limited environments. While it is well considered that biotic processes contribute to weathering and therewith also prepare the landscape for erosion, little is known to what degree different landforms form barriers and corridors of life across geological time scales. Here, we present an example of how to tackle this complex interplay of biology and landscape evolution by introducing the Collaborative Research Centre CRC 1211 ‘Earth – Evolution at the dry limit’. A CRC is a German Research Foundation funding program, bringing together scientists from different disciplines to tackle jointly complex emergent research questions for up to twelve years. The CRC 1211 focuses on the arid cores of the Atacama Desert and the Namib Desert. Main objective is to disentangle how the shaping of land-surfaces by past episodes of wetter climate coevolved with the evolution of life. It is hypothesized that aridity was interrupted by punctuated wetter periods, which left fingerprints in surface processes and the radiation of the biota, with climatic thresholds beyond which biota could adapt to and influence landscape development. Specific desert landscape elements such as soil surface crusts, desiccation cracks and subsoil water potentially form underexplored refugia of life at particular sites, while old channels and alluvial fan systems potentially structure its dispersal at small to intermediate scales ($< 100 \text{ m}^2$). In addition, there are large-scale ($> 10,000 \text{ km}^2$) gradients in surface processes and biodiversity, likely controlled by the intensity and duration of fog or rainfall. To substantiate these hypotheses we combine expertise from the fields of population and (phylo-) genetics, molecular biology, biogeography, ecology, soil sciences, Earth-surface sciences, geomorphology, meteorology, (paleo-) climatology, (isotope-) geochemistry and physical dating to discover and evaluate the trajectories and thresholds of the evolution and isolation of life. While presenting here our current research strategy, we invite scientists from all over the world to link their research on related questions for the joint development of a global picture on how evolution of life was triggered and regulated by land-surface processes.

1. Introduction

Water is the defining feature of the habitable Earth; it is essential for all life as we know it. Evolution of life in extremely water-limited environments, which cover significant portions on Earth, is not well understood. Akin to life, water-driven processes leave unique marks on the Earth’s surface. Mars is the only other planet known to bear the marks of water-driven surface processes, albeit fossil and of great age (e.g. von Paris et al., 2015). On Mars as well as on Earth, the slow surface processes that may operate even in the virtual absence of liquid water are essentially unknown. What is evident is that transient episodes of increased water availability leave long-lasting traces in extremely water-limited environments. Intriguingly, those traces of bursts in Earth-

surface evolution have rarely been related to bursts in biological colonization/evolution, and vice versa, although both relate to the same trigger: water.

The objective of the project *Earth – Evolution at the Dry Limit* is to pioneer the research on the mutual evolutionary relationships between Earth-surface processes and biota. The target areas are arid to hyper-arid systems, where both biota and Earth-surface processes are severely and predominantly limited by the availability of water. In doing this we aim to isolate the key fingerprints of biological activity at the (water) limit of the habitable Earth, and to characterize the Earth-surface processes operating in the (virtual) absence of liquid water. We aim to characterize thresholds for biological colonization and concurrent fluvial transformation of landscapes, identify the tipping point(s) of

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biotically and abiotically controlled Earth-surface systems, and establish detailed long-term terrestrial climatic records of the oldest and most arid zones on Earth. Chronometric and spatial information on the colonization and radiation of biota will be related to the landscape evolution and their common driver; climate. In achieving these goals we foresee major contributions to emerging concepts of evolutionary lag time (e.g. Guerrero et al., 2013), the interplay between geographical barriers and species migration in response to climate change (e.g. Burrows et al., 2014), species diversification in response to climatic and geological processes (e.g. Gillespie and Roderick, 2014), biogeomorphology (e.g. Corenblit et al., 2011) and the development and refinement of methodologies to date and determine rates of Earth-surface processes and biological evolution.

The project *Earth – Evolution at the Dry Limit* is predominantly funded as a Collaborative Research Centre (CRC 1211) by the German Research Foundation (DFG; <https://sfb1211.uni-koeln.de/>); however, it also encompasses research from international partners and other sources of funding. A CRC is established at a German university with the intention to sharpen the university's profile with respect to research and teaching, by bringing together scientists from different disciplines to solve emergent research questions that could not be answered by a single project alone. A CRC consists of up to three phases of up to four years duration each, which request individual applications that need to be positively evaluated in a two-step approach. The first step consists of a review by an international panel, and the second step involves a highly competitive evaluation procedure that assesses and compares proposed CRCs from all research fields. The CRC 1211 is currently in the first funding period (7/2016 - 6/2020; 9.7 M€), funding for the second phase (7/2020-6/2024; 11.2 M€) has been approved. The CRC collaborates closely with research partners in (alphabetic order) Argentina, Chile, Namibia, South Africa, Switzerland and the United Kingdom.

2. Background

At the dry limit both biological activity and Earth-surface processes undergo fundamental changes in response to the limiting factor water. All life on Earth has been and still is crucially dependent on the availability of water; and arid or hyper-arid conditions exert formidable selection pressure on biological systems. Environmental conditions favour certain biological communities over others, while the isolation of communities by landscape evolution (e.g. dissection) or climatic change exerts selection pressure on populations (Ali and Aitchison, 2014; Antonelli et al., 2009; Bahl et al., 2011; Gillespie and Roderick, 2014; Guerrero et al., 2013; Luebert et al., 2011b; Picard et al., 2008). Selection pressure on isolated communities will give rise to new phenotypes in floral and faunal populations and eventually to endemic species (Grenier et al., 2010; Luebert et al., 2011a; Schwarzer et al., 2010). By relating the phylogenetic relationships to ancestor populations, the timing of isolation can be inferred using modern molecular dating techniques (relaxed ‘molecular clock’; Antonelli et al., 2009; Guerrero et al., 2013; Jabbour and Renner, 2012; Luebert et al., 2011b; Macqueen et al., 2011; Picard et al., 2008; Weir and Price, 2011). A continuing challenge is linking this chronological information from molecular dating approaches to paleoclimatic reconstructions and/or changes in the landscape (Picard et al., 2008). If this challenge can be met, emerging novel hypotheses on relationships between climate (change) – Earth surface and biological evolution (Corenblit et al., 2011) can be tested.

Hyper-arid conditions, present in some of the Earth's extreme deserts such as the core region of the Atacama Desert in northern Chile, are capable of creating essentially lifeless environments (Fletcher et al., 2012; Neilson et al., 2012; Valdivia-Silva et al., 2012), which are characterized by the complete absence of higher organisms. Likewise, microbial life is substantially reduced in diversity, abundance and activity, though viable organisms may exist that may be reactivated under

appropriate conditions (Azua-Bustos et al., 2015; Bull and Asenjo, 2013; Knief et al., 2020; Schulze-Makuch et al., 2018; Wilhelm et al., 2018). However, abiotic processes will inevitably dominate in such environments (Dietrich and Perron, 2006; Ewing et al., 2006). With increasing water availability biological processes become increasingly important, finally dominating soil formation processes and modulating geomorphic evolution (Istanbulluoglu and Bras, 2005). Investigating the geo-biological process interactions that occur during the crossing of this threshold holds the potential to quantify the mutual dependency of life and Earth-surface evolution (Dietrich and Perron, 2006), and to constrain the minimum requirements of extreme biota (→exobiology, Fletcher et al., 2012; Navarro-Gozález et al., 2003; Valdivia-Silva et al., 2012).

Even subtle variations of environmental conditions in arid areas can support/limit the formation and survival of island populations (Borthagaray et al., 2010; Cáceres et al., 2007; Navarro-Gozález et al., 2003; Rietkerk et al., 2004); unsurprisingly, ancient arid environments often have a high proportion of endemic species and/or phenotypes (Durant et al., 2012) that are suitable to extract chronological information using, e.g., molecular dating approaches (Bahl et al., 2011). Populations in arid environments are therefore particularly suited to record past fluctuations in environmental conditions that allowed species establishment and subsequent isolation. In addition, isolated (paleo-) wetlands in the desert represent a resource for the reconstruction of past environmental conditions and past life by analysing the present-day as well as the fossil biota (Pigati et al., 2014).

