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Overview of the oxygen isotope systematics of land snails from North America

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Abstract

Continental paleoclimate proxies with near-global coverage are rare. Land snail $\delta^{18}O$ is one of the few proxies abundant in Quaternary sediments ranging from the tropics to the high Arctic tundra. However, its application in paleoclimatology remains difficult, attributable in part to limitations in published calibration studies. Here we present shell $\delta^{18}O$ of modern small (<10 mm) snails across North America, from Florida (30°N) to Manitoba (58°N), to examine the main climatic controls on shell $\delta^{18}O$ at a coarse scale. This transect is augmented by published $\delta^{18}O$ values, which expand our coverage from Jamaica (18°N) to Alaska (64°N). Results indicate that shell $\delta^{18}O$ primarily tracks the average annual precipitation $\delta^{18}O$. Shell $\delta^{18}O$ increases 0.5–0.7‰ for every 1‰ increase in precipitation $\delta^{18}O$, and 0.3–0.7‰ for every 1°C increase in temperature. These relationships hold true when all taxa are included regardless of body size (ranging from ~1.6 to ~58 mm), ecology (herbivores, omnivores, and carnivores), or behavior (variable seasonal active periods and mobility habits). Future isotopic investigations should include calibration studies in tropical and high-latitude settings, arid environments, and along altitudinal gradients to test if the near linear relationship between shell and meteoric precipitation $\delta^{18}O$ observed on a continental scale remains significant.

Keywords: Oxygen stable isotopes; Land snails; Latitudinal transect; Precipitation proxy; North America

INTRODUCTION

Developing and augmenting paleoclimate proxies and increasing the number of paleoclimate studies are necessary and urgent tasks to improve our understanding of climate change and variability at various spatiotemporal scales. In particular, proxies from the continental realm that offer hemispheric to near-global coverage are rare. For example, tree-ring records are generally limited to middle latitudes of the Northern Hemisphere, speleothems develop in cave settings only, and ice-core records are only accessible at the highest latitudes or very high elevations. In this context, land snail shells are an exceptionally valuable proxy because they exhibit a near-global spatial distribution within the continental realm (except Antarctica), ranging from the tropics to the high Arctic, and are present in almost every environment and biome, ranging from deserts to wetlands.

Within North America, more than 1200 species of land snails have been identified spanning nearly the entire continent and all terrestrial biomes except for hyperarid deserts and the high Arctic (Nekola, 2014). Approximately 40% of North American land snails have shells that are smaller than 10 mm in maximum shell length, with 10 families accounting for more than 75% of the small species, including Vertiginidae (106),[1] Polygyridae (80), Pristilomatidae (72), Oxychilidae (32), Gastrodontidae (30), Helicodiscidae (27), Succineidae (19), Pupillidae (16), Discidae (14), and Valloniidae (13) (Nekola, 2014). The same families are also common in the Quaternary fossil record of North America, as they are preserved in paleosols, loess sequences, and wetland, fluvial, alluvial, colluvial, and lake deposits. All class sizes of shells, from minute (<5 mm) to large (>20 mm), are frequently preserved in a variety of Quaternary sedimentary settings. Fossil shells of these and other taxa are also found at paleontological (Goodfriend, 1992, 1999) and archaeological

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[1] Number of species per family is given in parentheses.

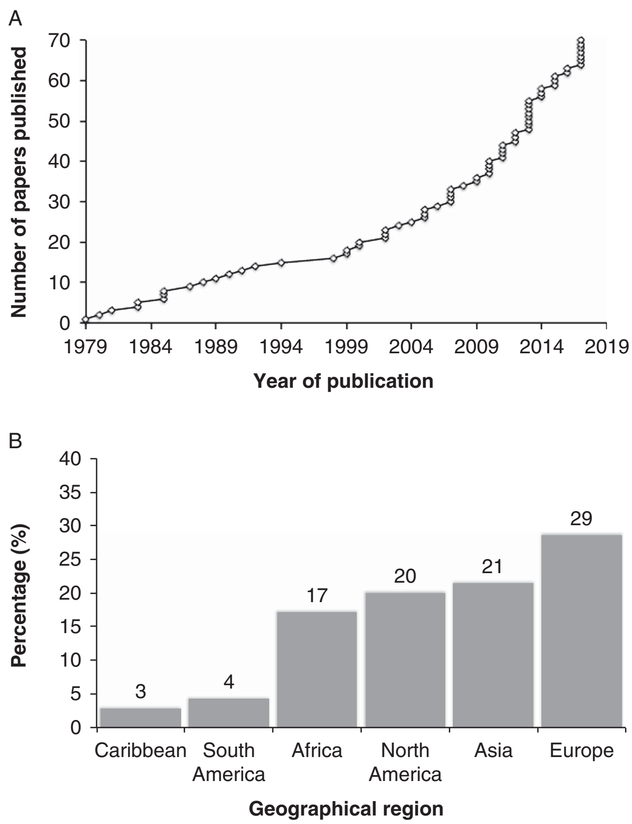

Figure 1. Summary of published studies (1979–2018) of oxygen isotopes of modern and fossil land snails worldwide. (A) Cumulative number of published articles by year of publication. (B) Proportion of studies published by major geographic region.

