Aminochronology and time averaging of Quaternary land snail assemblages from colluvial deposits in the Madeira Archipelago, Portugal

Evan New[a]*, Yurena Yanes[a], Robert A.D. Cameron[b], Joshua H. Miller[a], Dinarte Teixeira[c,d], Darrell S. Kaufman[e]

[a]Department of Geology, University of Cincinnati, Cincinnati, Ohio 45221, USA
[b]Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
[c]Institute of Forests and Nature Conservation, IP-RAM, Madeira Government, Madeira 9000-715, Portugal
[d]LIBRe—Laboratory for Integrative Biodiversity Research, Finnish Museum of Natural History, University of Helsinki 00014, Finland
[e]School of Earth and Sustainability, Northern Arizona University, Flagstaff, Arizona 86001, USA
*Corresponding author at: Department of Geology, 500 Geology Physics Building, 345 Clifton Court, University of Cincinnati, Cincinnati, OH 45221, USA.
E-mail address: newen@mail.uc.edu (E. New).

Abstract

Understanding the properties of time averaging (age mixing) in a stratigraphic layer is essential for properly interpreting the paleofauna preserved in the geologic record. This work assesses the age and quantifies the scale and structure of time averaging of land snail-rich colluvial sediments from the Madeira Archipelago (Portugal) by dating individual shells using amino acid racemization calibrated with graphite-target and carbonate-target accelerator mass spectrometry radiocarbon methods. Gastropod shells of *Actinella nitidiuscula* were collected from seven sites on the volcanic islands of Bugio and Deserta Grande (Desertas Islands), where snail shells are abundant and well preserved in Quaternary colluvial deposits. Results show that the shells ranged in age from modern to ~48 cal ka BP (calibrated radiocarbon age), covering the last glacial and present interglacial periods. Snail shells retrieved from two of the colluvial sites exhibit multimillennial age mixing (>6 ka), which significantly exceeds the analytical error from dating methods and calibration. The observed multimillennial mixing of these assemblages should be taking into consideration in upcoming paleoenvironmental and paleoecological studies in the region. The extent of age mixing may also inform about the time span of colluvial deposition, which can be useful in future geomorphological studies. In addition, this study presents the first carbonate-target radiocarbon results for land snail shells and suggests that this novel, rapid, and more affordable dating method offers reliable age estimates for small land snail shells younger than ~20 cal ka BP.

Keywords: Age mixing; Amino acid racemization; Carbonate-target ^{14}C dating; Land snails; Quaternary; Desertas Islands

INTRODUCTION

Time averaging, the age mixing of noncontemporaneous fossils, is an inherent quality of most geologic strata and important for understanding sedimentary and taphonomic processes (Kowalewski, 1996). When unknown, time averaging may complicate the interpretation of geologic horizons, because accumulations of fossils from different time intervals can be mixed in a single stratum, giving the erroneous appearance of contemporaneity (Kidwell and Bosence, 1991). Age mixing can also generate false patterns of fossil distribution through time. For example, an assemblage that spans a broad period of time can give the mistaken appearance of comparative contemporaneity between taxa. Quantifying time averaging is, therefore, an essential step before interpreting sedimentological, paleoecological, and/or paleoclimatic patterns from geologic deposits (Kowalewski, 1996; Kowalewski et al., 1998; Bush et al., 2002).

The degree of age mixing is primarily dependent on factors like fossil production (genesis) rates, destructive (decay) rates, and sedimentation (burial) rates (e.g., Tomašových et al., 2014). As a result, the time resolution across depositional settings and fossil assemblages can be substantially variable, ranging from short (years to decades) to long (millennial

to multimillenial) time scales (e.g., Tomašových et al., 2014; Albano et al., 2016, 2018). More importantly, not all taxonomic groups preserved jointly within a deposit will necessarily exhibit equivalent degrees of age mixing. For instance, specimens with durable hard parts (e.g., mollusks) may exhibit significant (multimillennial) time averaging, while less durable skeletons (e.g., echinoderms) are usually accumulated across more limited time spans (years to decades) due to higher taphonomic decay rates (Kowalewski et al., 2018). Similarly, the remains of short-lived organisms (such as those with a subdecadal life span) are more likely to be significantly time averaged than long-lived organisms due to the shorter life span (higher genesis rates). When fossils of short-lived organisms are examined, the likelihood of significant age mixing within a deposit increases (Kidwell and Bosence, 1991; Goodwin et al., 2004). Consequently, understanding the extent of time averaging can notably improve paleoecological and paleoenvironmental reconstructions from fossil assemblages.

Time averaging can be defined by scale, that is, the range of years across which age mixing has occurred; and by structure, that is, the distribution of specimen frequency through the observed age range of a fossil assemblage (Meldahl et al., 1997; Kowalewski et al., 1998). The standard method to evaluate the scale and structure of time averaging is by directly dating individual fossils within a geologic stratum and then using the ages of fossils to infer the extent and shape of age mixing (e.g., Flessa et al., 1993; Kowalewski and Bambach, 2008). Much of our knowledge of scale and structure of time averaging of fossils is based on Holocene (last 11.7 ka) remains of marine bivalves (e.g., Kidwell, 1998; Kidwell et al., 2005; Dominguez et al., 2016; Vidović et al., 2016; Schnedl et al., 2018), brachiopods (Carroll et al., 2003; Krause et al., 2010), and more recently echinoderms (Kosnik et al., 2017; Kowalewski et al., 2018). Estimates of time averaging in continental fossil assemblages have received less focus. Some published studies of time averaging in terrestrial fossils from both the Holocene and the mid–late Pleistocene include small mammal assemblages (Terry and Novak, 2015) and land snails (Yanes et al., 2007).

Land snail shells are abundant, easily identifiable, sensitive to climate change, and well preserved in many Quaternary continental settings. Accordingly, fossil shells have been increasingly used as paleoecological and paleoclimatic proxies (e.g., Goodfriend et al., 1996; Yanes et al., 2019). However, to prevent false or biased biological and paleoclimatic inferences from land snail assemblages, it is important to establish a robust chronological context and assess the degree of age mixing (Yanes et al., 2007).

A well-established and widely used method for dating Quaternary shells is amino acid racemization (AAR) calibrated with radiocarbon dating (e.g., Miller and Brigham-Grette, 1989; Goodfriend, 1992; Kowalewski et al., 1998; Kidwell et al., 2005; Yanes et al., 2007; Kosnik et al., 2008). Amino acid dating is based on the principle that all amino acids (except glycine) have two mirrored orientations of chirality (D and L). While alive, virtually all living organisms,

including snails, produce amino acids in the L orientation. Upon death, the D/L ratio increases from 0 toward equilibrium at 1.0 during the process of racemization, or epimerization for isoleucine/allo-isoleucine (e.g., Hare et al., 1980; Wehmiller and Miller, 2000). Different amino acids racemize/epimerize at different rates (e.g., Goodfriend, 1991; Goodfriend and Meyer, 1991). Because the rate of racemization/epimerization is dependent on both taxon and temperature, it is necessary to calibrate the method for the locality and taxon to be investigated by using an independent dating method, such as radiocarbon dating, which uses radiocarbon present in samples to determine a numerical age that can be then calibrated to calendar years. The relatively new carbonate-target accelerator mass spectrometry (AMS) radiocarbon dating method described by Bush et al. (2013) is rapid and cost-effective and has been increasingly used for dating Holocene marine carbonate-bearing fossils and calibration of AAR ages (e.g., Dominguez et al., 2016; Kosnik et al., 2017; Kowalewski et al., 2018).

For this study, we investigated previously undescribed snail-rich colluvial deposits from the Desertas Islands (Madeira, Portugal). This locality offers a wealth of paleobiological and paleoenvironmental information to assess regional climate and biotic evolution throughout its well-documented geological history (e.g., Cook et al., 1990) and diverse land snails throughout the fossil record spanning the past 150 ka (e.g., Cameron and Cook, 1992; Cook, 2008). The native land snail fauna of the archipelago, studied intensively since the early nineteenth century, is species rich (more than 250 species described) and mainly endemic (Waldén, 1983; Cook et al., 1990; Cameron and Cook, 1999; Abreu and Teixeira, 2008). As a result, these land snails have been the subject of multiple taxonomic, ecological, and morphological studies. However, the majority of land snail studies examine the Madeira Archipelago as a whole (e.g., Waldén, 1983; Cameron and Cook, 1989; Cook, 1996, 2008) or the human-populated islands of Madeira (Cook et al., 1990; Prada and Serralheiro, 2000) and Porto Santo (Cameron et al., 2006). Land snail studies focusing on the Desertas Islands are rare, and the records of fossil land snail shells have been largely overlooked (e.g., Wollaston, 1878; Cameron and Cook, 1999).

This study focuses on determining the age of fossil shells and quantifying the scale and structure of age mixing of snail assemblages using AAR calibrated with both graphite-target and carbonate-target AMS radiocarbon methods. We test the hypothesis that snail assemblages preserved in Quaternary colluvial deposits exhibit multimillennial-scale age mixing (beyond the radiocarbon dating and AAR calibration errors) and that the structure will be variable (e.g., right-skewed, left-skewed), as observed in late Pleistocene paleosols and dunes rich in land snails from the Canary Islands (Yanes et al., 2007). This research also tests the viability of the carbonate-target AMS radiocarbon dating for land snail shells and establishes the first chronology for these assemblages using multiple geochronological methods (i.e., AAR, graphite-target and carbonate-target AMS

radiocarbon). Our results provide new age data from Quaternary terrestrial invertebrate assemblages that will complement and expand upon the intensive work conducted in Holocene marine assemblages over the last few decades.