Similarly to the biota, Earth-surface processes are crucially dependent on the availability of water: the absence of which in any state (liquid, vapour, solid) largely signifies the demise of Earth-surface processes (only aeolian activity; internal tectonic & magmatic forces or extraterrestrial impacts would then be capable of modifying the Earth's surface; Dietrich and Perron, 2006). Severely water-limited systems on Earth are therefore valuable proxies for the field of planetary geomorphology (Dietrich and Perron, 2006; Fenton and Hayward, 2010; Tooth, 2012). However, there is still surprisingly little known about processes operating in almost purely or at least temporary abiotic end-member systems, finally triggering the pathways and thus evolution of life in wetter periods.

Because of enduring absence of water, periods of environmental change in (hyper-) arid regions frequently leave long-lasting traces (e.g. soils, fluvial incision and deposits, supergene alterations) in the landscape (Dunai et al., 2005; Evenstar et al., 2017; Evenstar et al., 2009; Owen et al., 2013; Rech et al., 2019; Ritter et al., 2018a; Ritter et al., 2018b; Sillitoe and McKee, 1996; Van der Wateren and Dunai, 2001; Vasconcelos et al., 1994). The long-term aridity may preserve these records over long time-scales, up to millions of years (Carrizo et al., 2008; Dunai et al., 2005; Evenstar et al., 2009; Evenstar et al., 2017; Jordan et al., 2014; Rech et al., 2019; Ritter et al., 2018a; Ritter et al., 2018b). Modern geochronological tools such as cosmogenic nuclides or decay chain-disequilibrium dating are now available to date these traces of environmental change (e.g. Cornu et al., 2009; Dunai, 2010). Noteworthy, the same environmental changes that shaped the Earth surface have the potential to induce and direct dispersal of species and subsequent isolation (Arndt et al., 2020; Böhnert et al., 2019; Luebert et al., 2011b; Merklinger et al., 2020; Picard et al., 2008; Ruhm et al., 2020; Weir and Price, 2011), allowing testing of hypothesized relationships between climate change, Earth surface- and biological evolution.

3. Research goals, hypotheses, perspective

The central hypothesis is that in severely water-limited systems biological evolution and Earth-surface evolution are both related to episodes/periods of wetter conditions in the past. Intermittent (wetter) periods that allow species migration also provide the energy and transport medium for accelerated surface modification. In contrast,

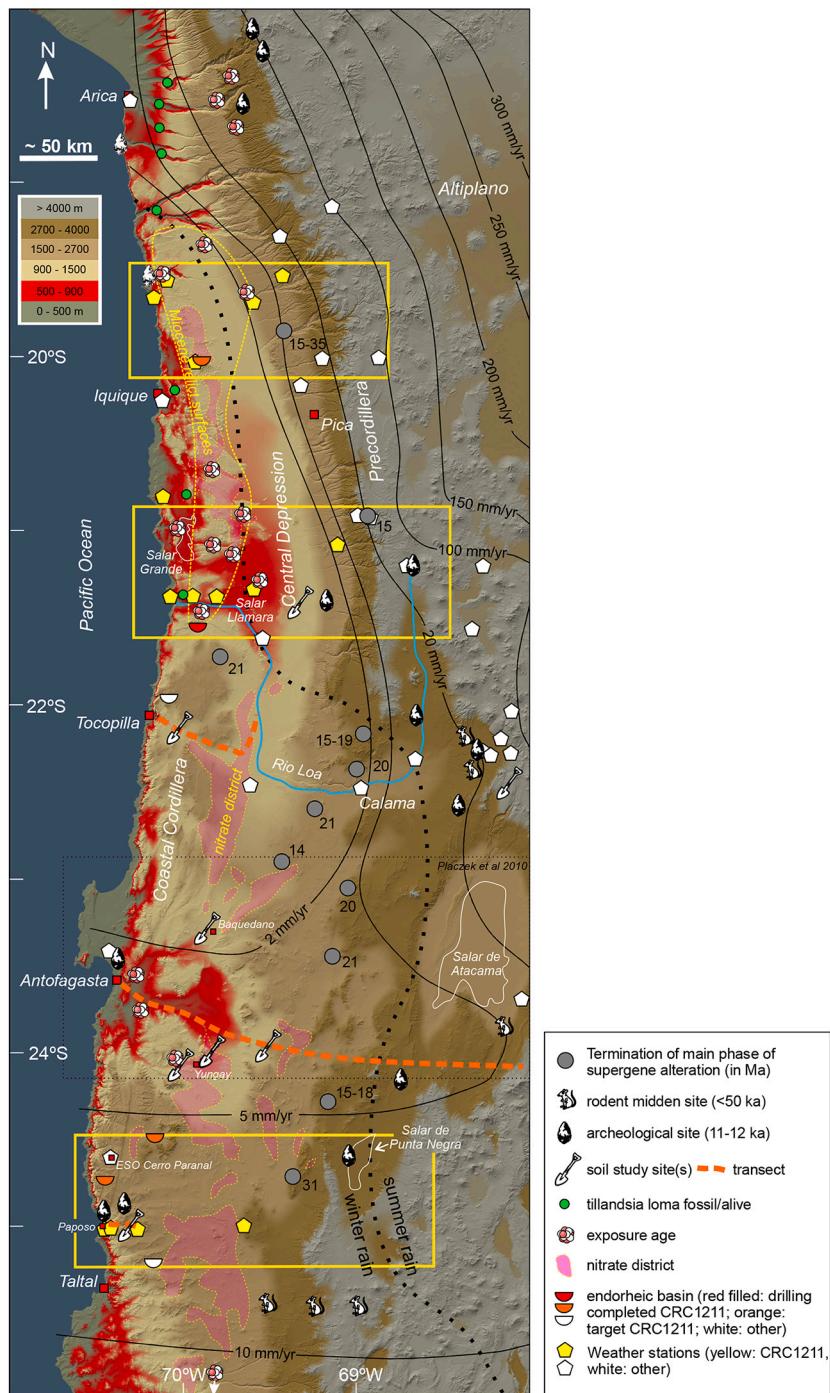


Fig. 1. Colour-shaded digital elevation model (derived from SRTM-data) with isohyets (Houston, 2006a), study sites and locations from the literature. The primary study area encompasses the Coastal Cordillera, the Central Depression and the western fringe of the Precordillera between $\sim 19.5^{\circ}$ and $\sim 23.5^{\circ}$ S. The yellow frames delineate common focus areas for CRC 1211 research. The elevation band between 500 and 900 m is highlighted in red hues; this altitude range has highest occurrence of fog and fog-precipitation (Cereceda et al., 2008b; Rutllant et al., 2003; Rutllant et al., 2013; Schulz et al., 2011). Sites from the literature are: nitrate districts (Erickson, 1981), terminations of phases of supergene enrichment of porphyry ore-deposits (Alpers and Brimhall, 1988; Bouzari and Clark, 2002; Sillito and McKee, 1996), rodent midden sites (Betancourt et al., 2000; Maldonado et al., 2005), earliest archaeological sites (Latorre et al., 2013), soil study sites (multiple studies sometimes at identical sites) (Amundson et al., 2012; Ewing et al., 2005; Ewing et al., 2006; Ewing et al., 2008; Fletcher et al., 2012; Quade et al., 2007; Rech et al., 2003; Valdivia-Silva et al., 2012), locations of *Tillandsia* lomas (Latorre et al., 2011; Pinto et al., 2006; own observations), exposure ages and erosion rates determined with cosmogenic nuclides (Amundson et al., 2012; Carrizo et al., 2008; Dunai et al., 2005; Evenstar et al., 2009; González et al., 2006; Jungers et al., 2013; Kober et al., 2007; Owen et al., 2003; Placzek et al., 2010). The stippled outline for Miocene relict surfaces is derived from Miocene exposure ages on sediment surfaces (Carrizo et al., 2008; Dunai et al., 2005; Evenstar et al., 2009; Evenstar et al., 2017; Ritter et al., 2018b). The endorheic basins in the Coastal Cordillera are filled primarily with clastic sediments (rather than evaporites, Diederich et al., 2020; Ritter et al., 2019). Major salars are indicated by white outlines (Chong, 1984). The Salar Llamara is fossil (Pueyo et al., 2001), i.e. could no longer pond water due to the dissection by the perennial Rio Loa, its outline is therefore not indicated.

prevailing (hyper-) arid conditions cause isolation, dieback or adaptation of species, and likewise fossilization of landscape features. Climatic thresholds that allow species migration and landscape modifications may be different at species level and for individual geomorphic processes. Hence, our overarching research goal is to relate water-limited biological evolution to water-limited Earth-surface evolution in a (paleo-) climatic context. We specifically exclude areas that are both water *and* temperature limited (e.g. Antarctica). As natural laboratories we chose old deserts, whose history of aridity provided sufficient time for recurring radiation/isolation and subsequent evolution of phenotypes with particular adaptation mechanisms to aridity and/or endemic species. As oldest deserts on Earth, the Atacama and the Namib deserts stand out as primary targets. Initially the focus is on the core of the Atacama Desert (Fig. 1), which contains the most arid areas on Earth and extensive areas of fossilized landscape (Carriño et al., 2008; Dunai et al., 2005; Evenstar et al., 2017; Evenstar et al., 2009; Houston, 2006a; Jordan et al., 2014; Rech et al., 2019; Ritter et al., 2018b), to be joined by comparative research in the Namib Desert in the second funding phase.