(Evans, 1972; Lubell, 2004) sites worldwide. Because of their ubiquity and excellent preservation potential, land snail shells offer unique opportunities to investigate climate and ecosystems of the past at broad spatiotemporal scales within the continental realm.

Increasingly, researchers are using the oxygen isotope composition ($\delta^{18}O$) of land snail shells to reconstruct aspects of Quaternary climate (Fig. 1). Land snails form their shells in isotopic equilibrium with snail body fluids, which, in turn, are strongly correlated with meteoric precipitation $\delta^{18}O$ values (Prendergast et al., 2015). Therefore, the $\delta^{18}O$ of snail shells can be used as a paleoenvironmental proxy if the dominant environmental factors controlling the oxygen isotopic system are reasonably well characterized (Balakrishnan and Yapp, 2004). Although several studies have tested and assessed the utility of land snails in paleoenvironmental studies, the majority of published articles have been limited in scope, targeting one or a few species and often exploring just a single biome or region.

In North America, for example, only six published studies have attempted to calibrate the $\delta^{18}O$ systematics of modern land snails. Yapp (1979) analyzed 30 aliquots of shells of ecologically disparate species, ranging from the Yucatan Peninsula (20°N) to Wisconsin (43°N), and observed that the difference ($\Delta^{18}O$) between the calculated $\delta^{18}O$ of the snail body fluid and the $\delta^{18}O$ of the average annual precipitation correlated with the reciprocal of the average annual relative humidity (RH) at those locales. Goodfriend and Ellis (2002) analyzed snails of the genus *Rabdotus* living in Texas and concluded that shell $\delta^{18}O$ values are primarily controlled by precipitation $\delta^{18}O$ values, rather than precipitation amount or evaporation rates. Balakrishnan et al. (2005b) studied land snails living in the southern Great Plains along an east-to-west transect between Oklahoma and New Mexico and concluded that RH, precipitation $\delta^{18}O$, and temperature all seemed to play roles in shell $\delta^{18}O$ values. Yanes (2015) found that the differences between the $\delta^{18}O$ values of the shells of modern snails of the genus *Succinea* retrieved from tropical (San Salvador, the Bahamas) and high (Fairbanks, Alaska) latitudes primarily record the differences in the $\delta^{18}O$ values of the meteoric waters at the two locales. Yanes et al. (2017) observed that small land snails from northwest Minnesota mainly tracked precipitation $\delta^{18}O$ values; however, coexisting species showed significantly different isotopic values. Finally, Yanes et al. (2018) observed that large body-size snails of the genus *Neohelix* from the Appalachian Mountains primarily record changes in precipitation $\delta^{18}O$ values and RH along an elevation transect between ~700 and ~1600 meters above sea level (m asl).

Despite the relative paucity of calibration studies, researchers are applying fossil land snail shell $\delta^{18}O$ values for paleoclimatic reconstructions at a rapid rate (Fig. 1A). It is therefore essential that systematic and comprehensive calibration studies be conducted to resolve how the fossil shell $\delta^{18}O$ data should be interpreted. Such calibration studies should have large spatial and ecological coverage so that future applications do not extrapolate beyond the limits of the data, and they should focus on taxa that are most common in the fossil record.

In this article, we present oxygen isotope data for several species of modern small land snails in North America collected across an unprecedented spatial scale, ranging from northern Florida (30°N) to northern Manitoba (58°N). We then augment this data with published oxygen isotope results on land snails from North America and the Caribbean, which expand our latitudinal coverage from Jamaica (18°N) to Fairbanks, Alaska (64°N). We also evaluate shell $\delta^{18}O$ values of modern land snails using instrumental climate data and discuss the usefulness and limitations of land snails as paleoclimatic proxies in North America. We then review possible mechanisms explaining the observed patterns and identify several avenues of potential research that we think will advance the field of land snail isotope research significantly.