STUDY AREA, MATERIALS, AND METHODS

Geographical and environmental setting

The Madeira Archipelago (32°39′4″N, 16°54′35″W) is located in the Atlantic Ocean 400 km north of the Canary Islands and 900 km southwest of Portugal (Fig. 1). The islands were formed by volcanic activity in a series of phases between 14.3 and 3.2 Ma (Geldmacher et al., 2000) and are divided into three island groups: Madeira, Porto Santo, and the Desertas Islands. While the climate of the Madeira archipelago is temperate across all the islands, the eastern islands (Fig. 1) from which samples were collected (Deserta Grande and Bugio) are semiarid.

Air temperatures are mild year-round with a mean of 21°C in Funchal, Madeira, ranging from 16°C in January to 23°C in August. This tempered seasonality due to the oceanic influence is ideal for AAR studies, as racemization/epimerization rate is sensitive to changes in ambient temperature. Aridity is largely dependent on topography, with lower coastal areas being generally drier than those inland with greater elevation (Santos et al., 2004). Evidence from dune deposits and plant remains indicates that the climate of Madeira has fluctuated over the last 150 ka, with evidence of increased aridity toward the present (Cameron and Cook, 1992). Parts of Madeira and the Desertas Islands show evidence of significantly increased aridity in the drier island environments due to fluctuations in climate and recent human impact via land clearance, fire, and grazing (Cameron and Cook, 1992).

The geology of the Desertas Islands is nearly entirely volcanic (basaltic) without presence of other rock types. Only small patches of colluvial silty-clay sediments with minor content of biogenic eolian carbonates (Goodfriend et al., 1996) can be found scattered around these two islands. Due to the lack of extensive carbonate-rich sediments and limestone throughout the Desertas Islands, the potential incorporation of dead carbon into snail shells (Pigati et al., 2004, 2010; Quarta et al., 2007; Hill et al., 2017) is likely limited in the study area.

Materials

Land snail shells were collected between 2012 and 2016 from seven different locations across two of the Desertas Islands: Bugio and Deserta Grande (Fig. 1). Whole snail shells were collected from deposits of colluvium (unconsolidated reworked sediment; Fig. 2). These deposits are all located on or at the base of exposures into erosive colluvial slopes and of varying texture, though predominantly loose unsorted sand and gravel. The colluvial sediments throughout The Desertas Islands are brown-reddish silty-clay sediments with some volcanic sand and lapilli (Fig. 2E and F), showing

moderate weathering (Goodfriend et al., 1996). To avoid racemization rate alterations due to daily and seasonal temperature fluctuations in surficial exposure, shells were collected from actively eroding slopes of unconsolidated sediments, buried under rocks or excavated by digging into looser sediments around them. Shells are likely to have reached the near surface only recently, as erosion carries surface material downslope. This should minimize the effects of seasonal temperature fluctuations on AAR rates. Each sample was collected from a single stratum of colluvium (Fig. 2).

We used only specimens of the abundant nominal species *Actinella nitidiuscula* (G.B. Sowerby I, 1824) (Gastropoda: Hygromiidae). While the nominate subspecies, *A. nitidiuscula nitidiuscula* (Fig. 3A) was found both alive and fossilized, the form *A. nitidiuscula saxipotens* (Wollaston, 1878) (Fig. 3B), listed at subspecific rank, was found only as fossils. Evidence of coexistence in deposits indicates that these two forms should be regarded as distinct but closely related species, and they are, informally, treated so here. *A. nitidiuscula* (sensu lato) is ideal for geochronologic and paleoclimatic studies, as it is endemic to the Madeiran Archipelago, abundant, and ubiquitous throughout the Holocene and late Pleistocene (Cook et al., 1990). Moreover, *A. nitidiuscula* is a small and thin species (shell width ≤12 mm), which is preferable, considering that small snails appear to require less calcium input and are therefore less likely to display contamination from recycled carbonate (Ellis et al., 1996; Pigati et al., 2004, 2010) as has been sometimes observed in larger land snail species living in carbonate-rich areas (e.g., Yanes et al., 2007; Hill et al., 2017). This inferred relationship between land snail shell size and recycling of carbonate is still being examined but was taken into consideration when selecting *Actinella* over larger and similarly abundant land snail species in this locality. For this study, carbonate uptake by snails is of limited concern, because the bedrock geology of Deserta Grande and Bugio Islands is nearly entirely basaltic. Only some small areas of colluvial sediments include some biogenic eolian carbonates. Thus, overall, Desertas snails have limited carbonate accessibility.

AAR dating

To test for the most informative amino acid in *Actinella nitidiuscula* shells from the Desertas Islands, we investigated racemization rates for seven amino acids: aspartic acid, glutamic acid, serine, alanine, valine, isoleucine, and leucine (Table 1). The extent of AAR was measured using reverse-phase liquid chromatography following Kaufman and Manley (1998). All sample preparation and analyses were performed in the Amino Acid Geochronology Laboratory at Northern Arizona University. Specimens were cleaned and prepared for analysis using methods described in Hearty and Kaufman (2009). A small fragment of each shell was used for AAR analysis ($n = 46$), and other fragments of the same shells were separated for subsequent graphite-target ($n = 6$) and carbonate-target ($n = 20$) radiocarbon dating.
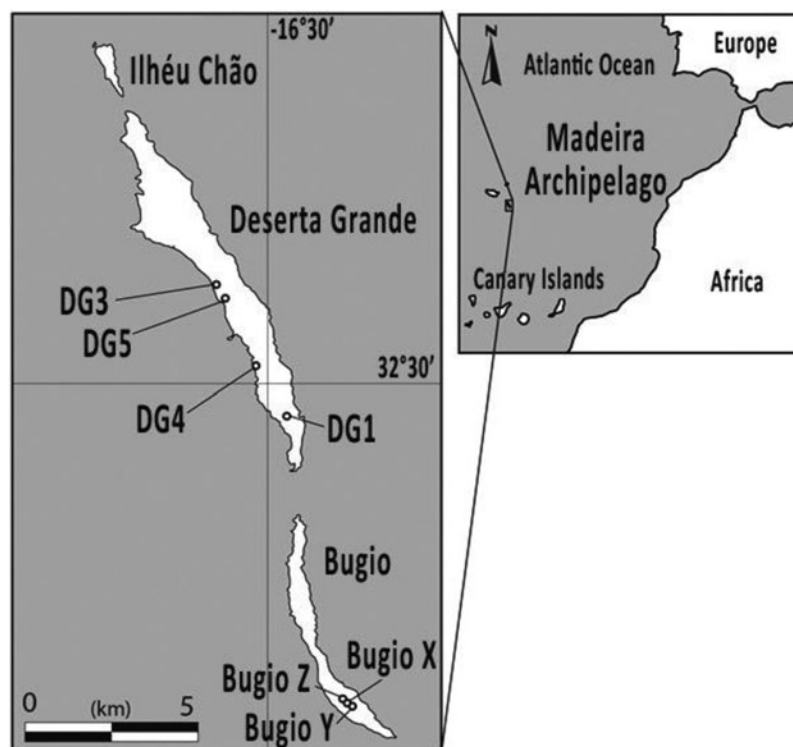
Figure 1. Location of the Desertas Islands chain, Madeira Archipelago. Circles depict colluvial sites from Deserta Grande and Bugio Islands dated in this study.

Shell fragments were cleaned and weighed before being dissolved in microreaction vessels and hydrolyzed for 6 h at 110°C before being dried in a vacuum desiccator and rehydrated using an adjusted distilled and deionized water solution. Samples were then injected onto a high-performance liquid chromatograph unit for analysis. The method uses precolumn derivatization of samples with *o*-phthaldialdehyde and chiral thiol, *N*-isobutyryl-ʟ-cysteine, to yield fluorescent diastereomeric derivatives of chiral primary amino acids (Kaufman and Manley, 1998). The racemization rate of glutamic acid (Glu) had the best fit (highest R^2 value from an ordinary least-squares linear model) when calibrated with radiocarbon dates and was chosen for all subsequent analyses.

Radiocarbon dating

To radiocarbon date snail shells, we used both the novel carbonate-target AMS (Bush et al., 2013) and the standard graphite-target AMS. Carbonate-target AMS was developed for carbonate samples to provide a lower-cost, lower-precision alternative to standard graphite-target AMS radiocarbon dating (Bush et al., 2013). Samples are prepared differently for the two techniques. For carbonate-target AMS, specimen-derived, finely powdered $CaCO_3$ is mixed with unbaked Sigma-Aldrich 400 mesh and 99.9% pure Fe, which is then poured into an aluminum cathode pressed for AMS measurement (see Bush et al. [2013] for additional details). In contrast, graphite-target AMS dating required filamentous graphite to be produced

from carbonate samples. While carbonate-target reduces preparation time and lowers analytical costs, there is evidence that the method has difficulties dating specimens older than 10 ka. Carbonate samples that Bush et al. (2013) dated to 10–12 ^{14}C ka BP showed ± 0.8–6.1% deviation, while those dated at 29–40 ^{14}C ka BP showed ± 27–108% deviation. As a result, subsequent studies using carbonate-target radiocarbon dating have limited analysis predominantly to Holocene samples (e.g., Hines et al., 2015; Grothe et al., 2016; Ritter et al., 2017; Kowalewski et al., 2018). We also note that previous work was focused on marine invertebrates only. Here, we expand tests of carbonate-target radiocarbon dating to terrestrial land snails, which can be powerful paleoclimate proxies for Quaternary terrestrial and atmospheric systems (see review in Yanes et al., 2019).