Related hypotheses that are tested are:

- o Aridity in the Atacama is long term (throughout the Cenozoic), but punctuated by wetter periods.
- o Major pluvial periods in the hyper-arid deserts relate to changes in global climate as well as regional feedback mechanisms involving tectonics, landscape development, atmospheric circulation and properties of the adjacent ocean.
- o Wetter periods can be identified in the genome of the biota and in archives of surface change; the expression is dependent on the species and environmental archive investigated, respectively.
- o The hyper-arid core of the Atacama is a long-term depositional environment for atmospheric and extraterrestrial deposition. As a result, some of the past trajectories of life are currently buried in soil.
- o Interaction of calcium sulphate and moisture is the dominant agent of surface preservation and change in the hyper-arid core of the Atacama, with crusts and desiccation cracks forming novel though little explored refugia for life.
- o At the small scale ($< 1 \text{ km}^2$), microrelief, subsoil water and related disturbances in the soil profile largely control genetic diversity at a given site.
- o At intermediate scale ($< 100 \text{ km}^2$), old landforms like alluvial fans, channels or zebra stripes structure above-ground and likely also below-ground biodiversity.
- o At the large scale ($10,000 \text{ km}^2$ and beyond), there are gradients in dominant surface processes from hyper-arid to arid environments; primarily controlled by fog and precipitation intensity and duration.
- o There are climatic thresholds beyond which biota can influence landscape evolution. This influence can have positive feedbacks on the corresponding ecosystems.
- o Species formation comes along with the acquisition of adaptation mechanisms to support survival under (hyper-) arid conditions.

To test these hypotheses, we define the following intermediate research goals:

- Isolate the key fingerprints of biological activity at the (water) limit of the habitable Earth.
- Characterize Earth-surface processes operating in the (virtual) absence of liquid water.
- Identify tipping point(s) between biotically and abiotically controlled Earth-surface systems.
- Derive the chronology of biological radiation, and investigate its modes, pathways and intrinsic climatic thresholds.
- Derive the chronology of Earth-surface processes, and determine their intrinsic climatic activation-thresholds.
- Obtain long-term terrestrial climatic records and achieve

paleoenvironmental reconstructions of the oldest arid zones on Earth, covering the time-scales of biological radiation and landscape evolution.

- Establish a predictive framework for the present climatic conditions based on land-based and remote observations.
- Develop/refine methodologies to date and determine rates of Earth-surface processes.

Since the processes investigated and methodologies applied operate at specific temporal and spatial scales, a related research program necessarily covers wide spatial and temporal ranges. The research design is aimed at maintaining significant overlap between subprojects and their specific ranges with those of others, particularly across disciplines. Spatial overlap is achieved by jointly studying the same focus areas (Fig. 1), and extrapolation of point data to gain regional information utilizing advanced remote sensing with extensive ground-proving. Spatial integration is intrinsic to some of our study objects. For instance, the point data of a cm-thick layer in a sediment sequence may hold the integral information of a catchment area of several 100 km^2 . Temporal overlap is provided by the average life time of common study objects (e.g. soils) and the - hypothesized (see above) - similar time scales of landscape and biological evolution. Fast operating, rare events can provide information about deep time, if the traces of these events are subsequently preserved, in some cases crossing orders of magnitude in time. For instance, sediments of an hour-long flood event may be preserved for millions of years in a suitable basin; one wet period, lasting several decennia/centuries, may lead to migration and subsequent isolation of species, which is recorded in the genes and genomes of newly evolved species and may be read by us millions of years later. The study of rapid events (e.g. a sheet-flow on a hill-slope) is necessary to interpret the meaning of long-term records (e.g. a sediment core of a location receiving hill-slope debris).

To structure the work, common focus areas have been selected based on the present and hypothesized past climatic gradients, the availability of features/records required for research of all projects, and logistic feasibility (Fig. 1). At the large scale, these focus areas span elevational gradients from the coast to the Precordillera near, e.g., Paposo, Aroma or Rio Tana, backed up with intensively monitored test sites including a new network of dust collectors and weather stations. The concept of focus areas does not preclude research outside of these areas; however, it requires that the majority of research is conducted within these areas.

4. Interdisciplinary cooperation

The main innovation potential of this coordinated research project lies in combining and relating the presently largely isolated research efforts in the fields of population and (phyo-) genetics, molecular biology, biogeography, ecology, soil sciences, Earth-surface sciences, geomorphology, meteorology, (paleo-) climatology, (isotope-) geochemistry and physical as well as biological dating methods. A key feature is that all disciplines involved work jointly in the same areas, with shared research objectives (Figs. 1 and 2). Current practice is that studies in one discipline commonly cherry pick findings (e.g. statements on timing of radiation, environmental and climatic change, or landscape evolution etc.) to support their corresponding statements, often without deeper knowledge of the potential pitfalls and limitations of the methods applied in the other fields. Furthermore, the evidence cited from the other disciplines is commonly not derived from the same area but from distal areas, often rendering the comparisons and relationships questionable. Our approach of jointly working in the same areas is designed to avoid these pitfalls and achieve a meaningful cross-relation of results between disciplines. Multiple joint interdisciplinary field excursions of project scientists and collaborators in the first project year, followed by joint field-work, confirmed the value of this approach. Sharing specialist knowledge in the field sensitized and informed the

