Climate shifts vs. edaphic humidity and the difficulty of palaeoreconstructions – a malacological study on stable isotopes in Quaternary dune sequences of Fuerteventura

CHRISTIANE RICHTER,1* CHRISTOPHER-BASTIAN ROETTIG,1 DANIEL WOLF,1 ANDREAS GÄRTNER,2 THOMAS KOLB3 and DOMINIK FAUST1

1Dresden University of Technology, Dresden, Germany
2Senckenberg Natural Historical Collections Dresden, Dresden, Germany
3Justus-Liebig-University Giessen, Gießen, Germany

Received 31 July 2020; Revised 26 February 2021; Accepted 3 March 2021

ABSTRACT: Dune palaeosurface sequences on the Eastern Canary Islands were investigated for stable isotope records in gastropod shells of the genus Theba. Due to the ecology of the taxon and the special oceanic insularity of the study site, we assume that δ18Oshell signals in our case mainly reflect shifts in δ18O of sea surface water. We found that a rapid decrease in δ18Oshell signals is associated with significant changes in gastropod associations. We suggest that these faunal changes were caused by strong (hot) winds at the end of glacial phases, that were described previously by Moreno et al. In addition, we assume that rapid declines in δ18Oshell signals due to marine transgressions were followed by geomorphologically stable phases, dominated by dust enrichment. Such palaeosurfaces correlate with maxima of gastropod biodiversity and with more negative δ13Cshell signals indicating a higher proportion of C3 plants. Based on our results, we also assume that these silty palaeosurfaces were associated with increased soil moisture conditions due to a higher water storage capacity of the finer substrate, independent of climatic moisture conditions. © 2021 The Authors Journal of Quaternary Science Published by John Wiley & Sons Ltd

KEYWORDS: biostratigraphy; Canary Islands; dust; Quaternary; δ18O

Introduction

The Quaternary period is characterized by strong climatic fluctuations, which significantly influence the morphology of our geosphere and biosphere. To better understand the cause–effect relationships of changing environmental factors and the resulting earth-surface processes, it is indispensable to investigate sediment archives of different kind and in different settings. In this context, dune palaeosurface sequences on the Canary Islands are ideally suited for investigating landscape evolution against the background of climate changes, sea-level fluctuations, wind system modifications and various other more site-specific parameters. As these deposits are rich in biogenic fossils, we use Quaternary gastropods as environmental proxies. Dune palaeosurfaces correlate with maxima of gastropod biodiversity and with more negative δ13Cshell signals indicating a higher proportion of C3 plants. Based on our results, we also assume that these silty palaeosurfaces were associated with increased soil moisture conditions due to a higher water storage capacity of the finer substrate, independent of climatic moisture conditions.

We aim to characterize in more detail the crucial factors that trigger these more diverse ecosystems associated with palaeosurfaces. In particular, we want to identify whether a higher ambient humidity played a role, either in the form of climatic humidity or by an increase in edaphic humidity due to altered substrate properties, as suggested by Richter et al. (2019). Richter et al. (2019) found increased biodiversity of snails related to palaeosurfaces as well as species that indicate a more pronounced plant cover. Rather, respective reddish silty layers were linked to palaeosurfaces formed during phases of interrupted sand supply and predominant deposition and preservation of Saharan dust that proceeded more or less independently from local climate conditions. Therefore, a major aim of this study was to investigate the significance of local climate on palaeosurface formation on Fuerteventura and to apply additional independent proxies to prove the hypothesis of Roettig et al. (2019). Richter et al. (2019) assumed deposition and preservation of Saharan dust that proceeded more or less independently from local climate conditions. Therefore, a major aim of this study was to investigate the significance of local climate on palaeosurface formation on Fuerteventura and to apply additional independent proxies to prove the hypothesis of Roettig et al. (2019).

*Correspondence: Christiane Richter, as above.
E-mail: christiane_richter@tu-dresden.de

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However, this is the first study for the eastern Canary Islands in which information on snail communities and isotope signatures are considered over a period of about 400 ka. By a lithological unit-wise sampling technique within the same test site, features of sandy layers and palaeosurfaces can be determined over a period comprising at least the last three glacial-interglacial cycles. This study combines lithostratigraphy with geochemical, bionstratigraphical and ecosтратigraphical methods. In this way, we gain new insights into Pleistocene environmental conditions on the eastern Canary Islands and processes involved in the formation of dune palaeosurface sequences. The central questions are: (1) Do we find fluctuations of the $\delta^{13}$C$_{shell}$ and $\delta^{18}$O$_{shell}$ signals over time and is it possible to derive climatic or environmental information from these signals? (2) Do $\delta^{13}$C$_{shell}$ and $\delta^{18}$O$_{shell}$ signals relate to phases of surface stability in comparison with aeolian deposition? (3a) Which palaeoenvironmental conditions were associated with the formation of palaeosurfaces on the eastern Canary Islands and what were the driving factors? (3b) Is palaeosurface formation on Fuerteventura caused by local climatic influences or by other sedimentary cycles, possibly triggered by global climate shifts?

Geographical setting and state of knowledge

The study area is located in the northern part of Fuerteventura, which belongs to the easternmost islands of the Canary archipelago. The studied sequence Encantado (28.63915°N/13.97679°W) was the best preserved section and therefore especially suitable for detailed analyses. Encantado is located south-west of Lajares at the Barranco Encantado (Fig. 1). An overview of the lithological units is given in Fig. 2, while a detailed lithological description can be found in Roettig et al. (2017).

The modern climate of Fuerteventura is part of the subtropical desert zone (see Peel et al., 2007). Surface runoff and streams are episodic and annual precipitation is <200 mm. The main source of precipitation relates to orographic moisture supplied by north-easterly trade winds, although the low altitudes of the eastern Canary Islands virtually prevent rainfall events (Juan et al., 2000).