A total of 20 *Actinella nitidiuscula* land snail specimens retrieved from seven colluvial deposits across Deserta Grande and Bugio Islands (Fig. 1) were analyzed by both AAR analysis and carbonate-target AMS radiocarbon dating, including two recently dead specimens analyzed to examine any potential dead carbon anomaly. Of these, four Pleistocene shells and two Holocene shells (six total) were also selected for graphite-target radiocarbon dating to assess the accuracy of the carbonate-target radiocarbon method. All radiocarbon analyses were performed at the Keck-Carbon Cycle AMS Facility at the University of California, Irvine. All samples were pretreated via cleaning and dilute HCl treatment to remove potential environmental contaminants. Calibration of radiocarbon years to calendar years was performed
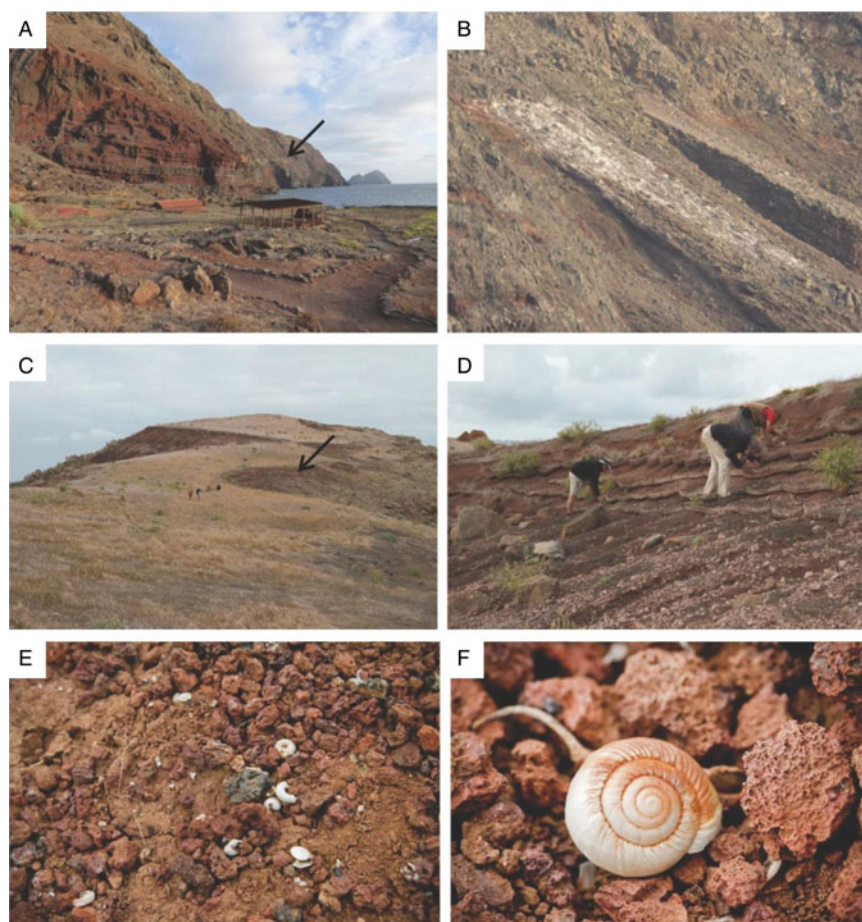
Figure 2. Field photographs of Quaternary colluvial deposits from the Desertas Islands of the Madeira Archipelago, Portugal. (A) General view of the abrupt volcanic landscape of Deserta Grande Island. Black arrow denotes colluvial sediments from site DG4. (B) Close-up view of the DG4 site in Deserta Grande Island. Shell samples were retrieved from unconsolidated brown-reddish silt-clay sediments on the side base of the slope. (C) Escarpments formed into the flat-topped hill from Bugio Island. Black arrows indicate site Bugio Y. (D) General view of colluvial brown-reddish silt-clay sediments at Bugio Y site. (E) Close-up view of loose colluvial sediment with volcanic lapilli-sand and fossil (white) land snail shells at Bugio X site. (F) Detailed view of Quaternary *Actinella nitidiuscula* shell preserved in colluvial unconsolidated sediments at Bugio X site (shell diameter = ~10 mm).

for all samples using the Calib Radiocarbon Calibration (v. 7.1) (Stuiver and Reimer, 1993). Radiocarbon dates were calibrated using the IntCal13 Northern Hemisphere calibration curve (Reimer et al., 2013). All ages are presented in calendar (cal) years or thousands of years (ka) before present (assumed AD 1950).

AAR calibration

A total of 17 shells from seven colluvial sites were used to generate a calibration curve for estimating calendar year ages from amino acid D/L ratios. These included 13 carbonate-target-dated shells and 4 graphite-target-dated shells. All these shells also underwent AAR. For Holocene shells, the carbonate- and graphite-based ages overlap, and we chose not to pursue additional correction or manipulation of the ages. The amino acid calibration was limited to shells with graphite-target radiocarbon ages younger than ~22 ^{14}C ka BP due to increasing offset between graphite- and

carbonate-target ages beyond that limit. Our resulting calibration was then used to estimate ages of 26 additional shells from two selected colluvial deposits from Deserta Grande Island (DG3 and DG4; Fig. 1), which were only analyzed using AAR.

We used nonlinear least squares to calculate the AAR–radiocarbon calibration. To obtain a 95% confidence estimate for the mean prediction of the calibration that incorporates our sampling of shell dates, we bootstrapped the calibration calculation 10,000 times by randomly resampling with replacement. After estimating ages of unknown shells in the two deposits on Deserta Grande Island (DG3 and DG4), the time averaging of the deposits was assessed using age-frequency distributions. Here, age refers to time of burial rather than ontogenetic age at death. These distributions depict an assemblages' representation of species abundance through time and offer opportunities to consider changes in preservation and sorting mechanisms. Standard moments of these distributions (skewness and kurtosis, measuring the

Figure 3. (color online) Photographs of the two land snail subspecies selected for amino acid racemization and ^{14}C accelerator mass spectrometry dating. (A) Modern individual of the extant *Actinella nitidiuscula nitidiuscula*. (B) Fossil individual of the extinct *Actinella nitidiuscula saxipotens*.

symmetry and "tailedness" of distributions, respectively) are used to describe the shape of recovered age distributions. To calculate uncertainty in skewness and kurtosis, we used a bootstrap algorithm (repeated 10,000 times) that incorporated the calculated confidence estimate of the overall calibration. For each AAR-dated shell, we iteratively sampled dates from a uniform distribution bounded by the calibration confidence interval at that age estimate. We then iteratively calculated kurtosis and skewness for each deposit. Finally, we calculated the resulting 95% confidence interval of these statistical moments for each deposit. A confidence interval of skewness that is entirely positive (>0.0) or negative (<0.0), provides evidence that the time averaging of a deposit is significantly skewed. A confidence interval for kurtosis that

Table 1. D/L amino acid ratios of 20 land snail shells from Deserta Grande and Bugio. The same individual shells were also dated by [14]C (Table 1), and all but three were used to calibrate the rate of amino acid racemization. Asterisks (*) denote modern (recently dead) shells.[a]

Lab ID (UAL)	Shell ID	Snail ssp.	D/L Asp	D/L Glu	D/L Ser	D/L Ala	D/L Val	D/L Ile	D/L Leu
15653	Bugio X-1	*saxipotens*	0.448	0.260	0.720	0.583	0.181	0.228	0.371
15654	Bugio X-2	*saxipotens*	0.443	0.237	0.675	0.551	0.140	0.218	0.348
15810	Bugio X-3	*saxipotens*	0.431	0.236	0.661	0.479	0.162	0.174	0.263
15811	Bugio X-4	*saxipotens*	0.445	0.237	0.693	0.471	0.149	0.154	0.254
15814	Bugio Y-1*	*nitidiuscula*	0.055	0.031	0.022	0.029	0.017	0.028	0.020
15644	Bugio Y-2*	*nitidiuscula*	0.058	0.025	0.023	0.048	0.013	0.018	0.032
15647	Bugio Z-1	*saxipotens*	0.441	0.188	0.802	0.503	0.130	0.145	0.297
15648	Bugio Z-2	*saxipotens*	0.404	0.184	0.735	0.533	0.129	0.140	0.290
15812	Bugio Z-3	*saxipotens*	0.446	0.169	0.786	0.367	0.118	0.135	0.217
15813	Bugio Z-4	*saxipotens*	0.418	0.355	0.105	0.578	0.179	0.189	0.290
15651	DG1-1	*nitidiuscula*	0.508	0.251	0.843	0.596	0.132	0.245	0.404
15652	DG1-2	*nitidiuscula*	0.484	0.231	0.559	0.580	0.103	0.185	0.353
15806	DG1-3	*nitidiuscula*	0.551	0.298	0.545	0.565	0.188	0.204	0.377
15807	DG1-4	*nitidiuscula*	0.538	0.292	0.496	0.571	0.182	0.189	0.367
15645	DG3-1	*saxipotens*	0.395	0.178	0.727	0.471	0.094	0.133	0.263
15646	DG3-2	*saxipotens*	0.414	0.193	0.678	0.454	0.087	0.124	0.258
15649	DG4-1	*saxipotens*	0.504	0.217	0.769	0.568	0.139	0.199	0.362
15882	DG4-2	*saxipotens*	0.433	0.186	0.747	0.504	0.108	0.137	0.294
15808	DG5-1	*nitidiuscula*	0.563	0.336	0.648	0.688	0.231	0.257	0.433
15809	DG5-2	*nitidiuscula*	0.542	0.308	0.505	0.594	0.256	0.257	0.440