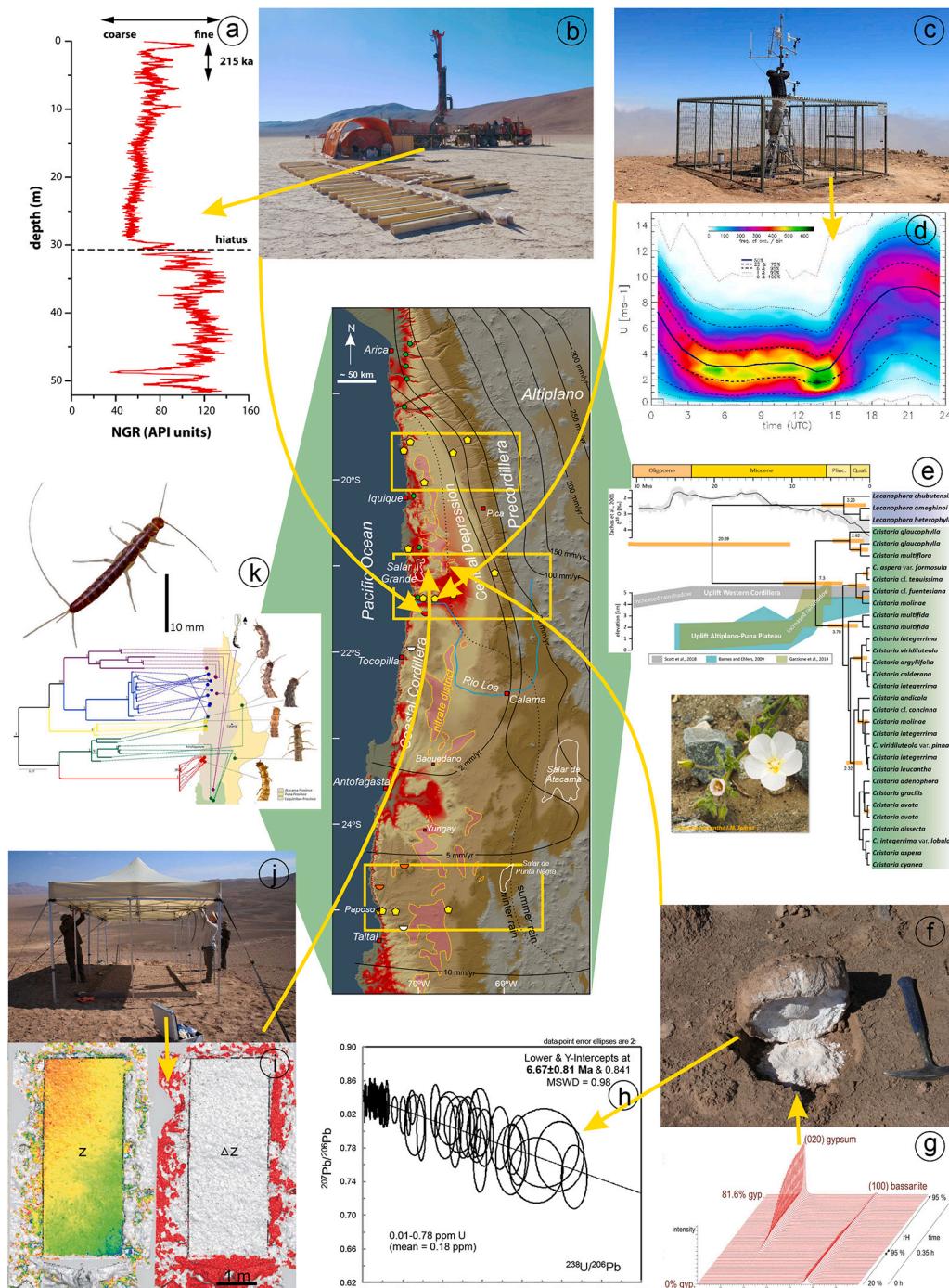


Fig. 2. Examples of joint research in the key focus areas of the CRC 1211 (yellow frames). a) Downhole natural gamma radiation (NGR) from a 52 m deep drill hole in an endorheic basin in the Coastal Cordillera, indicating profound long-term grain-size shifts that reflect differences in precipitation. The top 6 m of the sequence (indicated by arrow & 215 ka) was investigated by Ritter et al. (2019). b) The remaining part of the record was recovered by sonic-drill rig in 2017 (picture: V. Wennrich) and is still under investigation. c) Weather-station (one of fifteen installed by CRC 1211, yellow pentagons in Fig. 1; data accessible via: <https://www.crc1211db.uni-koeln.de/wd/index.php>; picture: M. May). d) 2-year, one-hourly windspeed data from depicted station (Schwein et al., 2020). e) Dated phylogeny of *Cristaria* in the Atacama Desert and its temporal correlation with global climatic and regional tectonic changes (after Böhnert et al., 2019). f) Fossil, partially exhumed calcium sulphate concretion (picture: T. Dunai). g) Kinetics of phase transformations of hydrous calcium sulphates under environmental conditions (data from Ritterbach and Becker, 2020). h) U-Pb dating of calcium sulphate concretion shown in f) (data and figure: A. Gerdes). i) and j) Irrigation experiment on a hillslope of the Coastal Cordillera with related lidar map of surface and surface modification (or absence thereof) before and after 45 l/m² artificial precipitation (May et al., 2020). k) Dated phylogeny of giant silverfish *Maindronia*, a Gondwana relict, which is unique to hyper-arid environments (picture and figure: R. Predel). Legend, where applicable, as in Fig. 1.

diverse practitioners about the needs and strengths of other disciplines to make scientific statements that are useful for one's own research.

5. Starting points and initial results

5.1. Climate and paleoclimate

A primary cause for aridity in the Atacama Desert is its location at the eastern boundary of the subtropical Pacific. In that region, large-scale atmospheric subsidence produces dry, stable conditions and maintains a surface anticyclone over the southeastern Pacific that hinders the arrival of mid-latitude disturbances (Takahashi and Battisti, 2007). The subtropical anticyclone drives equator-ward winds along the coast that, in turn, foster the transport of cold waters from higher southern latitudes (i.e. the Humboldt or Chile-Peru Current). The upwelling cold Humboldt Current inhibits the moisture capacity of onshore winds by creating a persistent inversion that traps any Pacific moisture below ~1,000 m above sea level (Houston, 2006b; Ruttlant et al., 2013) and leads to the formation of a persistent deck of stratus clouds (Cereceda et al., 2008a; Ruttlant et al., 2003; Takahashi and Battisti, 2007). These factors result in a marked regional cooling of the lower troposphere that is compensated by enhanced subsidence along the Atacama coast (Takahashi and Battisti, 2007), which leads to further drying of this area. Finally, the pronounced rain-shadow effect of the Andes to the east effectively inhibits easterly moisture transport (Houston and Hartley, 2003; Rech et al., 2010; Rech et al., 2019; Takahashi and Battisti, 2007). The high evaporation potential in most sections of the Atacama (Houston, 2006a) provides the finishing touch to the hyper-arid conditions.

Increased precipitation tends to occur throughout the Precordillera and Altiplano, when strong upper-level easterly winds enhance moisture transport from Amazonia during austral summer (December to February; Garreaud et al., 2003; Garreaud et al., 2009). As a consequence of the easterly moisture source, a rain shadow develops over the Precordillera and Atacama Desert, leading to a rapid decline in mean annual precipitation from over 300 mm per year at 5,000 m to less than 20 mm per year at 2300 m (Houston and Hartley, 2003). Below 2,300 m, associated with the Central Depression and the Coastal Cordillera, extreme hyper-aridity with a mean annual precipitation of less than 2 mm per year occurs (Houston, 2006b; Fig. 1). Winter rainfall, in contrast, is largely sourced from northerly and easterly moving frontal systems originating from the Pacific (Vuille and Ammann, 1997).

While the general patterns are known, historic observational data is spatially very patchy (Houston, 2006b). The precipitation data for the driest region (< 5 mm per year), covering approximately 120,000 km², relies on five meteorological stations only (Houston, 2006b), three of which are along the coast (Antofagasta, Iquique, Arica), none of which are in the Coastal Cordillera.

Consistent with the nearly fixed latitudinal position of the South American continent during the last 150 Ma (Hartley et al., 2005), and the existence of the Humboldt current following the establishment of the Antarctic Circumpolar Current after ~50 Ma due to the opening of the Drake passage (Cristini et al., 2012; Lagabrielle et al., 2009; Scher and Martin, 2006), it is likely that arid/semiarid conditions have prevailed over the Atacama region at least since the early Oligocene (Dunai et al., 2005; Hartley, 2003) and potentially since the late Cretaceous (Hartley et al., 2005). The onset and permanency of the hyper-arid conditions and its regional extent, however, is a matter of controversy. Geological evidence has been used to support arguments for a late Pliocene to Early Miocene onset of predominantly hyper-arid conditions (Amundson et al., 2012; Dunai et al., 2005; Evenstar et al., 2009; Gaupp et al., 1999; Hartley, 2003; Hartley and Chong, 2002; Hartley et al., 2005; Jordan et al., 2014; Jungers et al., 2013; Kirk-Lawlor et al., 2013; Placzek et al., 2010; Rech et al., 2006; Rech et al., 2019; Sáez et al., 2012; Wörner et al., 2002). The wide range of geological ages proposed

for this onset is partially due to the different proxies used (i.e. their sensitivity to climate), the records' resolution, and their location (near coastal sites vs. Andean foothills; the geographic spread of data covers 6 degrees of latitude, Fig. 1). The difficulty in resolving this key issue utilizing physics-based climate modelling is in part because of the uncertainty of the timing of the uplift of the Andes (Barnes et al., 2012; Ehlers and Poulsen, 2009; Garzione et al., 2008; Garzione et al., 2017; Insel et al., 2012; Mulch et al., 2010; Poulsen et al., 2010; Rech et al., 2006) and the contested significance of the rain-shadow effect for hyper-aridity in the Atacama (Garreaud et al., 2010; Lamb and Davis, 2003; Rech et al., 2019).