Overview of published land snail isotopic studies worldwide

Since Yapp's seminal article on the $\delta^{18}O$ of land snail shells was published nearly four decades ago (Yapp, 1979), approximately 70 articles have been published on the topic of stable isotopes in land snail shells (Supplementary Table 1). The bulk of these studies have attempted to use snail $\delta^{18}O$ values to reconstruct local precipitation $\delta^{18}O$ values for various periods of geologic time, primarily the Holocene and late

Pleistocene (Supplementary Table 1). However, inferences on precipitation $\delta^{18}O$ values from snail shells remain semiquantitative, as other climatic parameters such as RH, air temperature, water vapor, species ecology, and perhaps vital effects also appear to play a role in the snail oxygen isotope budget (Balakrishnan and Yapp, 2004).

Worldwide, ~37 studies have focused on modern calibration of the oxygen isotope composition of snail shells for a target region and taxa (Supplementary Table 1). However, nearly all published studies focusing on fossil shells generally include modern shell analyses for comparative purposes, an indispensable step if the species and locale have never been explored before. Some of these studies report site-specific and/or species-specific regression equations (Lécolle, 1985; Goodfriend and Ellis, 2002; Balakrishnan et al., 2005b; Zanchetta et al., 2005; Yanes et al., 2008, 2009; Prendergast et al., 2015), which is helpful, although we note that such equations are only valid for the taxa and location investigated. Balakrishnan and Yapp (2004) proposed a universal mathematical model that combines empirical and theoretical data that can be used to evaluate the impact of multiple atmospheric variables (meteoric precipitation $\delta^{18}O$, water vapor $\delta^{18}O$, RH, and temperature) on shell $\delta^{18}O$ values. The model is robust and can be applied to land snails in all parts of the world, but many studies conducted after their article was published in 2004 have not employed it, partly because of the large number of unknown variables and assumptions required.

Geographically, one third of the ~71 published articles on stable isotopes of land snail shells have been conducted in Europe (Supplementary Table 1; Fig. 1B), with fewer in North America (Yapp, 1979; Sharpe et al., 1994; Goodfriend and Ellis, 2000, 2002; Balakrishnan and Yapp, 2004; Balakrishnan et al., 2005a, 2005b; Zaarur et al., 2011; Stevens et al., 2012; Paul and Mauldin, 2013; Yanes, 2015; Yanes et al., 2017, 2018; Nash et al., 2018) and the Caribbean (Baldini et al., 2007; Yanes and Romanek, 2013). As stated previously, of the North American studies, only six conducted modern calibration assessments for shell $\delta^{18}O$ values (Yapp, 1979; Goodfriend and Ellis, 2002; Balakrishnan et al., 2005b; Yanes, 2015; Yanes et al., 2017, 2018), and all of them were limited in scope.

The vast majority of snail isotope studies worldwide have analyzed $\delta^{18}O$ values of entire shells rather than employing a time-series approach (Supplementary Table 1), although eight published articles have explored high-resolution oxygen isotope time series along shell growth direction (Goodfriend, 1992; Leng et al., 1998; Baldini et al., 2007; Yanes et al., 2011b, 2012, 2014; Rangarajan et al., 2013; Ghosh et al., 2017). In addition, one study focused on shell margin or last growth episode oxygen isotope values (Yanes and Fernandez-Lopez-de-Pablo, 2017), and two have analyzed snail body fluid $\delta^{18}O$ values in conjunction with shell $\delta^{18}O$ (Goodfriend et al., 1989; Prendergast et al., 2015).

Four studies used laboratory-controlled experiments to examine stable carbon isotope systematics in snail diet, shell, and body tissue (Stott, 2002; Metref et al., 2003; Liu et al., 2007; Zhang et al., 2014), although none have investigated the oxygen isotope composition of land snails under laboratory conditions. The absence of laboratory-based oxygen isotope studies is likely attributable to the difficulty in quantitatively constraining the relatively high number of environmental variables affecting the snail oxygen isotope composition (Balakrishnan and Yapp, 2004). Such experiments are extremely challenging, as they require establishing, stabilizing, and monitoring multiple climatic variables simultaneously and sustaining the snail communities healthy and alive, which can be difficult for long periods of time (>4 months).

Finally, three studies have measured clumped isotopes in land snail shells (Zaarur et al., 2011; Eagle et al., 2013; Wang et al., 2016). Some clumped isotope results showed that land snail calcification temperatures were significantly higher than ambient average annual temperatures or snail active period temperatures, especially at mid- to high latitudes (Zaarur et al., 2011). This suggests that snails preferentially add shell material when environmental conditions are at optimum (warmer) levels, which may vary between species (Wang et al., 2016). The results of these pioneering studies are intriguing and suggest that further investigations of clumped isotope paleothermometry in modern land snail shells from contrasting environments and ecologies are warranted.