[a]Abbreviations: Lab ID, UAL # (carbonate-target); Snail ssp., *Actinella nitidiuscula* subspecies; D/L Asp, aspartic acid; D/L Glu, glutamic acid; D/L Ser, serine; D/L Ala, alanine; D/L Val, valine; D/L Ile, isoleucine; D/L Leu, leucine.

is entirely less than 3.0 (the kurtosis value for a normal distribution) indicates that the time averaging of the deposit has very broad tails (i.e., weakly peaked or not peaked at all). Distributions with very thin tails (more strongly peaked) would have confidence intervals that are entirely greater than 3.0. Based on depositional setting, there is some expectation that colluvial deposits could produce time-averaged assemblages that are approximately uniformly distributed with respect to age (low-peaked) or more normally distributed; but it is unlikely that they would produce highly peaked age distributions. All calculations were written in R v. 3.4.1 (R Core Team, 2017).

Artificial time averaging from dating uncertainties

To fully quantify time averaging, the degree of age mixing of individual shells needs to be evaluated relative to the expected age variation brought about by uncertainties related to the dating methods. Evaluation of the quality of radiocarbon/AAR calibration can determine the extent and significance of artificial time averaging in tested samples (e.g., Kowalewski et al., 1998; Yanes et al., 2007; Dominguez et al., 2016; Kosnik et al., 2017). Multiple sources of uncertainty contribute to error in age estimates, including: regression uncertainties, analytical error, conversion of ^{14}C ages to calendar ages, reservoir age estimate, and effects of different postdepositional temperature history on the rate of AAR. We estimate an age uncertainly of around 1000 years.

RESULTS

Graphite- and carbonate-target radiocarbon results

The 20 carbonate-target radiocarbon-dated land snail shells from the Desertas Islands ranged in age from modern (~0.1 cal ka BP) to ~48 cal ka BP (calibrated radiocarbon age) (Table 1). These results reveal that snail-rich colluvial deposits in these islands include the transition from the last glacial maximum to the early Holocene (interglacial) interval. Comparisons between graphite- and carbonate-target radiocarbon-dated shells show a significant overlap for Holocene shells, with an offset of 20 to 80 years only (Fig. 4; Table 3). Early Pleistocene shells show a slightly larger offset but still within the analytical error (0.4 to 1.4 ka), and finally, Pleistocene shells older than 22 cal ka BP showed a significant age offset between 6.3 and 15.6 ka (Fig. 4; Table 3).

Although the survival time of land snail shells on the ground surface or "taphonomic active zone" in The Desertas Islands is unclear, considering the semiarid conditions of these islands, it is hypothesized that the snails possibly died within the last several decades or last century. Two modern (recently dead) fresh-looking shells collected from the soil surface exhibit apparent ^{14}C ages of one to three centuries (Table 2). As expected, recently dead snail shells showed D/L AAR ratios close to zero (Table 2).
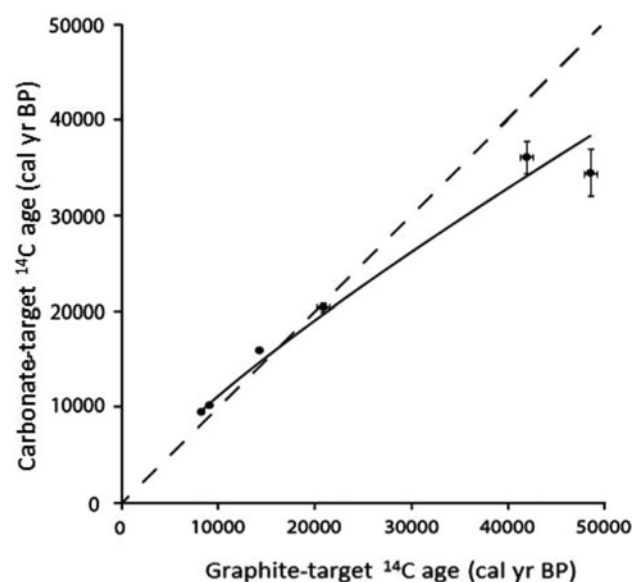

Figure 4. Relationship between carbonate-target to graphite-target accelerator mass spectrometry radiocarbon results (median calibrated ages) of four Pleistocene and two early Holocene *Actinella nitidiuscula* shells ($R^2 = 0.985$). Dashed line depicts 1:1 line. Error bars represent 2-sigma calibrated age range. Data are listed in Table 3.

Radiocarbon calibration of AAR values

After the effectiveness and limits of carbonate-target radiocarbon dating had been established (Fig. 4), a calibration curve was created using calibrated ^{14}C ages and AAR D/L ratios. For four samples older than 10 cal ka BP, graphite-target dates derived from the same shells were used rather than carbonate-target dates, due to greater reliability. The D/L ratios of glutamic acid (Glu) showed the highest correlation with calendar year calibrated ^{14}C ages (Fig. 5). Therefore, the Glu D/L ratios were selected for age estimation of Madeira Islands shells. Calibrated AAR age is represented by the following equation, where age is in years BP (Fig. 5):

$$AGE = 622{,}247 \; \text{D/L Glu}^{(2.404)} \qquad (1)$$

The strong correlation between D/L Glu and ^{14}C ages (Fig. 5) suggests that the influence of possible different temperature histories on the rate of AAR is limited.

Quantifying age mixing of snail-rich colluvial deposits

Two snail-rich colluvial deposits from Deserta Grande were selected to assess the scale and structure of time averaging in buried land snail assemblages, site DG3 and DG4 (Table 4). These two colluvial deposits were selected for their great abundance of pristine *Actinella* shells and other species of land snails that were accessible and easy to sample. The sites lacked clear soil structures or discernible

Table 2. Radiocarbon and calibrated ages of 20 *Actinella* land snail shells from Deserta Grande and Bugio analyzed via carbonate-target and graphite-target accelerator mass spectrometry radiocarbon dating. Asterisks (*) denote modern (recently dead) shells. Double asterisks (**) depict oldest shells (excluded from the calibration).[a]

Lab ID	Shell ID	Snail ssp.	^{14}C method	^{14}C age (yr BP)	SD (yr)	2-sigma cal yr BP	Median age (cal yr BP)
15653	Bugio X-1	*saxipotens*	Carbonate	16,060	480	18,346–20,544	19,410
15654	Bugio X-2	*saxipotens*	Carbonate	17,710	600	19,940–22,785	21,390
15810	Bugio X-3	*saxipotens*	Carbonate	17,080	540	19,288–21,964	20,640
194124	Bugio X-4	*saxipotens*	Graphite	17,800	60	21,342–21,810	21,570
15814	Bugio Y-1*	*nitidiuscula*	Carbonate	170	40	0–295	170
15644	Bugio Y-2*	*nitidiuscula*	Carbonate	365	40	315–502	420
15647	Bugio Z-1	*saxipotens*	Carbonate	8440	150	9015–9744	9410
15648	Bugio Z-2	*saxipotens*	Carbonate	8260	210	8597–9610	9200
15812	Bugio Z-3	*saxipotens*	Carbonate	8150	160	8641–9464	9090
194125	Bugio Z-4	*saxipotens*	Graphite	45,200	1400	46,054–50,000	48,610
15651	DG1-1	*nitidiuscula*	Carbonate	15,400	420	17,689–19,613	18,650
15652	DG1-2	*nitidiuscula*	Carbonate	15,970	460	18,296–20,409	19,310
15806	DG1-3**	*nitidiuscula*	Carbonate	31,400	3400	28,981–42,117	35,610
194120	DG1-4	*nitidiuscula*	Graphite	37,790	560	41,259–42,851	42,100
15645	DG3-1	*saxipotens*	Carbonate	8720	160	9477–10,195	9790
15646	DG3-2	*saxipotens*	Carbonate	8480	160	9031–9891	9470
194123	DG4-1	*saxipotens*	Graphite	12,555	35	14,644–15,127	14,870
15882	DG4-2	*saxipotens*	Carbonate	9860	190	10,726–12,001	11,350
15808	DG5-1**	*nitidiuscula*	Carbonate	31,000	3200	28,985–41,596	34,870
15809	DG5-2**	*nitidiuscula*	Carbonate	28,600	2400	27,856–37,754	32,680

[a]Abbreviations: Lab ID, UCI # (graphite-target) or UAL # (carbonate-target); Snail spp., *Actinella nitidiuscula* subspecies; ^{14}C age (yr BP); uncalibrated radiocarbon age.