Throughout the Neogene and Quaternary, the Atacama Desert experienced distinct spatial and temporal changes in the degree of aridity, however, the history and the forcing mechanisms for these orbital-scale fluctuations are yet poorly understood (Hartley and Chong, 2002; Jordan et al., 2014; Ritter et al., 2018a, 2018b). The reconstruction of changes in the sea-surface temperature (SST) of the adjacent ocean, which is regarded as one of the key drivers (Amundson et al., 2012; Garreaud et al., 2010; Houston and Hartley, 2003; Jordan et al., 2014; Ritter et al., 2019), is hampered by the scarcity of marine sediment cores of sufficient temporal range from the coastal southeastern Pacific. Marine sedimentary successions presently exposed along the Chilean coast, in contrast, date back to the middle Miocene and are already accessible with their well-preserved microfossils. (Ibaraki, 2001; Kiel and Nielsen, 2010; Le Roux et al., 2005; Nielsen and Glodny, 2009; Ortlib et al., 1996a; Ragaini et al., 2008). They open opportunities for quantitative reconstructions of coastal upwelling and SST changes.

For shorter time-scale, i.e. the late Pleistocene to Holocene, there is a consensus that at least the size of the area with hyper-arid conditions fluctuated. During glacial periods, Pacific frontal systems migrate 150–200 km further northward than during interglacial periods (Lamy et al., 1998; Lamy et al., 2000; Rojas et al., 2009; Stuut and Lamy, 2004), creating wetter conditions in southern areas (> 23°S) that are presently hyper-arid (Díaz et al., 2012; Maldonado et al., 2005; Quade et al., 2008). Also, the Andean foothills received more runoff from the Pre-cordillera during the latest glacial (Betancourt et al., 2000; Bobst et al., 2001; Gayo et al., 2012a; Gayo et al., 2012b; Latorre et al., 2013; Pfeiffer et al., 2018).

Publications on the paleoclimate of the Atacama commonly generalize local findings (e.g. evidence for a wetter period) to be valid for the entire Atacama Desert, ignoring present-day climatic gradients (Fig. 1), while it would be cautious to assume that such gradients existed in the past as well. Due to the scarcity of observational data (modern data and continuous paleoclimate proxy records) regional climate models that are specific to the Atacama are essentially untested, although they could help resolving the apparent discrepancy of paleoclimatic indicators. A prime goal, therefore, is to improve the observational database, both for the short and the long-term climate. Our own, first data indicate:

- The commonly used remote-sensing derived models overestimate the real precipitation in the Atacama Desert by up to two orders of magnitude (Schween et al., 2020). This finding is based on climate station data, including first data obtained from 15 climate stations, which were set up in 2017 in the three main focus areas of the CRC1211 (Figs. 1, 2c, 2d; open access database at <https://www.crc1211db.uni-koeln.de>).
- Synoptic analyses of long-term observational data along with high-resolution weather simulations indicate that a characteristic ensemble of weather conditions is responsible for the majority of current rain and dust events in the Atacama Desert (Böhm et al., 2020; Reyers and Shao, 2019; Reyers et al., 2019).
- Multi-disciplinary geoscientific analyses of up to ca. 6 m long sediment cores from endorheic (internally drained) basins show that climatic fluctuations were significantly out-of-phase in the northern and central parts of the Atacama throughout the Late Quaternary

(Diederich et al., 2020; Ritter et al., 2019). Amongst the explanations for the regional differences are cutoff lows off the Atacama coast, which according to paleoclimate modeling were more frequent during the Last Glacial Maximum than today (Reyers and Shao, 2019). The paleoclimatic information is currently expanded beyond the Quaternary by the investigation of a ca. 52 m long drill core from an endorheic basin of the central focus area (Fig. 1), which was recovered in 2017.

- Complementary information concerning pluvial phases in the Coastal Cordillera, though highly discontinuous and partly masked by tectonic activity, comes from reconstructions of hillslope (May et al., 2020; Medialdea et al., 2020), coastal alluvial fan (Bartz et al., 2020a, 2020b) and fluvial channel activities (Binnie et al., 2020).

5.2. Biological evolution

The Atacama Desert is not only considered as the most arid region on Earth, but also the most lifeless terrestrial ecosystem. Nevertheless, organisms do exist in diverse hostile habitats within this biome. The spatial and temporal occurrence of essentially all living organisms in the Atacama Desert is strongly dependent on the availability of water, which reaches the desert in the form of sparse rainfall or fog. Fog-derived moisture supports the biota along the coast below the inversion zone (Schulz et al., 2012; Ruhm et al., 2020) and on isolated patches inland (Latorre et al., 2011; Pinto et al., 2006), while rainfall events mainly occur along the eastern and southern margins of the Atacama Desert (Houston, 2006b). The corresponding runoff from the Andean foreslope supports riparian biomes (Latorre et al., 2013; Quade et al., 2008; Ruhm et al., 2020). The hyper-arid core of the Atacama Desert, receiving less than 2 mm rain per year on average, is assumed to be below the 'Dry Limit' for photosynthetic activity and primary production (Warren-Rhodes et al., 2006).

5.3. Present-day distribution of flora, fauna and microbiota

Present-day vegetation in the Atacama Desert is essentially restricted to the eastern and western sides of the hyper-arid core (Ruhm et al., 2020), i.e. on the western flank of the Andes – particularly on alluvial fans (referred to as fan vegetation) – and along the western edge of the Coastal Cordillera (referred to as Loma vegetation). These two vegetation types differ markedly in abiotic environmental factors. In terms of water supply for instance, the Loma vegetation is supported by fog, while the fan vegetation depends on irregular rainfall events and/or runoff from distal headwaters. Both of these major vegetation types of the Atacama Desert show a very patchy distribution (Dillon et al., 2009; Luebert, 2011; Maldonado et al., 2005; Pinto et al., 2006; Ruhm et al., 2020; Schulz et al., 2011) with unknown correlations to the underlying soil properties or regional climate. The azonal and patchy distribution of the primary producers could largely influence the occurrence and dispersal of consumers and decomposers, including heterotrophic microorganisms, protozoa and insects. These relationships have not been investigated in the Atacama Desert to date.

Assuming that such relationships exist, they may be reflected in co-migrational patterns and possibly even co-evolutionary developments, at least between higher organisms or higher organisms and their associated microeukaryotes. For bacterial taxa living in the desert, strong co-evolutionary processes are expected to be of minor relevance, considering that bacteria are often not that strongly dispersal-limited according to the long-standing assumption that "everything is everywhere" (Baas Becking, 1934), and based on the postulation that "biodiversity at the microbial level is fundamentally different from that of macroscopic animals and plants" (Finlay et al., 1999). However, bacterial endemism is meanwhile known to occur in isolated habitats, e.g., in animal hosts (Martiny, 2016). The scarcity of adequate host individuals in a desert ecosystem, which reinforces dispersal limitation, may actually promote co-dispersal and perhaps even co-evolutionary

processes in such host-bacteria associations. Besides, evidence is emerging that regional endemism can be observed in soil bacteria within specific genera, whereby observed diversity patterns have been reported to be affected by past climatic conditions (Andam et al., 2016; Choudoir and Buckley, 2018). Thus, the development of the present-day microdiversity of bacterial groups may be governed by analogous processes as seen for plant and animal species. If climate related diversification processes can be identified in the Atacama Desert microbiota, the CRC provides a valuable platform to compare these to diversification processes of higher organisms.

Several microbiological studies that were performed in the Atacama Desert focused on the detection of life in the hyper-arid core, driven by the fact that the core of the desert serves as model for Mars in astrobiology (Navarro-Gozález et al., 2003; Parro et al., 2011; Warren-Rhodes et al., 2007a, 2007b; Wierzchos et al., 2011). In these and further studies, the presence and viability of microorganisms in surface soils of the Atacama Desert has been validated, even for hyper-arid regions (e.g. Lester et al., 2007; Crits-Christoph et al., 2013; Schulze-Makuch et al., 2018; Knief et al., 2020), indicating that this area is not completely lifeless despite the absence of macroscopic vegetation. However, the mere presence of microorganisms or their biomarkers that can be detected does not necessarily indicate microbial metabolic activity (Wilhelm et al., 2018), an aspect that deserves more attention in future studies. Only very recent studies provide clearer evidence for the existence of viable microbial communities in these desert soils. They revealed that sudden water availability, e.g. upon rainfall, can trigger microbial life into activity or even growth, therewith likely sustaining the longer-term survival of the bacteria in this ecosystem (Jones et al., 2018; Fernández-Martínez et al., 2019; Schulze-Makuch et al., 2018). However, at the same time the sudden availability of water can apparently be detrimental for major parts of the desert soil microbiota (Azua-Bustos et al., 2018; Štoviček et al., 2017). It requires further studies to better understand these apparently contrasting results.