Lithological background

Quaternary sediments on Fuerteventura consist largely of aeolian dune sands that were relocated from the shelf during periods of marine regressions. They are predominantly composed of marine bioclastic carbonates (Roettig et al., 2017). These sands are occasionally mixed with different proportions of Saharan dust (Schneider et al., 2020), which is primarily transported by Calima events (Criado and Dorta, 2003; von Suchodoletz et al., 2009; Criado et al., 2011; Muhs, 2013). Roettig et al. (2019) relate the formation of silty palaeosurfaces to phases of reduced sand supply coinciding with significant marine transgressions. The Quaternary dune and dust deposits partly contain volcanic fallout deposits (lapilli and tephra) or coarse components from reworked basaltic bedrock or caliches (carbonated crusts). During the final stages of surface stability, the deposits partially underwent multiple erosion and reworking. In modern times, numerous gullies of barranco and wadi systems deeply dissected the aeolianite sequences, allowing far-reaching lateral tracking of lithological units along the gully walls. A short stratigraphic overview of the investigated sequence Encantado is given in Fig. 2 and Table 1, while more detailed descriptions of the lithological units can be found in Roettig et al. (2017). Chronological ages are based on infrared stimulated luminescence dating on feldspar (see Roettig et al., 2017) and are presented in Fig. 2. According to the dating results, the deposits at the base of the sequence have an age of at least 365.5 ± 34.8 ka ranging to a Holocene age at the top of the deposits (see Roettig et al., 2020).

Stable oxygen isotopes

Stable isotope signals in gastropod shells provide information about environmental influences during the time of shell carbonate precipitation. Since carbonate precipitation occurs mainly during phases of snail activity (Goodfriend et al., 1989), the recorded environmental influences correspond to certain daytimes and seasons, which are dependent on the species-specific behaviour of the gastropods. The influences on these stable isotope signals are complex. However, many publications show a correlation between $\delta^{18}$O signals in snail shells and mean annual $\delta^{18}$O signals of local precipitation (e.g. Lécolle, 1985; Zanchetta et al., 2005; Kehrwald et al., 2010; Colonese et al., 2014; Prendergast et al., 2015). Local precipitation in turn is a function of the source effect, temperature effect, continentality/rainout effect, altitudinal effect and amount effect (see e.g. Moreno et al., 2014). Furthermore, the global and local circulation of air masses is subject to seasonal and daily fluctuations and was most likely also different for glacial and interglacial periods as well as stadial and interstadial phases.

Despite the strong dependence of $\delta^{18}$O in snail shells on the local precipitation signal, the overprinting of the signal by evaporation processes can also be very strong, affecting both the absorbed precipitation as well as the metabolism and transpiration of the snail itself (see Goodfriend and Magaritz, 1987). Evaporation processes are mainly dependent on aridity/rainfall humidity, wind movement and temperature and thus differ depending on the local climate (see e.g. Yapp, 1979). In addition, these evaporation processes can vary daily and seasonally (see Magaritz and Heller, 1983).

The most important factors that influence the $\delta^{18}$O signal in shell sands are illustrated in Fig. 3. The respired gases $O_2$ and $CO_2$ seemingly do not affect the $\delta^{18}$O signals of shells. They are essential for the oxidation of glucose and thus for the generation of energy in the mitochondria, but apparently do not get incorporated in the shell aragonite of terrestrial gastropods (also see Balakrishnan et al., 2005). Similarly, oxygen from ingested food and the ground does not seem to significantly affect the $\delta^{18}$O shell signals from Theba (see Yanes et al., 2011; comp. Zhang et al., 2018). We for now neglect these factors in the following approach.) However, it is also important to consider species-specific differences. Different metabolisms, microhabitats and behaviour bias the $\delta^{18}$O$_{shell}$ signal. Thus, $\delta^{18}$O$_{shell}$ records the activity periods of the snail species, which as in continental climate can have two periods of rest, while in tropical climates they can last year-round. On Fuerteventura, species of the genus Theba keep one aestivation period during the driest and hottest summer months (see McQuad et al., 1979).

For the interpretation of $\delta^{18}$O signals in snail shells across time, we also have to consider that influencing variables presumably fluctuated between glacial and interglacial as well as stadial and interstadial periods. Thus, there is a bias, for example, by differences in the altitude effect and continental effect due to sea level high- and lowstands, the amount effect, in sea surface temperatures and in evaporation rates due to different relative humidities, etc.

Stable carbon isotopes

The interpretation of $\delta^{13}$C signals in land snail shells allows us to reconstruct the prevalent palaeovegetation via indirect
conclusions on ingested food. However, for the interpretation of the signals, it is important to consider all carbon sources for the shell composition and individual nutritional preferences of the respective species. Current studies show that $\delta^{13}C$ signals from shell aragonite of terrestrial gastropods are primarily a function of the isotope signals of snail nutrition (Stott, 2002; Liu et al., 2007; McConnaughey and Gillikin, 2008; Yanes et al., 2013). If the food spectrum of a snail species is known, the $\delta^{13}C_{\text{shell}}$ signal can potentially be used to derive the palaeovegetation from the incorporated $^{13}C$ to $^{12}C$ ratio in the snail shell. In some Helicidae, the $\delta^{13}C_{\text{shell}}$ signals allow us to derive the proportion of ingested highly xerophilous plant species (C4 and CAM) compared to less xerophilous to mesophilous plant species (C3) (Goodfriend and Magaritz, 1987; Goodfriend, 1990) and therefore can indicate humidity conditions (see Goodfriend, 1990; Prendergast et al., 2017). This principle is based on the different metabolic mechanisms of these plant groups, which cause the incorporation of different $\delta^{13}C$ signals in the respective plant species. Hence, the $\delta^{13}C_{\text{plant}}$ signal is an indicator of long-term water use efficiency in plants (Ehleringer, 1989; Marshall et al., 2007). On the Canary Islands, Yanes et al. (2008, 2013) investigated

Figure 1.
(a) Topographic map of the Canary Islands (Source: modified from stepmap.de). (b) The study area south–west of Lajares with the black arrow indicating the study site. (c) The studied outcrop ‘Encantado’ marked by the black arrow (Source: modified from maps.google.de). [Color figure can be viewed at wileyonlinelibrary.com]
δ¹³C signals in land snail shells of the genus *Theba*. Therefore, they also measured δ¹³C signals of C3, C4 and CAM plants in the Eastern Canary Islands and obtained values between −29.0 and −13.0‰, while related δ¹³Cshell signals of *Theba* geminata from the same localities showed values between −10.1 and 1.7‰ (Yanes et al., 2008, 2013). The most positive δ¹³C signals of the shells were attributed to a diet based on C4 plants. As many gastropod species are specialized to feed only on a specific group of plants, algae or fungi, Yanes et al. (2008, 2013) investigated the nutritional preferences of *Theba*. They found that *Theba* geminata feeds on C4, C3 and CAM plants without preferences for a particular group and that the δ¹³C signals of snail body tissues reflected the ingested plant types in their quantitative spatial distribution at the snail habitat. They also found that δ¹³C signals of the soft body were positively correlated with δ¹³C shell signals (Yanes et al., 2013).