Table 3. Comparison of calibrated radiocarbon age derived from graphite-target and carbonate-target accelerator mass spectrometry radiocarbon dating of *Actinella nitidiuscula* snail shells from the Desertas Islands.[a]

Shell ID	Location	Lab ID (UCI)	Graphite-target ^{14}C age (cal yr BP)	SD (yr)	Lab ID (UCI)	Carbonate-target ^{14}C age (cal yr BP)	SD (yr)	Offset (yr)
Bugio Z-2	Bugio	203580	9199	20	15648	9201	210	2
DG3-1	Deserta Grande	203579	9822	20	15645	9786	160	36
DG4-1	Deserta Grande	194123	14,873	35	15649	15,492	340	619
Bugio X-4	Bugio	194124	21,567	60	15811	19,802	490	1765
DG1-4	Deserta Grande	194120	42,102	560	15807	35,370	3400	6732
Bugio Z-4	Bugio	194125	48,612	1400	15813	33,781	2700	14,831

[a]Abbreviations: Lab ID, UCI # (graphite-target); SD, standard deviation; Offset, difference between graphite-target and carbonate-target calibrated ages.

stratigraphy. Shells were drawn from actively eroding slopes of unconsolidated silt-clay sediments at the base of unstable colluvial slopes.

From site DG3, 15 analyzed shells ranged in age between ~3.5 and ~13.6 cal ka BP, with a median age of 10.8 cal ka BP. The frequency distribution is left-skewed (skewness 95% CI: −1.5, −0.4), that is, older specimens occur more frequently in the assemblage than younger specimens. Kurtosis estimates are wide, but bracket 3.0 (kurtosis 95% CI: 2.5, 5.4). Fourteen of the 15 dated shells ranged from ~7.4 to ~13.6 cal ka BP and appear normally distributed within this range. The remaining shell represents a substantially younger shell of ~3.5 cal ka BP (Fig. 6A).

From site DG4, the ages of 11 analyzed shells ranged from ~7.3 to ~13.5 cal ka BP, with median shell age of 10.6 cal ka

BP. The frequency distribution is largely symmetric, with no clear relationship in the assemblage between age and frequency when examined at a 1 ka time resolution (skewness 95% CI: −0.6, 0.6; kurtosis 95% CI: 1.4, 2.8) (Fig. 6B).

DISCUSSION

Scale of time averaging in Quaternary colluvial deposits

The age ranges of dated shells within the two analyzed deposits in Deserta Grande Island point to variation in age (>6 ka) exceeding the error expected by various sources of uncertainties. Accordingly, the results support our hypothesis of real
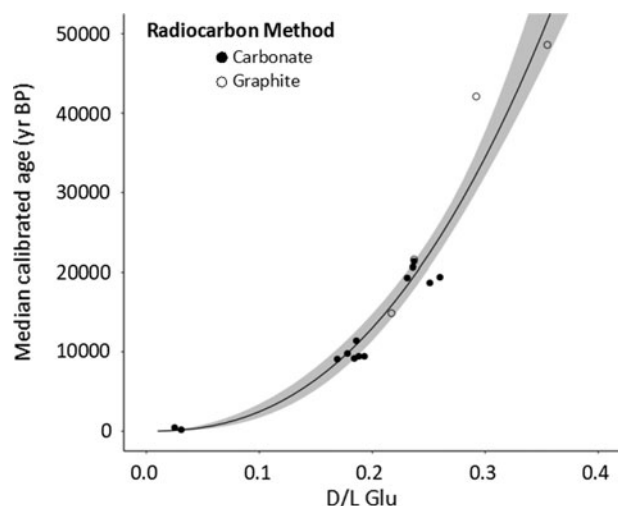
Figure 5. Relationship between glutamic acid D/L ratio and ^{14}C ages of the 17 *Actinella nitidiuscula* shells used to calibrate the rate of amino acid racemization (AAR). Each dot depicts a single shell dated by both methods (AAR and ^{14}C). Whiskers represent 2-sigma range of calibrated ages. Carbonate- and graphite-target ^{14}C dating results were used in the regression analysis. Gray band represents 95% CI of the calibration curve. As an estimate of goodness of fit, ordinary least-squares regression of log-transformed data yields $R^2 = 0.96$. Data are listed in Tables 1 and 2.

multimillennial age mixing of shells within colluvial deposits from The Desertas Islands. The scale of age mixing documented here was not significantly impacted by potential dead carbon intake by the snails (e.g., Hill et al., 2017), because the studied islands are poor in carbonate sediments and recently dead (modern) shells yielded ^{14}C ages younger than ~300 years that could potentially be explained by a post-bomb effect after the 1950s (Quarta et al., 2007). Even if snails' carbonate intake is possible, the effects of carbonate ingestion (<300 years) cannot explain the large degree of age mixing within colluvial sediments (>6 ka). These facts support the idea that carbonate ingestion by *Actinella* was probably limited, more so than for snails living in carbonate-rich areas, and therefore, we argue the radiocarbon results should not be significantly distorted by dead carbon offsets.

Multimillennial-scale time averaging has been observed in several late Pleistocene and Holocene buried continental shelly assemblages. Similar studies conducted on Helicidae snail shells have found evidence of similar magnitude of age mixing in late Quaternary carbonate-rich paleosols, paleodunes, and cave sediments from other oceanic islands (Goodfriend, 1989; Goodfriend and Mitterer, 1993; Yanes et al., 2007), suggesting that multimillennial-scale time averaging may be pervasive in Quaternary land snail assemblages in colluvium from islands with semiarid to arid habitats. Given the potential of fossil land snail shells as paleoenvironmental and paleoecological proxies (e.g., Goodfriend et al., 1996; Yanes et al., 2019), these results reinforce the necessity for improving our understanding of time averaging in continental sedimentary records.

Table 4. D/L glutamic acid (Glu) values and numerical ages for specimens from two colluvial deposits (DG4 and DG3) from Deserta Grande Island, Madeira, Portugal. Ages were derived from the calibration equation: Age = 622,247 · D/L Glu $^{(2.404)}$ as shown in Fig. 5.

Lab ID (UAL)	Shell ID	Snail ssp.	Median age (yr BP)	Lower age (yr BP)	Upper age (yr BP)	Glu D/L
15892	DG3-1	*nitidiuscula*	12,690	11,020	14,460	0.198
15893	DG3-2	*nitidiuscula*	11,490	9860	13,230	0.190
15894	DG3-3	*nitidiuscula*	12,380	10,720	14,160	0.196
15895	DG3-4	*nitidiuscula*	10,640	9030	12,370	0.184
15896	DG3-5	*nitidiuscula*	7600	6170	9190	0.160
15897	DG3-6	*nitidiuscula*	13,630	11,940	15,410	0.204
15898	DG3-7	*nitidiuscula*	9170	7630	10,850	0.173
15899	DG3-8	*nitidiuscula*	9820	8250	11,530	0.178
15900	DG3-9	*nitidiuscula*	10,360	8770	12,090	0.182
15901	DG3-10	*nitidiuscula*	7490	6070	9060	0.159
15902	DG3-11	*nitidiuscula*	10,920	9310	12,660	0.186
15903	DG3-12	*nitidiuscula*	13,000	11,320	14,770	0.200
15904	DG3-13	*nitidiuscula*	12,530	10,870	14,310	0.197
15905	DG3-14	*nitidiuscula*	3510	2540	4650	0.116
15906	DG3-15	*nitidiuscula*	10,500	8900	12,230	0.183
15881	DG4-1	*saxipotens*	12,690	11,020	14,460	0.198
15882	DG4-2	*saxipotens*	9430	7870	11,120	0.175
15883	DG4-3	*saxipotens*	9170	7630	10,850	0.173
15884	DG4-4	*saxipotens*	11,930	10,280	13,690	0.193
15885	DG4-5	*saxipotens*	12,840	11,170	14,620	0.199
15886	DG4-6	*saxipotens*	10,360	8770	12,090	0.182
15887	DG4-7	*saxipotens*	8920	7390	10,580	0.171
15888	DG4-8	*saxipotens*	13,470	11,790	15,250	0.203
15889	DG4-9	*saxipotens*	10,920	9310	12,660	0.186
15890	DG4-10	*saxipotens*	7260	5860	8830	0.157
15891	DG4-11	*saxipotens*	7380	5970	8950	0.158

[a] Abbreviations: Lab ID, UAL # (carbonate-target); Snail ssp., *Actinella nitidiuscula* subspecies; Lower age, lower age limit derived from error range of AAR calibration expressed in years BP; Upper age, upper age limit derived from error range of AAR calibration expressed in years BP.