In general, the distribution of bacteria or microbial biomarkers in the hyper-arid core of the Atacama Desert is not even, but patchy (Gómez-Silva et al., 2008; Warren-Rhodes et al., 2007a, 2007b; Warren-Rhodes et al., 2019). Moreover, microbial occurrence appears to be largely restricted to specific habitats, which provide protection against the extreme physicochemical and climatological conditions. Past water availability may also be a driver of microbial life, as supported by the finding that the occurrence of microbial traces in the study sites of the desert core is correlated with (paleo-) aqueous habitats such as playas (Warren-Rhodes et al., 2007a, 2007b). Along this line, the sheltered subsoil is recently getting more credit. Schulze-Makuch et al. (2018) found microbial metabolic activity in three subsurface samples upon a rain event and considered the subsurface as an appropriate habitat for microbial communities. Warren-Rhodes et al. (2019) pointed back to soluble salts and mineralogy influencing water bioavailability, being particularly relevant in deeper sediments, thus leading to a patchy colonization pattern triggered by osmotic stress. Detailed biogeographic studies analyzing the distribution of bacteria in Atacama Desert soils along with site-specific environmental parameters, such as soil properties and climate, with the aim to better explain the current distribution are still scarce. Likewise, biogeographic patterns of host-associated bacteria in the Atacama Desert remain currently completely unknown.

The presence of microeukaryotes is also strongly dependent on water as well as on organic material. Distribution patterns of microeukaryotes in the Atacama Desert are mostly unknown. Generally, free-living soil inhabiting protists are known to form resting stages in order to survive periods of drought and nutrient limitation, similar to many desert-dwelling bacteria, so that many of them show a broad, even cosmopolitan distribution on Earth. Due to the hostile environmental conditions in the Atacama Desert, protist diversity is strongly reduced in these soils (Conley et al., 2006; Lynch et al., 2012), and it is unclear whether specialized endemic lineages of protists may have developed in desert soils or saline lakes under these extreme conditions in association

with a specific microbiome. Refuges for protists are found in more specific habitats in the Atacama Desert, such as the digestive tract of insects (Arndt et al., 2020; Detwiler and Janovy Jr, 2008). A high level of specialization to particular habitats, along with distribution patterns of genotypes that are correlated to those of insect host species and specific plant microbiomes, as well as a higher likelihood of endemism, are expected for these protists reflecting short-term and long-term evolutionary processes in the Atacama.

Insect life is expected to be largely dependent on the presence of organic biomass as food source, and biogeographic patterns of the Atacama fauna are assumed to be correlated to floristic patterns. Among the typical insects in the Atacama Desert are species of darkling beetles (*Tenebrionidae*) and silverfish (*Zygentoma*), which have developed specific mechanisms to cope with water limitation (e.g. Goutchie and Crowe, 1979; Marcuzzi and Lafissa, 1977; Watson and Irish, 1988). These insects are wingless and show lower passive dispersal compared to wind-dispersed seed plant diaspores (Cepeda-Pizarro et al., 2005), so that their migration processes will be strongly affected by the continuous availability of organic material in form of plants or windblown detritus. Moreover, deep valleys such as that of the Rio Loa (Fig. 1) may represent dispersal barriers for these organisms. Thus, landscape features can result in habitat fragmentation and this again would argue for a decoupling of dispersal and colonization patterns between these insects and flowering plants (Zúñiga-Reinoso and Predel, 2019). In order to better understand the origin and diversification of the present-day Atacama flora and fauna, its distribution and dispersal patterns have to be studied. By comparing the present-day distribution and divergence times of selected groups of plants and insects, as well as of protozoa and bacteria, colonization patterns and co-migration events of the biota in the Atacama Desert can be unraveled.

5.4. Evolution of life

The patchy distribution of the flora, fauna and microbiota in the Atacama Desert can be considered as the result of contemporary environmental factors and historical contingencies. Landscape evolution has influenced dispersal and thus the evolution and diversification of plant, insect and protist groups, likewise as climatic conditions and nutrient availability have driven and still drive dispersal and isolation processes of biological populations. Isolated communities will give rise to novel phenotypes in floral and faunal populations and eventually to endemic species. Although only addressed based on a few selected groups, Tenebrionid and in particular plant diversification are probably the best studied processes within the biota of the Atacama Desert (Dillon et al., 2009; Flores and Pizarro-Araya, 2006; Guerrero et al., 2013; Heibl and Renner, 2012; Luebert, 2011; Luebert et al., 2011a, 2011b; Luebert and Wen, 2008; Pizarro-Araya and Jerez, 2004). The radiation of a group of flowering plants (*Heliotropiaceae*) in the Atacama Desert took place after periods of isolation at ~14, ~7 and 5 Ma (Dillon et al., 2009; Luebert and Wen, 2008). Similar dates have been inferred for the radiation of *Nolana* (*Solanaceae*), the most diverse plant family of the Atacama Desert (Dillon et al., 2009). Since dispersal and establishment are believed to be strongly dependent on hygric phenomena, the rather recent radiations suggest that wetter periods have interrupted the long-term aridity inferred from the geological record. Nevertheless, the long-lasting aridity in the Atacama Desert may not only have led to co-migrational patterns between groups of organisms, but possibly even to co-evolutionary processes.

Different modes of dispersal are conceivable for plants, animals, protists and bacteria, including long-distance dispersal (e.g. by wind) as well as short-distance migration processes. These would have impact on the genetic structure of populations. By means of population genetics, gene flow among populations can be estimated and therefore the connectivity of the populations inferred, which can be interpreted or correlated in light of dispersal modes, climatic and soil conditions. Likewise, the soil serves as an archive of life and can harbor

biomolecules and seed banks, indicating former or temporarily inactive dispersal corridors, i.e. regions with biotic corridors that intermittently connect the vegetation patches we observe today as separate. The detection of such corridors will help to explain the present-day distribution of the biota.

The soils of the Atacama Desert harbor and influence the conditions of life since millions of years. Both, the distribution and the specific properties of soil organic carbon (SOC) in Atacama soils can be used as a fingerprint of past life in the desert, thereby helping to disentangle historical dispersal corridors, provided that the biomarkers have not yet been fully degraded. Previous studies in the Atacama Desert have revealed that SOC is much lower than in other desert soils (Lester et al., 2007). Labile surface organic carbon in the region around Yungay (Fig. 1) was shown to reach very low limits, ranging from 2–125 µg per gram of soil for the KMnO₄ oxidizable fraction (Fletcher et al., 2012; Valdivia-Silva et al., 2012). Likewise, the study of Navarro-Gómez et al. (2003) reported a strong depletion of most organic molecules in this region, while more complex mixtures of organic compounds were detected in less arid sites. Mörchen et al. (2019) found that with increasing distance to the coast and thus aridity, SOC stocks decreased in the topsoil. Intriguingly, relatively large amounts of organic matter were found at depths below 15 cm, with peaking SOC concentrations between 40 and 150 cm depth in the soil, irrespectively of the presence or absence of visible vegetation. The authors thus concluded that this subsoil carbon accrual provides the potential for deep(er) biosphere food-webs and they demonstrate the need to dig into soil for discovering traces of life in comparable environments. A detailed assessment of the patchy distribution of soil organic matter stocks within the desert, along potential dispersal routes as well as, at microscale, across mineral surfaces serving as microhabitats for soil microorganisms, is largely missing.