**Biostratigraphic background**

Richter et al. (2019) examined species compositions on Fuerteventura over the last ca. 360 ka and found that the gastropod associations changed fundamentally. Based on the occurrence of specific communities, they derived eight different biozones (malacozones) (Fig. 4). As can be seen in Fig. 4, the genus *Theba* is very robust and occurs continuously throughout the profile. This makes *Theba* particularly suitable for stable isotope analyses, because of the continuous
Table 1. Description of the lithological units of section Encantado. Sub units a–e indicate the succession of lithofacies types from the bottom to the top of the referring units.

| Lithological unit | Sub-unit | Description |
|-------------------|----------|-------------|
| Unit 1            |          | Sallow greyish-brown strongly loamy sand; contains basalt debris, lapilli, gastropod shells and insect nests |
| Unit 2            |          | Reddish-brown silty to slightly loamy sand; contains lapilli, gastropod shells and insect nests |
| Unit 3            |          | Ochre coloured silty sand; contains lapilli, gastropod shells and insect nests |
| Unit 4            |          | Greyish-ochre coloured sand; enriched with carbonate cement; contains highly concentrated carbonatically cemented insect nests |
| Unit 5            | b        | Light ochre coloured sand; contains lapilli, gastropod shells and insect nests |
|                   | a        | Sallow ochre coloured silty sand; contains lapilli, gastropod shells and insect nests |
| Unit 6            | b        | Ochre-brown to pinkish coloured silty, slightly loamy sand with volcanic imprint; more loamy to the top; carbonate gravel at the base; basalt debris in top; contains lapilli, gastropod shells and insect nests |
|                   | a        | Greyish-brown slightly loamy sand; contains lapilli and highly concentrated cemented insect nests |
| Unit 7            | c        | Sallow ochre-brown slightly loamy sand; strongly loamy and dark-brown to the top; contains root-shaped clay cutans and gypsum concretions as well as coated gastropod shells and insect nests |
|                   | b        | Pinkish ochre-grey coloured slightly loamy sand with volcanic imprint; shows greasing effect; contains many gastropod shells and insect nests |
|                   | a        | Whitish-ochre coloured sand; contains few biogenic fragments and many crotovines with material from Unit 7b |
| Unit 8            | c        | Light pink coloured loamy sand with volcanic imprint; more loamy to the top; shows greasing effect; contains lapilli, partly coated gastropod shells and insect nests; bioturbation at the top |
|                   | b        | Reddish-ochre coloured sand; contains few gastropod shells and many crotovines |
|                   | a        | Light ochre coloured sand; contains few gastropod fragments |
| Unit 9            |          | Ochre-brown slightly loamy sand; strong reddish-brown and more loamy to the top; contains lapilli, gastropod shells and insect nests; bioturbation at the top |
| Unit 10           |          | Ochre-yellow sand with a strong reddish-brown colour and sub-polyhedral structure at the top; contains lapilli, gastropod shells and insect nests; crotovines |
| Unit 11           |          | Greyish-brown coloured loamy sand; strong brown and more loamy to the top; contains lapilli, gastropod shells and insect nests; top contains basalt debris and shows bioturbation |
| Unit 12           | e        | Ochre-brown to pinkish coloured sand with volcanic imprint; contains lapilli, gastropod shells and carbonatically cemented insect nests |
|                   | d        | Ochre-brown coloured, slightly loamy sand; more loamy to the top; contains lapilli, coated gastropod shells and insect nests |
|                   | c        | Sallow greyish ochre-brown to pinkish coloured substrate with volcanic imprint; contains lapilli, gastropod shells and coated insect nests |
|                   | b        | Ochre-brown coloured slightly loamy sand; contains lapilli as well as coated gastropod shells and insect nests |
|                   | a        | Light ochre coloured sand, slightly loamy to the top; contains layered enrichments of lapilli and gastropod shells, as well as insect nests; bioturbation at the top |
| Unit 13           |          | Dark-brown slightly loamy sand; more loamy and reddish brown to the top; contains gypsum concretions. coated gastropod shells and insect nests; bioturbation at the top |

Figure 3. Variables influencing the $\delta^{18}O$ signals of land snail shells [according to Siegenthaler (1979) and Schmidt et al. (1999), modified]. [Color figure can be viewed at wileyonlinelibrary.com]

(1) rain signal depending on air masses (marine source signal, temperature effect, amount effect, continentality/rainout effect, altitude effect)

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occurrence on the one hand and the numerous already existing isotope investigations for representatives of this genus on the other. *Theba* spp. in this study refers to a species complex that includes *Theba arinagae*, *Theba geminata* and probably two new species of the genus (see Richter et al., 2019) – due to their similar ecological behaviour, we assume that these different species perform comparable fractionation processes.

**Methods**

**Raman spectroscopy and XRD analysis**

The mineralogical composition of empty shells of two modern *Theba* individuals, as well as from samples E-8 and E-1 (four shells of each sample) was analysed via Raman spectroscopy. Three to six measurements were performed on different, randomly selected regions of each shell. All analyses were done using a Bruker Senterra R200-L Raman spectrometer working with a 785-nm laser at 100% of 100-mW power. Further analytical parameters were chosen as follows: a 20× objective (NA = 0.4, wd = 1.3 mm), a slit of 25 × 1000 µm, an integration time of 5 s and 12 co-additions, and a spectral range of 60–1520 cm\(^{-1}\). An Olympus BX51 confocal microscope was coupled to the Raman spectroscope. Calibration of the system was done against the 520.4 cm\(^{-1}\) line of a silicon standard target.