Most published research assessing the scale of time averaging has traditionally focused on marine bivalve assemblages retrieved from shallow-water environments raging in age from late Pleistocene to modern. Published work suggests that the extent of age mixing can be quite variable, ranging from multiannual to multimillennial (e.g., Meldahl et al., 1997; Kowalewski et al. 1998, 2018; Kidwell et al., 2005; Barbour Wood et al., 2006; Kosnik et al., 2009; Albano et al., 2016, 2018; Ritter et al., 2017; and numerous references therein). In contrast, the few land snail studies retrieved from paleosols and paleodunes (Yanes et al., 2007), cave sediments, and colluvial deposits (this study) indicate consistent multimillennial mixing. Deposits displaying extensive age mixing have also been reported in studies of non-molluscan fauna from Holocene and late Pleistocene settings, indicating that multimillennial time resolution is not limited to molluscan assemblages. This includes taphonomic and geochronological studies on other durable taxa like freshwater
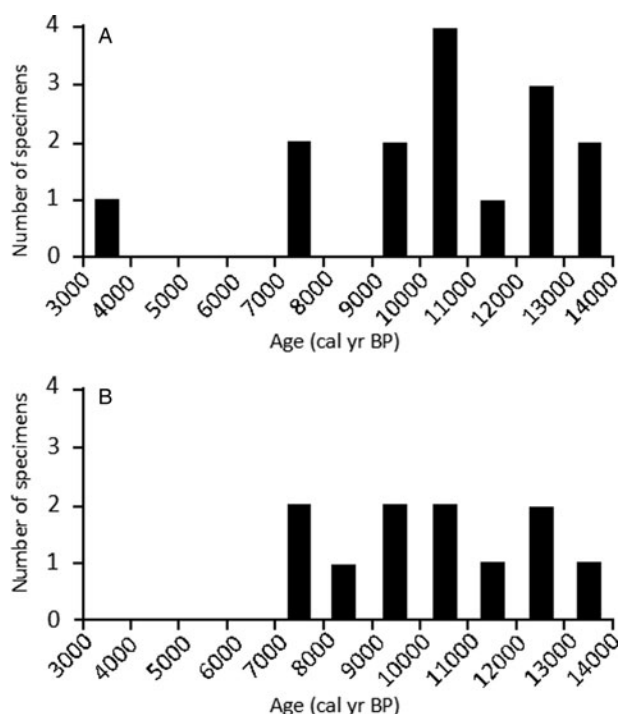
Figure 6. Age-frequency distributions of individual shell ages from colluvial sites in Deserta Grande Island, Madeira Archipelago, Portugal. (A) Structure of age mixing from site DG3 determined from dating 15 shells. (B) Structure of age mixing from site DG4 examined by dating 11 shells. The 1000-year bin size was chosen based on an age range that would eliminate the most gaps while also preserving structure of age distribution. Data are listed in Table 4.

ostracods (Michelson and Park, 2013), brachiopods (Barbour Wood et al., 2006; Krause et al., 2010), corals (Edinger et al., 2007), and terrestrial vertebrate assemblages (Hadly, 1999; Terry, 2009, 2010).

In addition to measuring the scale of time averaging by taxa and location, several studies have specifically examined how changes in burial depth could affect age mixing, either through direct comparison of age mixing at different depths or via examination of taphonomic processes. Buried specimens (those interred more than several centimeters beneath the surface) do not show significant differences in the scale of time averaging with increasing depth, as revealed through direct assessment of time averaging or examination of ecological fidelity in marine bivalves (e.g., Kosnik et al., 2008, 2009), land snails (Goodfriend, 1989; Yanes et al., 2011), and small mammals (Terry and Novak, 2015).

Taphonomy may control the scale of time averaging. Studies of comparative taphonomy (e.g., Brett and Baird, 1986) have shown that many factors, such as local sedimentation rates and environmental energy, can influence fossil preservation and, as a result, local time averaging. Similarly, a direct comparative study between marine mollusk and echinoid test preservation in a single site (Kowalewski et al., 2018) demonstrated that different taxa in the same deposit can exhibit different degrees of time averaging due to the intrinsic properties of those taxa, that is, more fragile echinoid tests display a

smaller (yearly to decadal) scale of age mixing than more resilient (multimillennial) marine mollusks. While land snail shells from forested (humid) areas can experience high rates of shell destruction from enhanced shell dissolution in wet/acidic environments (e.g., Albano., 2014), snail shells from semiarid habitats tend to be more resilient (e.g., Yanes et al., 2011; Yanes, 2012).

All in all, the degree of age mixing can vary notably as a result of characteristics such as location, environment, ecology of taxa, burial conditions, and taphonomy (e.g., Tomašových et al., 2014). In our snail assemblages from the Desertas Islands, the documented multimillennial resolution is feasibly explained by (1) the relatively brief life span (1 to 2 years) of *Actinella nitidiuscula*, which should result in high rates of shell production; (2) the relatively high durability of gastropod shells occupying semiarid habitats, that is, low rates of shell decay; and/or (3) the apparent slow burial/sedimentation rates in these volcanic (basaltic) islands.

Structure of time averaging in Quaternary colluvial deposits

"Structure of time averaging" refers to the frequency distribution of specimen ages through the observed age range of the assemblage (e.g., Meldahl et al., 1997). The age distributions of the two sampled land snail assemblages from the DG3 and DG4 sites display different shapes (Fig. 6). Shell age distributions from DG3 display higher kurtosis and a more normal distribution, while shells from DG4 display a more platykurtic (less peaked) age distribution. Age-frequency distributions suggest that younger specimens are overall the least abundant in this depositional setting, pointing to high taphonomic durability of oldest specimens. Inconsistency in the shape of age-frequency distributions, including different samples in the same horizon, has been observed in Quaternary land snails (Yanes et al., 2007) and in marine bivalves in both buried (Kosnik et al., 2009) and surficial deposits (Ritter et al., 2017; Kowalewski et al., 2018).

Taphonomy and sediment reworking play a large role in the structure of time averaging of faunal deposits (e.g., Flessa et al., 1993; Olszewski, 2004; Kosnik et al., 2009). In less sturdy skeletal remains such as brittle invertebrate shells and small mammal bones, older remains will inevitably experience a higher rate of destruction than younger examples. This can result in right-skewed distributions (indicating higher survivorship among younger fossil specimens) that are taphonomically driven, as is found in most studies of marine bivalves (Dexter et al., 2014; Ritter et al., 2017) and terrestrial vertebrates (e.g., Hadly, 1999; Terry, 2009; Terry and Novak, 2015). However, in one study on Quaternary land snails by Yanes et al. (2007), shell assemblages displayed a trend toward left-skewed distribution, suggesting a higher survivorship of older specimens.

The right-skewed trend continues even in nonsurficial assemblages, as deeper age-frequency distributions remain leptokurtic (Kosnik et al., 2009; Terry and Novak, 2015).

However, as before, a right-skewed distribution is most visible in shell ages pooled from multiple collection sites. Sediments that have undergone significant reworking, such as glacially reworked sediments, show less consistent age distribution (Briner et al., 2014). The structure of time averaging in colluvium, in particular, may be highly variable. This is likely because colluviation is a process of sediment reworking defined by erosion and transport of preexisting sediment driven by soil water saturation and physical disturbances (e.g., Leopold and Völkel, 2007). As a result, the reworking of sediment to form colluvial deposits may incorporate multiple source units, including previously buried shells and other fossil materials (Lang and Hönscheidt, 1999; Leopold and Völkel, 2007). While the present study and the study by Yanes et al. (2007) suggest that terrestrial mollusks do not appear to follow the same preservation and burial process as marine counterparts, future studies with higher numbers of dated shells will be used to further test the structure of age mixing in land snail assemblages across taxa, locations, and depositional settings.

Implications for shell geochronology

Mollusks and specifically land snail shells dated via AAR calibrated with graphite-target radiocarbon have been well established in developing local geochronologies (e.g., Goodfriend, 1989; Yanes et al., 2007; Hearty and Kaufman, 2009). The results presented here reinforce the use of land snail shells as excellent specimens for quantification of time averaging due to their ubiquity, abundance, and frequent shell durability in Quaternary settings. Graphite-target radiocarbon dating is limited by time and expense, while the carbonate-target method allows for faster and cheaper analysis of multiple localities and taxa. AAR analysis is applicable beyond the range of radiocarbon dating, but typically relies on an independent dating method to calibrate the rate of AAR to derive numerical ages. While initial carbonate-target results limited its effective dating range back to around 10 ^{14}C ka BP (e.g., Bush et al., 2013; Grothe et al., 2016; Ritter et al., 2017), our results show a good correlation with amino acid d/l ages up to ~15–22 cal ka BP (Fig. 4), pushing its use into the late Pleistocene, at least for *Actinella nitidiuscula* land snail shells from the Desertas Islands and possibly other small (<12 mm) land snail taxa from semiarid regions. These findings are promising for paleoclimate and paleoecological studies using late Pleistocene and Holocene land snails, because a larger number of ancient shells retrieved from archaeological and paleontological settings can be dated for a given budget. With the methods and approach presented here, the temporal resolution of poorly stratified or reworked settings, like cave deposits, which are usually rich in continental faunas, can finally be resolved.

Implications for time span of colluvial deposition

Although the observed time range of the Deserta Grande Island sites DG3 and DG4 were relatively constrained (>6 ka), they could tentatively inform understanding about the timing of colluvial deposition. Colluvium formation is an irregular erosional process driven largely by gravity but influenced by climate and weathering of source sediments; it can occur in different climates and environments and in different orientations and under different conditions (Leopold and Völkel, 2007). These properties make colluvial sediments very complex geoarchives to study; constraining the period of colluvial deposition is particularly difficult. Studies dating colluvial deposits (e.g., Kwaad and Mucher, 1979; Lang and Hönscheidt, 1999) have shown that the period of colluvial deposition cannot be adequately expressed through dating of interred objects alone. However, the shell ages reported here, if corroborated by further sedimentological analysis, may indicate the time of sediment deposition when shells were transported and buried under colluvial sediments (Williams and Polach, 1971). Youngest snail shell ages within colluvial units may indicate periods of recent colluvial sedimentation, whereas older ages may inform about earlier sediment deposition times. While dating of interred fossils may indicate time of colluvial deposition, further sedimentary and geochronologic studies are required to fully understand the timing of colluvial sediment accumulation.