The aim of the biological research in the CRC 1211 is to investigate the origin and diversification of the Atacama Desert flora and fauna, the (historical) biogeography of selected taxa and of microbial communities, and the biological processes occurring under extreme aridity. This includes the identification and assessment of factors relevant to these phenomena: water availability, climate, topography and nutrient availability. Knowledge about the limits for biological processes in the desert will in turn help to assess the role of the biota in landscape formation and conservation, as plant cover or the formation of biological soil crusts can influence landscape evolution. To shed light into the open research questions, work in the CRC 1211 concentrates on the following topics:

- Compare the evolution of the current biota in the Atacama Desert with the development of the desert itself. Preliminary studies with selected plant species suggest that there is likely a discrepancy between age of the desert and plants, a finding which now has to be substantiated for other taxonomic groups. Hence, work is extended to further plant species, insects and protists, whose geographic distribution and genetic differentiation is compared and correlated with landscape morphology and evolution (Arndt et al., 2020; Böhner et al., 2019; Merklinger et al., 2020, Ruhm et al., 2020, Zuniga-Reinoso and Predel, 2019) as well as with human impact (Stoll et al., 2020).
- As different organisms depend on each other, specific focus is laid on co-migrational and co-evolutionary processes. Such research reveals whether the dispersal patterns of members of the current biota that developed in an already (hyper-) arid desert coincide, meaning that formation of different species and dispersal occurred under similar environmental conditions (Arndt et al., 2020).
- Allocate corridors for above-mentioned (co-) migration processes. The azonal and patchy occurrence of living organisms in the Atacama Desert is unlikely to be the result of passive long-distance dispersal only. Evidence for the existence of corridors comes for instance from the observation that the Loma vegetation had a more contiguous

distribution in the past, probably associated with more humid phases (Schulz et al., 2011). We thus search for such corridors, along fog and aridity gradients and both above-ground as well as in soil (Jaeschke et al., 2019; Mörchen et al., 2019), which should have preserved the residues of past life to some extent due to the prolonged dryness. Using biomarkers at different soil depths may then help to identify the residues of former living cells (Amelung et al., 2008; Koegel-Knabner, 2000), whereas past nutrient formations can, e.g., be traced via altered $\delta^{18}\text{O}$ isotope compositions of soil phosphates (Tamburini et al., 2012; Amelung et al., 2015; Bauke et al., 2018). Remoistening the ground may finally help to identify under which conditions life in soil can be re-activated (e.g. Jones et al., 2018), assuming that this reactivation of life will work more easily the more recently spores and dormant microorganisms were deposited.

- Identify barriers of species dispersion and limits of life. In general, successful dispersal decreases with increasing distance and is often limited due to barriers of inhospitable environments (Martiny et al., 2006; Ruhm et al., 2020; Zuniga-Reinoso and Predel, 2019). Regions with water limitation, as observed in the hyper-arid core of the desert, represent such barriers. Limited soil nutrient availability or unusual nutrient stoichiometry may represent another barrier. In this regard soils may be both a habitat and a barrier of life, particularly since texture-driven controls of water availability and nutrient stoichiometry vary with depth and along climatic gradients (Mörchen et al., 2019; Knief et al., 2020).
- Identify hotspots in soil and at the land surface that serve as refugia for life. Such refugia can be a microdepression, below or within a surface crust, a surface channel or merely the deeper soil. The latter may contain unexpected carbon accrual due to, e.g., xeropreservation of roots, as well as alterations in water-dispersible colloid composition (Mörchen et al., 2019; Moradi et al., 2020). The analyses must therefore include an analysis of dust deposition, as a refugium of the past may nowadays be buried within an altered land surface. Disregarding such processes will likely result in a failure of discovering past corridors of life, not only in the Atacama Desert, but also in other hyperarid ecosystems and possibly also on Mars.

5.5. Earth-surface evolution

Three main N-S trending geomorphic zones constitute the driest portion of the Atacama: the Coastal Cordillera, the Central Depression and the western Andean flank rising to the Precordillera (Fig. 1). Due to the widespread coincidence in direction of these zones with climate zoning (particularly between 19° and 23° S, Fig. 1) and/or the source areas of their sediments, the Earth-surface features and sediments in the Coastal Cordillera have the greatest propensity to record the history of extreme hyper-aridity, whereas those in the Central Depression and along the western Andean flank better record precipitation fluctuations through time in the Precordillera.

The Coastal Cordillera is constructed from a block-faulted Paleogene landscape (Allmendinger and González, 2010; Allmendinger et al., 2005; Carrizo et al., 2008; Dunai et al., 2005; Mortimer and Saric, 1975; Tosdal et al., 1984). The range is cut by canyons and bordered to the west by a high cliff (600–1900 m) and a zone of marine terraces (Ortlieb et al., 1995; Ortlieb et al., 1996b; Radtke, 1989; Regard et al., 2010). To the east, the longitudinal Central Depression is infilled by Neogene deposits shed from the Precordillera, which have since been locally structurally disturbed (Evenstar et al., 2009; Evenstar et al., 2017; Mortimer and Saric, 1975). In the Andes, stratovolcanoes rise above the Andean plateau and are surrounded by internal drainage basins (Mortimer, 1973). The old tectonically dissected landscape in the Coastal Cordillera has a marked lack of fluvial landscape features and is best preserved between Arica and Antofagasta (Fig. 1, Carrizo et al., 2008; Dunai et al., 2005; Mortimer and Saric, 1975). In the core of this area, Miocene surface ages are widespread (Fig. 1, Carrizo et al., 2008; Dunai et al., 2005; Evenstar et al., 2009; Evenstar et al., 2017; Ritter

et al., 2018b). South of Antofagasta this old land surface is skeletally preserved above younger regional erosion surfaces (Mortimer and Saric, 1975), which were active into the Pliocene (Amundson et al., 2012; Jungers et al., 2013; Placzek et al., 2010). A narrow, few kilometers wide, band along the entire coast receives precipitation as fog and rare rainstorms, causing localized denudation and corresponding deposition in the Coastal Cordillera (Baker et al., 2013; Bartz et al., 2020; Carrizo et al., 2008; González et al., 2006; Vargas et al., 2006; Walk et al., 2020).

The Central Depression (Pampa Tamarugal) is an elongate, N-S basin, which terminates at the coast north of Arica (Fig. 1). The surface of the Pampa rises towards the Andean flanks, and although some deep canyons cross the Pampa to the sea, the basin acts as base level for most of the streams descending from the Andes. It is consequently an area of ephemeral lakes and salt flats and holds a corresponding sedimentary record since the Oligocene (Hartley and Evenstar, 2010; Kirk-Lawlor et al., 2013; Pueyo et al., 2001; Ritter et al., 2018a). The southern terminus of the study area ($\sim 25.5^\circ\text{S}$) is largely coincident with the disappearance of endorheic basins in the Coastal Cordillera and Central Depression (Rehak et al., 2010), witness to the increasing long-term availability of water to the south.

Due to the long-term hyper-aridity, large portions of the Atacama Desert are covered by calcium sulfate dust and crusts originating from atmospheric deposition (Erickson, 1981; Michalski et al., 2004; Rech et al., 2003; Wang et al., 2015). These are particularly well preserved in the northern portion of the study area (area of Miocene relict surfaces in Fig. 1). Likewise, the Atacama Desert is known for its economic nitrate and iodate deposits (Erickson, 1981; Erickson, 1983), whose preservation and accumulation by atmospheric deposition are intrinsically linked to long-term hyper-arid conditions (Böhlke et al., 1997; Michalski et al., 2004; Perez-Fodich et al., 2014; Reich and Bao, 2018).

While the general patterns are known, quantitative data is spatially very patchy. Our current knowledge on the Earth-surface evolution in the Atacama is characterized by early, sweeping, often qualitative descriptions considering regional gradients in climate and landscape (Brüggen, 1950; Erickson, 1981; Erickson, 1983; Mortensen, 1929; Mortimer, 1980; Mortimer and Saric, 1975) and highly sophisticated modern quantitative, but regionally biased and patchy, information. The majority of studies on soils (Ewing et al., 2006; Ewing et al., 2008; Jordan et al., 2014; Rech et al., 2003; Rech et al., 2019), hillslope processes and sediment transport (Amundson et al., 2012; Jungers et al., 2013; Kober et al., 2007; Owen et al., 2003; Owen et al., 2011; Owen et al., 2013; Placzek et al., 2010), as well as the climatic development (Betancourt et al., 2000; Díaz et al., 2012; Gayo et al., 2012a; Latorre et al., 2013; Maldonado et al., 2005; Nester et al., 2007; Pfeiffer et al., 2018; Quade et al., 2008), widely skirt the zone of extreme hyper-aridity ($< 2 \text{ mm/a}$) and are carried out in areas that today receive rare but appreciable amounts of precipitation (rainstorms, Chong, 1984; Jordan et al., 2014; Jordan et al., 2015; Jordan et al., 2019) and/or depend on runoff from the Precordillera (Chong, 1984; Houston, 2006b). To date only a handful of studies investigated the Earth-surface processes in the driest part containing the Miocene relict surfaces (Carrizo et al., 2008; Cosentino et al., 2015; Cosentino and Jordan, 2017; Dunai et al., 2005; Evenstar et al., 2009; Loveless et al., 2009; Ritter et al., 2018b). As result of the different areas investigated, each with potentially different climatic history, and the different sensitivity and nature of proxies used, there is no consensus on the duration of hyper-aridity in the Atacama or of the intensity/duration of transient wetter periods in the past.