Results are compared with data of aragonite (R040078, R060195, R150021) and calcite (R040070, R040170, R050009, R050048, R050127, R050130, R050307, R150020, R150075) that were analysed at 780–785 nm and published in the RRUFF database (Lafuente et al., 2015).

To obtain an independent control of the Raman spectroscopic results, one complete *Theba* shell of samples E-8 and E-1 was cleaned as described below, pulverized in an agate mortar and analysed via X-ray diffraction (XRD; Bruker D2 Phaser with a Cu anode operating at 30 kV, 10 mA). Parameters of the analyses were a 2θ range of 5.002–66.976°, a step size of 0.010° and a counting time of 0.2 s per step.

**Stable isotope analysis**

From the section Encantado, which is described in the previous section and in Roettig et al. (2017), we took 26 sediment samples over a thickness of 15 m analogous to lithological units as shown in Figs. 5 and 7. From these, we extracted four complete adult shells with a similar number of 4–4½ whorls per sample for isotope measurements. We analysed exclusively shells of the genus *Theba*, to minimize taxon-specific differences in metabolic fractionation processes. Furthermore, we analysed stable isotope signals of four modern *Theba* shells. Since recent environmental conditions apparently do not enable gastropods to live at the immediate profile locations, the modern empty *Theba* shells were sampled beneath rotten plant.
material from a valley floor close to the study site. All shells were broken and cleaned in an ultrasonic bath, while adhering loamy or carbonatic accretions were removed with a brush and sandpaper also from the internal surface of the shells. Subsequently, shells were air dried and ground with a porcelain pestle. Measurement, calculation and corrections were conducted by an external laboratory (Prof. Dr Joachimski, Geozentrum Nordbayern). Therefore, 0.3 mg of the homogenized carbonate powders was merged with 100% phosphoric acid at 70°C using a Gasbench II connected to a ThermoFisher Delta V Plus mass spectrometer. Results are indicated as delta notation. All values were set in relation to the common standard for carbonates, V-PDB (Vienna-Pee Dee Belemnite). Further- more, reproducibility and accuracy were monitored by replicate analysis of laboratory internal standards calibrated to international standards NBS 19, NBS 18 and LSVEC. Calcite oxygen isotope values were corrected for aragonite using the phosphoric acid fractionation factors given by Rosenbaum and Sheppard (1986) and Kim et al. (2007). The analytical precision of the two laboratory internal standards that were applied was 0.08 and 0.04‰ for δ13C and 0.08 and 0.06‰ for δ18O.

Biodiversity index

The Shannon Index (1948) is used to quantify biodiversity. This index is open upwards and inclines with increasing species richness and equitability, respectively. Equitability describes whether all species are present with similar abundances and indicates if a biotope is stable or rather unstable, and dominated by certain stress factors (see Magurran, 1988).
The Shannon biodiversity index was calculated as demonstrated in Shannon (1948).

Results
Stable isotope analysis
The stable isotope signals for δ13C and δ18O of the Encantado section (Supporting Information Tables S1 and S2) are plotted in Figs. 5 and 7.

As the number of samples is at the lower end of the usual sample quantities used (compare e.g. to Colonese et al. (2014) who measured 3–6 shells per lithological unit or Yanes et al. (2013) who measured 4–10 shells per lithological unit), we assume less representative medians for datasets with a high variability. δ13C signals for Encantado vary between −6.95 and 1.46‰. There is a significant difference between δ13C medians of samples from palaeosurfaces (−5.90‰) compared to all other samples of the profile (−4.71‰) (Kruskal–Wallis test: \( p = 0.002 \)). Accordingly, samples of palaeosurfaces (samples E-10, E-12, E-19, E-20, E-25 and E-26) are characterized by more negative δ13C signals. In addition, the samples of tephric layers (E-3, E-5, E-14, E-15, E-17 and E-23) show more negative δ13C signals compared to the surrounding layers. Accordingly, the differences between δ13C medians of these tephra-rich samples and the mean of the δ13C medians of the underlying and overlying samples averages −0.6‰ (calculated as follows):

\[
\text{Difference} = \text{Median}_x - (\text{Median}_k + \text{Median}_l)/2
\]

\( x \) Sample \( x \)
\( k \) Sample superjacent to sample \( x \)
\( l \) Sample subjacent to sample \( x \)

In comparison, these differences in δ13Cshell signals compared to the surrounding substrate are −1.1‰ for palaeosurfaces and 0.8‰ for all other samples on average (Fig. 6). This shows that tephric samples have significantly more negative δ13Cshell values compared to the surrounding substrate than all other samples that are neither tephras nor palaeosurfaces (Kruskal–Wallis test: \( p = 0.015 \), Fig. 6).

If we exclude the samples with the largest standard deviations (above 2‰), namely samples E-3, E-7, E-8 and E-17, we can detect an inverse correlation between δ13Cshell and the Shannon index (taken from Richter et al., 2019). The corresponding correlation factor after Pearson is −0.49 with a level of significance of \( p = 0.034 \), which corresponds to a residual risk of 3.4% for the relation to be random.

δ18Oshell signals vary between −1.49 and 2.26‰, and do not correlate with δ13Cshell or any other proxy of the malacological analyses. δ18Oshell values are particularly high for samples E-4, E-7, E-10, E-16, E-18, E-20, E-22, E-25 and E-27, showing no continuous pattern related to palaeosurfaces.

Modern shells in this study showed δ18O values between −0.55 and −0.93‰, which are more negative compared to the uppermost part of the Encantado profile (sample E-27). Sample E-27 is characterized by a median δ18Oshell signal of 1.23‰ and, due to its allocation to lithological units 1–3, is presumed to correspond to an age of around 16 ka before present (Roettig et al., 2017).

Mineralogical analysis
Mineralogical analyses applying Raman spectroscopy on two shells of modern Theba and samples E-8 and E-1 (four specimens each) yielded almost pristine aragonite on 34 of 39 spots (Supporting Information Fig. S1). The patterns of the remaining five measurements, i.e. three on one shell of sample E-8 and two on one shell of sample E-1, gave reason to assume subordinate presence of calcite. XRD analyses on complete shells of E-8 and E-1 showed patterns indicative for the presence of pure aragonite (Supporting Information Fig. S1).