CONCLUSIONS

Land snail shells from two colluvial deposits in the Desertas Islands of the Madeira Archipelago (Portugal) showed an ~6 ka-scale age mixing, exceeding the age variability caused by dating imprecision. This magnitude of time averaging should be considered and applied in future paleobiological and paleoclimatic research in the region. The majority of previous studies examining time averaging and age-frequency distribution have shown a typically right-skewed distribution inconsistent with results presented here. This may represent sampling deficiencies, or alternatively, a shell burial model of age distribution less dominated by taphonomic (destructive) processes.

The results reported here suggest that Quaternary land snails can be effectively dated using the carbonate-target radiocarbon dating method up to ~15–20 cal ka BP. This method allows for relatively inexpensive analysis of multiple individual specimens that makes large-scale dating of assemblages more feasible, particularly when used in conjunction with AAR analysis. This study illustrates that the carbonate-target method opens new opportunities to significantly improve the geochronological context of snail assemblages from unstratified and reworked deposits in archaeological and paleontological investigations.

ACKNOWLEDGMENTS

with AAR analyses and John Southon (UCI) for AMS ^{14}C analyses. The detailed and constructive reviews by associate editor Jeff Pigati and two anonymous reviewers greatly improved the quality and clarity of this article.

REFERENCES

Abreu, C., Teixeira, D., 2008. List of molluscs (Mollusca). In: Borges, P.A.V., Abreu, C., Aguiar, A.M.F., Carvalho, P., Jardim, R., Melo, I., Oliveira, P., Sérgio, C., Serrano, A.R.M., Vieira, P. (Eds.), *A List of the Terrestrial Fungi, Flora and Fauna of Madeira and Selvagens Archipelagos*. Direcção Regional do Ambiente da Madeira and Universidade dos Açores, Funchal and Angra do Heroísmo, pp. 237–244.

Albano, P.G., 2014. Comparison between death and living land mollusk assemblages in six forested habitats in Northern Italy. *Palaios* 29, 338–347.

Albano, P.G., Filippova, N., Steger, J., Kaufman, D.S., Tomašových, A., Stachowitsch, M., Zuschin, M., 2016. Oil platforms in the Persian (Arabian) Gulf: living and death assemblages reveal no effects. *Continental Shelf Research* 120, 21–34.

Albano, P.G., Gallmetzer, I., Haselmair, A., Tomašových, A., Stachowitsch, M., Zuschin, M,., 2018. Historical ecology of a biological invasion: the interplay of eutrophication and pollution determines time lags in establishment and detection. *Biological Invasions* 20, 1417–1430.

Barbour Wood, S.L., Krause, R.A., Kowalewski, M., Wehmiller, J., Simões, M.G., 2006. Aspartic acid racemization dating of Holocene brachiopods and bivalves from the southern Brazilian shelf, South Atlantic. *Quaternary Research* 66, 323–331.

Brett, C.E., Baird, G.C., 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *Palaios* 1, 207–227.

Briner, J.P., Kaufman, D.S., Bennike, O., Kosnik, M.A., 2014. Amino acid ratios in reworked marine bivalve shells constrain Greenland Ice Sheet history during the Holocene. *Geology* 42, 75–78.

Bush, A.M., Powell, M.G., Arnold, W.S., Bert, T.M., Daley, G.M., 2002. Time-averaging, evolution, and morphologic variation. *Paleobiology* 28, 9–25.

Bush, S.L., Santos, G.M., Xu, X., Southon, J.R., Thiagarajan, N., Hines, S.K., Adkins, J.F., 2013. Simple, rapid, and cost effective: a screening method for analysis of small carbonate samples. *Radiocarbon* 55, 631–640.

Cameron, R.A.D., Cook, L.M., 1989. Shell size and shape in Madeiran land snails: do niches remain unfulfilled? *Biological Journal of the Linnean Society* 36, 79–96.

Cameron, R.A.D., Cook, L.M., 1992. The development of diversity in the land snail fauna of the Madeiran archipelago. *Biological Journal of the Linnean Society* 46, 105–114.

Cameron, R.A.D., Cook, L.M., 1999. Land snail faunas of the Deserta Islands, Madeiran archipelago, past and present. *Journal of Conchology* 36, 1–15.

Cameron, R.A.D., Cook, L.M., Goodfriend, G.A., Seddon, M.B., 2006. Fossil land snail faunas of Porto Santo, Madeiran Archipelago: change and stasis in Pleistocene to recent times. *Malacologia* 49, 25–59.

Carroll, M., Kowalewski, M., Simoes, M.G., Goodfriend, G.A., 2003. Quantitative estimates of time-averaging in terebratulid brachiopod shell accumulations in a modern tropical shelf. *Paleobiology* 29, 381–402.

Cook, L.M., 1996. Habitat, isolation and the evolution of Madeiran landsnails. *Biological Journal of the Linnean Society* 59, 457–470.

Cook, L.M., 2008. Species richness in Madeiran land snails, and its causes. *Journal of Biogeography* 35, 647–653.

Cook, L.M., Cameron, R.A.D., Lace, L.A., 1990. Land snails of eastern Madeira: speciation, persistence and colonization. *Proceedings of the Royal Society of London B* 239, 35–79.

Dexter, T.A., Kaufman, D.S., Krause, R.A., Barbour, S.L., Simões, M.G., Warren, J., Yanes, Y., Romanek, C.S., Kowalewski, M., 2014. A continuous multi-millennial record of surficial bivalve mollusk shells from the São Paulo Bight , Brazilian shelf. *Quaternary Research* 81, 274–283.

Dominguez, J.G., Kosnik, M.A., Allen, A.P., Hua, Q., Jacob, D.E., Kaufman, D.S., Whitacre, K., 2016. Time-averaging and stratigraphic resolution in death assemblages and Holocene deposits: Sydney Harbour's molluscan record. *Society for Sedimentary Geology* 31, 563–574.

Edinger, E.N., Burr, G.S., Pandolfi, J.M., Ortiz, J.C., 2007. Age accuracy and resolution of Quaternary corals used as proxies for sea level. *Earth and Planetary Science Letters* 253, 37–49.

Ellis, G.L., Goodfriend, G.A., Abbott, J.T., Hare, P.E., von Endt, D.W., 1996. Assessment of integrity and geochronology of archaeological sites using amino acid racemization in land snail shells: examples from central Texas. *Geoarchaeology* 11, 189–213.

Flessa, K.W., Cutler, A.H., Meldahl, K.H., 1993. Time and taphonomy: quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. *Paleontological Society* 19, 266–286.

Geldmacher, J., van den Bogaard, P., Hoernle, K., Schmincke, H.-U., 2000. The [40]Ar/[39]Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). *Geochemistry, Geophysics, Geosystems* 1, 1–26.

Goodfriend, G.A., 1989. Complementary use of amino-acid epimerization and radiocarbon analysis for dating of mixed-age fossil assemblages. *Radiocarbon* 31, 1041–1047.

Goodfriend, G.A., 1991. Patterns of racemization and epimerization of amino acids in land snail shells over the course of the Holocene. *Geochimica et Cosmochimica Acta* 55, 293–302.

Goodfriend, G.A., 1992. Rapid racemization of aspartic acid in mollusc shells and potential for dating over recent centuries. *Nature* 357, 399–401.

Goodfriend, G.A., Cameron, R.A.D., Cook, L.M., Courty, M., Fedoroff, N., Livett, E., Tallis, J., 1996. The Quaternary eolian sequence of Madeira: stratigraphy, chronology, and paleoenvironmental interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 120, 195–23

Goodfriend, G.A., Meyer, V.R., 1991. A comparative-study of the kinetics of amino-acid racemization epimerization in fossil and modern mollusk shells. *Geochimica et Cosmochimica Acta* 55, 3355–3367.

Goodfriend, G.A., Mitterer, R.M., 1993. A 45,000-yr record of a tropical lowland biota: the land snail fauna from cave sediments at Coco Ree, Jamaica. *Geological Society of America Bulletin* 105, 18–29.

Goodwin, D.H., Flessa, K.W., Téllez-Duarte, M.A., Dettman, D.L., Schöne, B.R., Avila-Serrano, G.A., 2004. Detecting time-averaging and spatial mixing using oxygen isotope variation: a case study. *Palaeogeography, Palaeoclimatology, Palaeoecology* 205, 1–21.

Grothe, P.R., Cobb, K.M., Bush, S.L., Cheng, H., Santos, G.M., Southon, J.R., Edwards, R.L., Deocampo, D.M., Sayani, H.R.,

2016. A comparison of U/Th and rapid-screen 14C dates from Line Island fossil corals. *Geochemistry, Geophysics, Geosystems* 17, 833–845.

Hadly, E.A., 1999. Fidelity of terrestrial vertebrate fossils to a modern ecosystem. *Palaeogeography, Palaeoclimatology, Palaeoecology* 149, 389–409.

Hare, P.E., Hoering, T.C., King, K., Jr. (Eds.) 1980. Biogeochemistry of Amino Acids: Papers Presented at a Conference at Airlie House, Warrenton, Virginia, October 29 to November 1, 1978. Wiley, New York.

Hearty, P.J., Kaufman, D.S., 2009. A Cerion-based chronostratigraphy and age model from the central Bahama Islands: amino acid racemization and ^{14}C in land snails and sediments. *Quaternary Geochronology* 4, 148–159.