Amongst the overarching goals of the CRC 1211 is to utilize landscape features and sedimentary archives to reconstruct the temporal and spatial variability of climate and thresholds for long-term landscape evolution in the Atacama Desert, as interplay between climatic, biotic and abiotic factors. This entails the following objectives:

- To evaluate for the first time the potential of Neogene sediments in

endorheic basins of the Coastal Cordillera for (near-) continuous reconstruction of local erosion and sedimentation (Diederich et al., 2020; Ritter et al., 2019);

- To quantitatively interpret topographic and hydrologic patterns concerning long-term and transient regional differences in runoff and erosion (Bartz et al., in 2020; Binnie et al., 2020, May et al., 2020; Medialdea et al., 2020; Mohren et al., 2020; Ritter et al., 2018b; Walk et al., 2020);
- To investigate the formation of calcium sulphates, chlorides and nitrates to better understand their potential for the reconstruction of humidity changes and role for landscape modulation (Ritterbach and Becker, 2020; Voigt et al., 2020).

5.6. Method development

Some methodological challenges and tasks have to be met by the CRC 1211. These for instance concern the sulphates, nitrates and phosphates in the soils of the Atacama Desert, including their poorly understood sources (atmospheric, marine, microbial activity) and cycling (Michalski et al., 2004). Besides, new proxies may need to be developed to extract paleoclimate information from the widespread evaporites (e.g. Gázquez et al., 2015).

Of particular importance are new methodological developments to obtain better age control on the Cenozoic continental clastic sediments and evaporites. Dating of continental sediments that are devoid of age-indicating fossils are currently largely restricted to luminescence techniques (e.g. Optically Stimulated Luminescence, OSL), paleomagnetics, and, if present, dating of organic matter (via ^{14}C) and volcanic ashes. Under suitable conditions sediment surfaces can be dated with exposure and burial dating utilizing cosmogenic nuclides.

The corresponding datable age ranges are < 50 ka for ^{14}C -dating (Wagner, 1998) and < 1 Ma for OSL dating (Ankjærgaard et al., 2013; Zander and Hilgers, 2013). No theoretical upper time limits exist for paleomagnetics (Merrill and McFadden, 1999), volcanic ashes (McDougall and Harrison, 1999) and stable cosmogenic nuclides (^3He and ^{21}Ne , Dunai, 2010; Dunai et al., 2005; Evenstar et al., 2017; Evenstar et al., 2009). However, for discontinuous records paleomagnetic age models require tie-points from other techniques (usually volcanic ash dating; e.g. Sáez et al., 2012). Dating of volcanic ashes in the Atacama as yet is limited by the scarcity of datable minerals in the distal deposits and the widely missing chemical link (fingerprint) to the volcanic sources. Burial dating utilizing in-situ produced (Balco and Rovey, 2008) or meteoric cosmogenic nuclides (Lebatard et al., 2008; Lebatard et al., 2010; Wang et al., 2011) can be applied in some cases, but datable age ranges are limited by the half-lives of the nuclides applied (Dunai, 2010; Granger and Muzikar, 2001). Straightforward dating of carbonates and gypsum in continental sediments is hampered by low uranium concentrations and significant contributions from detrital impurities, thus requiring new chemical and/or analytical protocols (Hansman et al., 2018; Mangenot et al., 2018). Notwithstanding this diverse tool box, in practice many early Quaternary and Miocene sediment records are not yet accurately datable.

In the framework of the CRC 1211, major progress in method development concerns the following aspects:

- Stable isotopic signatures in nitrates and phosphates in water-dispersible colloids of soil profiles have been shown to provide insights into past biological activity in sediments that are currently barren in organic carbon (Moradi et al., 2020).
- Information on the paleo-humidity was obtained by the determination of $\Delta^{17}\text{O}$ on hydration water in evaporites (Herwartz et al., 2017; Surma et al., 2018).
- It has been shown that the utilization of small-sample techniques for AMS ^{14}C dating (Melchert et al., 2019; Rethemeyer et al., 2019; Stolz et al., 2017; Stolz et al., 2019) on compounds isolated by modern preparative gas and liquid chromatography systems

('compound specific radiocarbon dating') has a high potential to assess the nature and timing of past biological activity at sites that are currently devoid of biological activity.

- Pairs of stable and long-lived cosmogenic nuclides (i.e. $^3\text{He}/^{53}\text{Mn}$) were developed for burial dating; with substantial ground work to be covered in order to achieve reliable analysis of ^{53}Mn (Schiffer et al., 2018; Schiffer et al., 2019).
- The combination of established dating techniques has provided reasonable age control for clastic sedimentary records from different settings: paleomagnetics (inclination and intensity), OSL and ^{14}C on endorheic basins (Diederich et al., 2020; Ritter et al., 2019), OSL, K-feldspar post infrared-stimulated luminescence (pIR-IRSL), quartz electron spin resonance (ESR) and ^{10}Be exposure dating on coastal alluvial fans (Bartz et al., in press a; Bartz et al., 2020b) and pIR-IRSL and ESR on hillslopes (Medialdea et al., 2020).

6. Concluding statement

In summary, understanding the complex interplay of processes that controlled the evolution of life at the dry limit cannot be provided by a single discipline alone. Many of the processes described above are nonlinear, some controlled or triggered by sudden events, others by slow adaptation mechanisms. The results achieved to date indicate that the dispersal of life is scale-dependent, sometimes buried below present land-surface, and certainly covering time-scales that repeatedly escape the analytical window of a particular dating technique. A Collaborative Research Centre is a viable instrument to unravel the complex functioning of such (eco)systems. However, even a Collaborative Research Centre can only work in certain priority areas, drawing on the expertise available at the participating universities. We thus invite scientists from all over the world to participate in this endeavour via sharing samples, data, models and knowledge as well as in upcoming joint workshops and scientific discourses in order to arrive at a better understanding of the origin and spread of life not only in the Atacama desert, but also in other extreme environments on our planet.

Declaration of Competing Interest

None.

Acknowledgements

We are grateful to our fellow collaborators in Chile, at the Universidad Católica del Norte Antofagasta; Universidad Antofagasta; Centro de Estudios Avancados en Zonas Aridas (CEAZA, La Serena); Centro del Desierto de Atacama (CDA, PUC Santiago) and SERNAGEOMIN, for their involvement in the research and their on-site support, in particular to Eduardo Campos from the UCN Antofagasta. Christian Tiede, Damián López and Daniela Hülle are thanked for their invaluable administrative and logistical support in Cologne.

The research outlined in this white paper relies on the contributions of all principal Investigators of CRC 1211 at the University of Cologne (UoC), University Bonn (UB), University of Heidelberg (UH), University of Frankfurt (UF), RWTH Aachen (RWTH), the Forschungszentrum Jülich (FZJ) the Geoforschungszentrum Potsdam (GFZ); and associated researchers in Germany: at the Heidelberg University of Education (HUE); Leibnitz Institute of Plant Genetics and Crop Plant Research (IPK), Leibnitz Centre for Agricultural Landscape Research (ZALF), Max Planck Institute for Plant Breeding Research (MPIPZ), Saarland University (SU), University of Münster (UM); Universität Würzburg (UW); in the UK: at the Edinburgh Napier University (ENU), in Chile at the Universidad Católica del Norte, Antofagasta (UCN); Universidad Antofagasta (UA); Centro de Estudios Avancados en Zonas Aridas (CEAZA, La Serena); Centro del Desierto de Atacama (CDA, PUC Santiago), Universidad de Concepción (UC), Universidad Austral del

Chile (UACH), SERNAGEOMIN; in Argentina: Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), in Namibia: Geological Survey of Namibia (GSN); Gobabeb Research and Training Centre (GRTC), National Botanical Research Institute (NBRI); and South Africa: University of Cape Town (UCT).

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During the first phase 19 project-affiliated postdoctoral researchers, 24 doctoral- and 51 research students contributed essentially to the CRC 1211. Funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – Project-ID 268236062 – SFB 1211.

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