Discussion
Geochemical alteration
All data were calibrated for aragonite as almost all mineralogical analyses of Theba shells from different stratigraphic levels did not show any calcite. Although parts of one shell from sample E-8 and E-1 contained local traces of calcite, these may result from the incorporation of ground-derived calcite by the snail rather than mineral conversion. Mineral conversion to calcite would probably significantly influence the stable isotope results (see Lécuyer et al., 2020). However, δ18Oshell and δ13Cshell signals do not correlate across the sequence and show no synchronous shifts. It is conceivable that different stable isotope ratios for palaeosurfaces compared to sandy layers may be due to different conditions for aragonite–calcite transformation processes in the respective environment. However, such effects would also have been revealed in the studies by Yanes et al. (2011). They analysed Theba shells in sand palaeosurface sequences on the eastern Canary Islands regarding their microstructure (by XRD and raster electron micrographs) and stated that aragonite–calcite transformation is negligible for the stable isotope analyses of terrestrial gastropod shells in these Quaternary deposits, independent of the lithofacies. This is also corroborated by the XRD and Raman analyses of this study, comparing modern Theba shells with Theba shells from the lowermost palaeosurface (sample E-8) as well as the lowermost sandy layer (sample E-1), and therefore seems to be applicable also for much older stratigraphic layers with ages over 300 ka. Accordingly, we consider that the prevalent fluctuations between palaeosurfaces compared to sandy layers in our sequence not to reflect
diagenetic patterns, but are dominated by other influences. Also, Xuefen et al. (2005) investigated the aragonite–calcite transformation of terrestrial gastropod shells in Chinese long-term loess records as well as in laboratory experiments and found that temperature and pressure did not appear to influence the observed aragonite–calcite transformation in these terrestrial loess deposits. However, they found mineral conversion in the gastropod shells towards calcite in the lowermost strata of the deposits, indicating age-dependent calcite formation due to the metastable state of aragonite. They identified an age of 420–658 ka BP, from which the calcite transformation presumably takes place. Since we see a fluctuation between palaeosurfaces and sandy layers regardless of the age, and no differences between younger and older strata, there is no evidence for an age-related aragonite–calcite transformation in our sequence. Therefore, we propose that calcite formation plays a negligible role in the analysed shell samples.

δ\textsuperscript{13}C\textsubscript{shell} – C3 plants in palaeosurfaces and the role of edaphic humidity

We presume the most positive δ\textsuperscript{13}C\textsubscript{shell} signals at Encantado to be related to a higher consumption of C4 plants, while more negative values indicate a higher consumption of C3 plants (see ‘Geographical setting and state of knowledge’). There is a general trend for samples that are related to palaeosurfaces such as samples E-10, E-12, E-19, E-20 and E-26 to coincide...
with the most negative median values of δ²⁸Cshell, which, in turn, indicate moister conditions. Sample E-8 is an exception to this pattern, which may be due to an outlier in the measured δ²⁸Cshell signals. The large standard deviation of 2.39‰ indicates that the median value for this sample may not be representative.

It may be conceivable that fluctuations in potentially ingested ground-derived carbonate biased these δ²³Cshell values, as also carbonate contents at the Encantado site are continuously decreased within palaeosurfaces (see Roetig et al., 2019). Goodfriend and Hood (1983) assumed that up to 33% of land snail shell carbonate can be derived from the parent material. However, the carbonate content across the Encantado sequence is never <40% (Roetig et al., 2017) and the availability of lithogenic carbonate was therefore always saturated. This would suggest that the amount of incorporated ground-derived carbonate in the snail shell should have been constant. However, Yanes et al. (2008) measured δ¹³C in carbonate-rich sediments of Lanzarote and gained values between −1.4 and 1.6‰, which shows that the influence of calcium carbonate on gastropod shells would not only depend on the amount of ingested carbonate but also on its composition. In contrast to Goodfriend and Hood (1983), studies by Stott (2002) and Metref et al. (2003) showed that δ¹³C signals from snail shells are directly related to the δ¹³C signals of their soft tissues, but neither was influenced by the consumption of carbonate or atmospheric CO₂. To test this, we apply the flux balance model from Balakrishnan and Yapp (2004). For the δ¹³C values of atmospheric CO₂, we take an average of ~6.7‰ for glacial phases (Leuenberger et al., 1992) and of ~8.4‰ (Graven et al., 2017) for modern (interglacial) times (Keeling et al., 1989) in the equations. The CO₂ partial pressure under full interglacial conditions was about 190 p.p.m. (Oeschger et al., 1984), about 280 p.p.m. for pre-industrial times (Neftel et al., 1985) and 360 p.p.m. at present (Keeling and Whorf, 2002). Accordingly, there was an increase of 170 p.p.m. for the CO₂ partial pressure of the atmosphere for interglacial compared to glacial times. Applying the flux balance model mentioned above and keeping all other variables constant (e.g. T = 16 °C, ϕ = 0, δ¹³CIN = −10‰), this increase of the δ¹³C signals of the atmosphere would have caused a decrease of 0.05‰ in the δ¹³C signals of the gastropod shells for interglacial compared to glacial times. Comparing this order of magnitude to the maximal variability of the measured δ¹³C values of the gastropod shells of 8.41‰, we reason that the influence of atmospheric CO₂ would play a minor role compared to the influence of the ingested diet. However, we assume that possibly significant differences apply for metabolisms and lime storage behaviour of different taxa. In the study of Goodfriend and Hood (1983) cited above, they investigated several tropical Jamaican taxa (e.g. of Eutrochatta and Pleurodonte) even belonging to different clades. With a focus on Helix aspersa, Stott (2002) and Metref et al. (2003) investigated the same species under laboratory conditions, thus reducing the number of influencing factors. Based on the close relationship between Theba and Helix, both pertaining to the family Helicidae, we for now assume the δ¹³Cshell signal in Theba to be food-dominated.