Hill, E.A., Reimer, P.J., Hunt, C.O., Prendergast, A.L., Barker, G.W., 2017. Radiocarbon ecology of the land snail *Helix melanostoma* in northeastern Libya. *Radiocarbon* 59, 1–22.

Hines, S.K.V, Southon, J.R., Adkins, J.F., 2015. A high-resolution record of Southern Ocean intermediate water radiocarbon over the past 30,000 years. *Earth and Planetary Science Letters* 432, 46–58.

Kaufman, D.S., Manley, W.F., 1998. A new procedure for determining DL amino acid ratios in fossils using reverse phase liquid chromatography. *Quaternary Science Reviews* 17, 987–1000.

Kidwell, S.M., 1998. Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios* 30, 977–995.

Kidwell, S.M., Best, M.M.R., Kaufman, D.S., 2005. Taphonomic trade-offs in tropical marine death assemblages: differential time averaging, shell loss, and probable bias in siliciclastic vs. carbonate facies. Geology 33, 729–732.

Kidwell, S.M., Bosence, D.W.J., 1991. Taphonomy and time-averaging of marine shelly faunas. In: Allison, P.A., Briggs, D.E.G. (Eds.), *Taphonomy: Releasing the Data Locked in the Fossil Record*. Plenum, New York, pp. 115–209.

Kosnik, M.A., Hua, Q., Kaufman, D.S., Kowalewski, M., Whitacre, K., 2017. Radiocarbon-calibrated amino acid racemization ages from Holocene sand dollars (*Peronella peronii*). *Quaternary Geochronology* 39, 174–188.

Kosnik, M.A., Hua, Q., Kaufman, D.S., Wüst, R.A., 2009. Taphonomic bias and time-averaging in tropical molluscan death assemblages: differential shell half-lives in Great Barrier Reef sediment. *Paleobiology* 35, 565–586.

Kosnik, M.A., Kaufman, D.S., Hua, Q., 2008. Identifying outliers and assessing the accuracy of amino acid racemization measurements for geochronology: I. Age calibration curves. *Quaternary Geochronology* 3, 308–327.

Kowalewski, M., 1996. Time-averaging, overcompleteness, and the geological record. *Journal of Geology* 104, 317–326.

Kowalewski, M., Bambach, R.K., 2008. The limits of paleontological resolution. In: Harries, P.J. (Ed.), *High-Resolution Approaches in Stratigraphic Paleontology*. Springer, New York, pp. 1–48.

Kowalewski, M., Casebolt, S., Hua, Q., Whitacre, K.E., Kaufman, D.S., Kosnik, M.A., 2018. One fossil record, multiple time resolutions: disparate time-averaging of echinoids and mollusks on a Holocene carbonate platform. *Geology* 46, 51–54.

Kowalewski, M., Goodfriend, G.A., Flessa, K.W., 1998. High-resolution estimates of temporal mixing within shell beds: the evils and virtues of time-averaging. *Paleontological Society* 24, 287–304.

Krause, R.A., Barbour, S.L., Kowalewski, M., Kaufman, D.S., Romanek, C.S., Simoes, M.G., Wehmiller, J.F., 2010.

Quantitative comparisons and models of time-averaging in bivalve and brachiopod shell accumulations. *Paleobiology* 36, 428–452.

Kwaad, F.J.P., Mucher, H., 1979. The formation and evolution of colluvium on arable land in northern Luxembourg. *Geoderma* 22, 173–192.

Lang, A., Hönscheidt, S., 1999. Age and source of colluvial sediments at Vaihingen-Enz, Germany. *Catena* 38, 89–107.

Leopold, M., Völkel, J., 2007. Colluvium: definition, differentiation, and possible suitability for reconstructing Holocene climate data. *Quaternary International* 162–163, 133–140.

Meldahl, K.H., Flessa, K.W., Cutler, A.H., 1997. Time-averaging and postmortem skeletal survival in benthic fossil assemblages: quantitative comparisons among holocene environments. *Paleobiology* 23, 207–229.

Michelson, A.V., Park, L.E., 2013. Taphonomic dynamics of lacustrine ostracodes on San Salvador Island, Bahamas: high fidelity and evidence of anthropogenic modification. *Palaios* 28, 129–135.

Miller, G.H., Brigham-Grette, J., 1989. Amino acid geochronology: resolution and precision in carbonate fossils. *Quaternary International* 1, 111–128.

Olszewski, T.D., 2004. Modeling the influence of taphonomic destruction, reworking, and burial on time-averaging in fossil accumulations. *Palaios* 19, 39–50.

Pigati, J.S., Quade, J., Shahanan, T.M., Haynes, C.V., Jr., 2004. Radiocarbon dating of minute gastropods and new constraints on the timing of late Quaternary spring-discharge deposits in southern Arizona, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 204, 33–45.

Pigati, J.S., Rech, J.A., Nekola, J.C., 2010. Radiocarbon dating of small terrestrial gastropod shells in North America. *Quaternary Geochronology* 5:519–32.

Prada, S., Serralheiro, A., 2000. *Stratigraphy and Evolutionary Model of Madeira Island*. Bocagiana/Museu Municipal do Funchal 200. Museu Municipal do Funchal (História Natural, Madeira, 13 p.

Quarta, G., Romaniello, L., D'Elia, M., Mastronuzzi, G., Calcagnile, L., 2007. Radiocarbon age anomalies in pre- and post-bomb land snails from the coastal Mediterranean basin. *Radiocarbon* 49, 817–26.

R Core Team, 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org, accessed 5/10/2018.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., *et al.*, 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55, 1869–1887.

Ritter, M., Erthal, F., Kosnik, M.A., Coimbra, J.C., Kaufman, D.S., 2017. Spatial variation in the temporal resolution of subtropical shallow-water molluscan death assemblages. *Palaios* 32, 572–583.

Santos, F.D., Valente, M.A., Miranda, P.M.A, Aguiar, A., Azevedo, E.B., Tome, A.R., Coelho, F., 2004. Climate change scenarios in the Azores and Madeira islands. *World Resource Review* 16, 473–491.

Schnedl, S.-M., Haselmair, A., Gallmetzer, I., Mautner, A.-K., Tomašových, A., Zuschin, M., 2018. Molluscan benthic communities at Brijuni Islands (northern Adriatic Sea) shaped by Holocene sea-level rise and recent human eutrophication and pollution. *The Holocene* 28, 1801–1817.

Stuiver, M., Reimer, P.J., 1993. Extended ^{14}C data base and revised CALIB 3.0 ^{14}C age calibration program, *Radiocarbon* 35, 215–230.

Terry, R.C., 2009. The dead do not lie: using skeletal remains for rapid assessment of historical small-mammal community baselines. *Proceedings of the Royal Society of London B* 277, 1193–1201.

Terry, R.C., 2010. On raptors and rodents: testing the ecological fidelity and spatiotemporal resolution of cave death assemblages. *Paleobiology* 36, 137–160.

Terry, R.C., Novak, M., 2015. Where does the time go? Mixing and the depth-dependent distribution of fossil ages. *Geology* 43, 487–490.

Tomašových, A., Kidwell, S.M., Barber, R.F., Kaufman, D.S., 2014. Long-term accumulation of carbonate shells reflects a 100-fold drop in loss rate. *Geology* 42, 819–822.

Vidović, J., Nawrot, R., Gallmetzer, I., Haselmair, A., Tomašových, A., Stachowitsch, M., Ćosović, V., Zuschin, M., 2016. Anthropogenically induced environmental changes in the northeastern Adriatic Sea in the last 500 years (Panzano Bay, Gulf of Trieste). *Biogeosciences* 13, 5965–5981.

Waldén, H.W., 1983. Systematic and biogeographical studies of the terrestrial Gastropoda of Madeira. *With an annotated Check-list.* Annales Zoologici Fennici 20, 255–275.

Wehmiller, J.F., Miller, G.H., 2000. Aminostratigraphy dating method in Quaternary geology. *Quaternary Geochronology: Methods and Applications* 4, 187–222.

Williams, G.E., Polach, H.A., 1971. Radiocarbon dating of arid-zone calcareous paleosols. *Bulletin of the Geological Society of America* 82, 3069–3086.

Wollaston, T.V., 1878. *Testacea Atlantica* 9, 588.

Yanes, Y., 2012. Shell taphonomy and fidelity of live, dead, Holocene and Pleistocene land snail assemblages. *Palaios* 27, 127–136.

Yanes, Y., Aguirre, J., Alonso, M.R., Ibáñez, M., Delgado, A., 2011. Ecological fidelity of Pleistocene–Holocene land snail shell assemblages preserved in carbonate-rich paleosols. *Palaios* 26, 406–419.

Yanes, Y., Al-Qattan, N., Rech, J.A., Pigati, J.S., Dodd, J.D., Nekola, J.N., 2019. Overview of the oxygen isotope systematics of land snails from North America. *Quaternary Research* 91, 329–344.

Yanes, Y., Kowalewski, M., Ortiz, J.E., Castillo, C., de Torres, T., de la Nuez, J., 2007. Scale and structure of time-averaging (age mixing) in terrestrial gastropod assemblages from Quaternary eolian deposits of the eastern Canary Islands. *Palaeogeography, Palaeoclimatology, Palaeoecology* 251, 283–299.