Accordingly, we consider that negative peaks in median δ¹³Cshell values to be mainly caused by an increase in C₃ plants. In support of this, the δ¹³Cshell signals are negatively correlated to the Shannon biodiversity index (see ‘Results’). Gastropod biodiversity (Shannon index and species richness, respectively) is highest for minima in δ¹³Cshell median values, equally indicating moister conditions. The most negative signals of δ¹³Cshell median values (which imply moister conditions) can be allocated to palaeosurfaces. Additionally, we find an increase in C₃ plants in samples from tephric layers (samples E-3, E-5, E-14, E-15 and E-17). The more negative δ¹³Cshell signals of the tephric layers compared to the subjacent and superjacent substrate (see ‘Results’) indicate that also tephric input is related to a significant increase relative to the basic substrate of the lithological units. As volcanism usually occurs independently from climatic cycles, we consider that the volcanic ash had a significant effect on the distribution of C₃ vs. C₄ plants. The volcanic ash probably led to a refinement of the sediment, increasing its water retention capacity. Under the very arid climate conditions in the Eastern Canary Islands, dew plays a major role in the availability of water. In this context, a higher water storage capacity in finer substrates may have caused a higher edaphic humidity, significantly affecting biota. Hence, there is evidence of a substrate-induced increased edaphic humidity independent of changes in local climatic conditions. This fact also suggests that the higher humidity that relates to the silty palaeosurfaces may equally have been caused by edaphic humidity in a finer substrate, instead of a significantly wetter climate. This study shows the importance of differentiating between climatic and edaphic humidity to disentangle large-scale climate shifts from small-scale sedimentary effects.

Validation of the results with modern shell δ¹³C signals

Modern δ¹³Cshell signals of this study vary between −6.68 and −8.39‰. Yanes et al. (2008) investigated carbon isotope ratios of four modern shells of Theba geminata from Montaña Costilla close to the study area and obtained results from −6.0 to −9.4‰. All these modern δ¹³Cshell values are more negative than the fossil values of the Encantado profile and indicate a high proportion of C₃ plants in the current environment.

However, as modern gastropod shells were missing from the upper terrace of the study site, we took the modern gastropod shells from a microhabitat in the valley floor close by. Consequently, the measured modern δ¹³Cshell signals have to be treated with care and are possibly influenced by the different relief and soil water regime. We expect that the occurrence of C₃ plants in many places on the eastern Canary Islands (see Yanes et al., 2013) is equally biased by the relief and the degree of anthropogenic impact, as related substrate differences (e.g. erosion or the deposition of former silty surface sediments in depth lines) strongly influence the distinction of the plant cover (Rodríguez et al., 2005; Mora et al., 2012). Yanes et al. (2008) measured δ¹³Cshell signals of Theba geminata from two different localities at La Graciosa (north of Lanzarote). Values varied between −4.6 and 1.7‰. This scatter of values is comparatively high and with 6.3‰ almost as wide as the variation between all fossil samples of Encantado, which show a scatter of 8.41‰. This shows a strong difference between microhabitats under similar climatic conditions either due to different substrates (disclosed surface layer) or relief (see also Magaritz and Heller, 1983). Accordingly, we recommend comparing only shells of the same profile location to make environmental reconstructions across time.

The absence of gastropods at the upper terrace of our study site indicates a stressed ecosystem and unfavourable conditions, which is additionally supported by the sparse vegetation. However, the recent surface is not comparable to that of prehistoric times. Anthropogenic influence caused an enrichment of certain nutrients and severe erosion, which led to degradation of the surface and a significantly lower water retention capacity (see Rodríguez et al., 2005; Mora et al., 2012). As the surface of our recent stability phase in

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Influences on δ18O in shells of the genus Theba – a special model for the oceanic setting of Fuerteventura

Based on the high oceanity of our study site and the specific behaviour of Theba, we propose to simplify particular influences on the δ18Oshell signals based on the following assumptions. (i) We neglect the influence of evaporation. Goodfriend et al. (1989) showed that the δ18O signal in Theba body fluids is strongly related to that of the shell carbonate, while shell growth mainly takes place during the active phases of snails (Goodfriend et al., 1989). Furthermore, snails are usually active under relative humidity conditions above 85% (e.g. Thompson and Cheny, 1996; Balakrishnan and Yapp, 2004). Theba is active primarily at night (Yanes et al., 2008), absorbing mainly dew (Goodfriend et al., 1989). For the coastal areas of Fuerteventura, at night, the land–sea wind system flattens and moisture from the ocean reaches the island via (trade) winds. Due to nocturnal cooling, dew condenses under water-saturated conditions (dew point = 100% relative humidity). For these conditions, we suggest to neglect evaporation for the dew as well as transpiration by the snail (cf. Yanes et al., 2011). We neglect the influence of daytime activity phases due to rain events and associated effects of increased evaporation processes on the δ18Oshell signals due to the low annual rainfall amounts on Fuerteventura (127 mm for LaJares) and the relatively low amount of rainwater intake compared to dew (Goodfriend et al., 1989). (ii) We propose that δ18O values of environmental waters ingested by Theba in our setting correlate with δ18O of the marine surface seawater in proximity to the island. The study site is located at a distance of 4 km from the sea. Measurements on environmental waters on the Eastern Canary Islands have been carried out by Yanes et al. (2008), who measured meteoric water samples. According to these studies, the location of Tao on Lanzarote with a comparable distance to meteoric water samples. According to these studies, the location of Tao on Lanzarote with a comparable distance to the ocean showed values of −2.0 to −2.6‰. Modelled mean annual δ18O values of precipitation for Fuerteventura by Terzer et al. (2013) amount to −2 to −4‰. However, the mean annual δ18O signals of precipitation have not yet been measured for the study site, nor have the (mean annual) δ18O signals of dew in this oceanic setting. Measurements by Ostlund et al. (1987) from west of the Canary Islands show mean ocean surface δ18O signals of 1.08‰. We expect the shift between δ18O in precipitation and δ18O of sea surface water and their bias by rainout effect, altitude effect, etc., to be smaller than in settings that are further inland or hillier. As δ18O rain is also influenced, for example, by sub-cloud evaporation, there furthermore is a difference between δ18O rain signals and δ18O signals of non-rainfall environmental waters. Accordingly, Kaseke et al. (2017) found dew to be more depleted in 18O compared to rainwater. We make the assumption that mean annual δ18O signals of the surface seawater and mean annual δ18O signals of the environmental waters (consumed by Theba) at our study site are correlated. Applying the flux balance model by Balakrishnan and Yapp (2004), and setting humidity in this equation to 1.0 (100%), temperature to the average annual minimum temperature (16 °C) and theta to 0 (which applies for the steady state between the haemolymph and the imbibed environmental waters/dew) and taking the average δ18O signals of the modern gastropod shells of this study (−0.67‰) as a basis, we obtain mean δ18O, signals of the imbibed water of −1.52‰. Thus, we propose for our highly oceanic insular environment that the δ18Oprecipitation signal and accordingly δ18Oshell might be correlated with marine isotope signals. These, in turn, considered for the same location across time may have the potential to reflect the global ice coverage, indicating glacial–interglacial cycles.

δ18Oshell and sedimentation patterns – the shift between sea-level fluctuations and palaeosurfaces

Based on the previous section, we attempt a first approach in Fig. 8 to correlate δ18O signals of our terrestrial gastropods with marine isotopic signals in foraminifers of the photic zone. However, it should be kept in mind that a detailed correlation of δ18O in gastropod shells, likewise the type of sediment archive (aeolianite sequence) is not entirely suitable for producing continuous proxy curves. As a result of complex geomorphological processes, aeolianite sequences reveal sedimentation phases with varying sedimentation rates and interruptions of sedimentation due to surface stability. Moreover, sedimentation gaps may result from the post-sedimentary erosion of sediment layers. Finally, the temporal resolution is rather an approximation given the standard deviation of luminescence ages.

If, referring to Roettig et al. (2019), we assume that the succession of sandy layers and palaeosurfaces is related to marine sea-level fluctuations, δ18O signals in our gastropod shells should similarly reflect these glacial–interglacial cycles. However, the signals of stable oxygen isotopes in the gastropod shells do not correlate continuously with the succession of palaeosurfaces and sandy layers, respectively. Possible explanations for these deviations are: (i) despite the composition of the source signals of environmental waters ingested by the gastropods, other factors were (temporarily) more dominant; and (ii) the signals reflect marine isotope signals and thus glacial–interglacial cycles, but the succession of sand sheets and palaeosurfaces does not. Sedimentation patterns therefore may be influenced by multiple factors. For example, sand accumulation is highly dependent on the availability of sand, which, in turn, is controlled by sea-level fluctuations (as regressions cause the exposure of shelf areas), but also the distance between the deposition sites and the sand source (as during glacial times sea level drops markedly (e.g. Denton et al., 2010); the beach could have been too far away to serve as a sand source). By contrast, we assumed a more humid climate during colder phases, so the shelf area was possibly covered with vegetation that hindered sand transport and possibly also led to a dust-dominated layer on our site. Furthermore, prevailing wind directions and wind strength or the covering of potential sand sources by volcanoclastic deposits (see Roettig et al., 2019) heavily influence the deposition of dune sands. For example, the palaeosurface related to sample E-1.0 is not accompanied by a decrease of δ18Oshell. Consequently, it could be assumed that the interglacial deposits have not been preserved or that the respective deposits were not formed at the same time as a transgression took place.

As already mentioned, the temporal resolution of glacial and interglacial periods of the aeolianite sequences is fraught with many uncertainties. However, although we have to evaluate the results with caution, there is a trend for palaeosurfaces to directly relate to rapid decreases in the δ18Oshell signals of

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Figure 8. The Encantado section plotted with malacozonation and derived environmental conditions according to Richter et al. (2019) (left), biodiversity, and distribution of Hemicycla spp. indicating a distinct plant cover (modified from Richter et al., 2019), δ13C signals of the gastropod shells that indicate the drought stress level of consumed plants (green to orange scale) as well as δ18O signals of the gastropod shells which reflect the precipitation/dew signal that we have in our particular study location is assumed to be related to the marine signal (blue to red scale). Purple arrows on the left side mark changes of the biozones while orange arrows indicate marine transgressions as derived from δ18Oshell signals; both are assumed to correspond to glacial terminations (e.g. T I to T III described by Moreno et al., 2001). For comparison, red and blue curves show δ18O signals of planktonic foraminifera (red) generated by Hodell et al. (2013) and of a synthetic Greenland temperature curve (GLT_syn) from Barker et al. (2011) (blue) calculated from the deuterium record of the Antarctic EDC ice core for the last 400 ka. The black curves on the right show wind strength (Si/Al) proxies from marine cores of the Canary Basin (Roettig et al., 2001).

As mentioned above, we relate rapid decreases in δ18O of gastropod shells on Fuerteventura to marine transgressions that in most cases were followed by the formation of palaeosurfaces.

Marine transgressions: hot winds bring extinction—and subsequent stability induces new communities?

As mentioned above, we relate rapid decreases in δ18O of gastropod shells on Fuerteventura to marine transgressions that in most cases were followed by the formation of palaeosurfaces.
As a trend, these rapid decreases in the heavy $^{18}$O isotope are linked to significant changes in the malacoanufla and the formation of new malacozones (MZs). These changes become obvious, for example, between the stratigraphic positions of samples E-7 (MZ B) and E-8 (MZ C) marked by the disappearance of *Obelus pumilio* that prefers mild conditions and does not tolerate too hot summers (see Richter et al., 2019). The subsequent bioconcentration had been established in the following palaeoasurface with *Canariella plutoria*, *Ferussaciac fritschi*, *Hemicicula vilismata*, *Hemicicula sarcostoma*, etc. Another shift applies between samples E-10 (MZ C) and 11 (MZ D) with the eradication of most species such as *Cochlicella* sp. nov., *Cryptella auriculata* and *Hemicicula paeteliana*. As soon as a finer substrate is preserved, which has a higher water retention capacity (sample E-12), a new gastropod community establishes with *Pommatias* sp. *lanzarotensis* and re-establishment of *Cryptella auriculata*. There are further rapid decreases in $^{18}$O$_{shell}$ with a change of the malacozone between samples E-16 (MZ F) and E-17 (MZ D), and E-18 (MZ D) and E-19 (MZ E(b)). Sample E-19 again coincides with the dusty facies of a palaeoasurface and leads to re-establishment of a new gastropod community (Upper *Pommatias* fauna). There is lithofa evidence for the previous samples E-16 to E-18 that they were additionally disturbed by erosion caused by event-like surface runoff and strong volcanic influence, as indicated in thin sections, which show an increased proportion of volcanic glasses (see Roettig et al., 2019). This geomorphological instability might have led to the erosion of a potential palaeoasurface and also may explain the low gastropod biodiversity related to samples E-16 to E-18. The faunal change between samples E-23 (MZ E(b)) and E-24 (MZ H) is not related to significant changes in $^{18}$O$_{shell}$ signals or the formation of a palaeoasurface, respectively. Here, the faunal change could either have been caused by too intense volcanic activity, or the related strata may have been eroded. The stratigraphic resolution of this upper section is not sufficient to provide a solid interpretation.

However, we assume that the overall displacement of species was related to climatic and/or environmental changes in the study area, which are also reflected in the rapid decreases in $^{18}$O$_{shell}$ presumably linked to significant transgressions that introduced interglacial and interstadial periods, respectively. We propose that the most important climatic/environmental features causing abrupt faunal changes may have been linked to strong winds during these transitional phases, as found by Moreno et al. (2001) in marine cores of the Northern Canary Basin. They revealed that wind strength maxima and vast dust input occurred during precessional minima associated with higher seasonality and related to glacial–interglacial transitions. These would have caused hotter summers with hot and dry winds, which, in turn, may have led to the disappearance of more sensitive gastropod species. These hot and dry winds additionally brought vast amounts of dust. However, the accumulation of dust caused a considerable refinement of the substrate that finally resulted in a kind of opposite effect on hydrological conditions. As seen by tephric layers (samples E-2, E-5, E-15 and E-23) such substrate refinement had a positive effect on the local flora independent of direct climatic changes. A dominance of C3 plants in finer tephric layers indicates wetter conditions. Therefore, we assume that geomorphic stability during marine transgressions and an enhanced water storage capacity of the silty palaeoasurface favoured the establishment of new gastropod communities independent from changes in local climatic conditions. This is in line with the results of Richter et al. (2019), who found that palaeoasurfaces are related to higher gastropod abundances and increased availability of resources such as food, but are not necessarily linked to a change in the biozone. To substantiate this, more investigations on the influence of certain environmental factors are necessary. Moreover, a higher number of shell measurements on gastropod material would help to improve the representativeness, while further luminescence dating could help to obtain a more complete picture of this complex system at high resolution.

**Conclusions**

Multiple factors influence $^{18}$O signals in terrestrial gastropod shells. These factors are assumed to vary in their character and dominance across time. However, we assume that $^{18}$O signals in *Theba* shells of the investigated highly oceanic island Fuerteventura predominantly reflect shifts in marine sea surface $^{18}$O signals. Thus, they allow a chronological allocation of our deposits with respect to sea-level fluctuations caused by glacial–interglacial cycles. We assume that rapid decreases in $^{18}$O signals of the shells indicate significant transgressions related to increasing global temperatures that follow glacial maxima. These decreases in $^{18}$O in the shells simultaneously relate to palaeoasence borders with changing gastropod associations (Richter et al, 2019) that indicate stronger environmental changes. We assume that these faunal transitions were caused by strong hot winds together with higher seasonality that characterized the end of glacial phases. These atmospheric patterns were primarily forced by precession minima, as shown, for example, by Moreno et al. (2001). Rapid decreases in $^{18}$O$_{shell}$ were followed by geomorphologically stable phases that related to dust accumulation and preservation dominating formation of the palaeoasurface. Palaeoasurfaces in our deposits were coupled with an increased gastropod biodiversity and soil moisture, as indicated by a higher proportion of C3 plants derived from more negative $^{13}$C$_{shell}$ signals. We propose that the formation of palaeoasurfaces was not primarily an effect of changing local climatic conditions. Rather, the ecosystems on Fuerteventura seem to respond to changes in the substrate caused by input of either dust or tephric material. Our study demonstrates the importance of distinguishing between climatic and edaphic humidity to separate large-scale climate shifts from small-scale sedimentary effects. We therefore propose that stable isotope signals can be a valuable proxy for palaeoclimatic and palaeoecological reconstructions, especially at oceanic islands, and allow us to link them with glacial–interglacial and accordingly to stadial-interstadial shifts. Nevertheless, we recommend using stable isotope signals in gastropod shells in combination with analyses of the gastropod assemblages and a solid stratigraphic background.

**Supporting information**

Additional supporting information can be found in the online version of this article.

**Table S1.** $^{13}$C signals with mean values and related standard deviation for Encantado (E-1 to E-27) and modern snail shells (modern) collected at a comparatively moist valley floor close by.

**Table S2.** $^{18}$O signals with mean values and related standard deviation and medians for Encantado (E-1 to E-27) and modern snail shells (modern) collected at a comparatively moist valley floor close by.

**Figure S1.** a) Raman spectra of alpine calcite, as well as calcite and aragonite specimens from the RRUFF database, b) Raman spectra of the two modern *Theba* shells, c) Raman spectra of the four *Theba* shells of sample E3-8, d) Raman spectra of the four *Theba* shells of sample E3-1, e) XRD spectra of one shell from sample E3-8 and one shell from sample E3-1 plotted against reference spectrum of aragonite PDF 75-2230.
Acknowledgements. This work was funded by the German Research Foundation (DFG, FA 239/18-1). Furthermore, the work of the first author was financed through a Graduate research fellowship of the TU Dresden. We gratefully thank the reviewers for the extensive time invested and their very constructive advice, which significantly improved the manuscript. We would also like to thank Prof. Dr Yurena Yanes and Dr Klaus Groh for their help in the identification of Canary gastropod species as well as Prof. Dr Joachimske for stable isotope measurements. Furthermore, we thank Philipp Baumgart and Florian Schneider for their support during fieldwork. The authors have no conflicts of interest to declare.

Data availability statement
The authors confirm that the data supporting the findings of this study are available within the article and its Supporting Information.

Abbreviations. MZ, malacozone; XRD, X-ray diffraction.

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