Land snail physiology and ethology

Although many terrestrial gastropods are detritivores that live among leaf litter or under rocks at the soil-air interface, as a whole they exhibit a range of trophic states (including numerous herbivores and even some carnivores) and microhabitat preferences (from subterranean to arboreal) (Wilbur and Yonge, 1964; Pearce and Örstan, 2006; Meyer and Yeung, 2011). Land snails form their shells under a relatively limited range of environmental conditions, generally when temperatures are between ~10 and ~27°C and RH is greater than ~75 (Herreid, 1977; Balakrishnan and Yapp, 2004; Pearce and Örstan, 2006). Accordingly, snail activity and life cycles may vary significantly between species, latitudes, or contrasting habitats. The extreme conditions at high latitudes characterized by colder temperatures, marked seasonality, and shorter growing seasons, likely result in a decrease in snail metabolic rates and a reduction in annual growth rates (Gaitán-Espitia and Nespolo, 2014). For example, large body-size snails appear to tolerate freezing temperatures (Ansart and Vernon, 2004) and drier conditions (Nevo et al., 1983; Yanes et al., 2012) better than their smaller counterparts, which may result in differing active periods (Yanes et al., 2017). Thus, specific taxa may exhibit different tolerance ranges, activity, and behavior at various latitudes, and possibly within and between microhabitats (Yanes et al., 2017).

In low-latitude and maritime climates, where temperature and precipitation are relatively constant and RH remains high (>75%, on average) year-round, land snails may be active throughout all seasons (Yanes et al., 2008, 2009, 2011, 2013; Yanes and Romanek, 2013). In contrast, land snails in

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temperate and cold regions are expected to be most active during the warmer months (Yanes, 2015), whereas in hot or arid environments they are mainly active during wet periods or at night when RH is high (Cook, 2001). This complex behavior across contrasting environments has significant implications for interpreting shell $\delta^{18}O$ records because reconstructed climate parameters may only reflect the season, or time of day, that snails are active, rather than mean annual conditions, and may be biased toward microclimatic conditions. The main challenge in this field of study is that specific details regarding snail active periods and behavior are virtually unknown for most (if not all) land snail species in North America. Therefore, isotope geochemists must make assumptions about expected snail active periods when relating the snail isotopic data to climate data, assigning them to specific seasons, or using a range of temperatures and humidity levels to discuss active periods in general.

Land snail shell formation

Land snail shell calcification is performed by the mantle, an organ composed of two epithelia separated by connective tissue and located at the inner surface of the shell (Wilbur and Yonge, 1964). Accretionary shell growth takes place at the shell margin, and the mantle edge is the most active calcification zone (Wilbur and Yonge, 1964). The epithelial cells of the mantle obtain the calcium and bicarbonate ions necessary to form shell from the hemolymph or snail's internal body fluid. These ions are primarily obtained from the diet (e.g., carbon from consumed plant matter and, to a lesser extent, carbonate rocks) and the environment (e.g., oxygen from imbibed environmental water) (Goodfriend and Hood, 1983; Goodfriend et al., 1989).

Unlike marine mollusk shells, which are often arranged in several layers of two different calcium carbonate polymorphs, most species of land snails build a shell composed of a single layer of aragonite, which is a metastable polymorph of calcium carbonate. The mineral portion of the snail shell can account for >90% of the total mass for many species and is covered by a thin outer layer known as the periostracum, a protein-rich film that decays quickly after snail death. Fortunately, aragonite shells are fairly resistant to decay and can be preserved in the geologic record for thousands, and sometimes millions, of years (Pearce, 2008; Rech et al., 2011). Moreover, potential diagenetic alteration can be examined through various techniques including X-ray diffraction, scanning electron microscopy, and Raman spectroscopy, among others (Rech et al., 2011).

Environmental controls on land snail shell $\delta^{18}O$ values

The $\delta^{18}O$ values of aquatic mollusk shells (both marine and freshwater) are primarily determined by two environmental variables: (1) the $\delta^{18}O$ values of the host water and (2) temperature during calcification (Epstein et al., 1951; Grossman and Ku, 1986). The systematics of oxygen isotopes in land snail shells are more complicated, with at least four environmental variables contributing to shell $\delta^{18}O$ values: (1) $\delta^{18}O$ values of local precipitation, (2) RH, (3) temperature, and (4) $\delta^{18}O$ values of ambient water vapor (Balakrishnan and Yapp, 2004). Shell $\delta^{18}O$ values thus depend not only on local and regional climate conditions, but also on the interaction of species ecology and behavior with meso- and microclimatic conditions that can vary both between and within sites (Yanes et al., 2017). To accurately interpret shell $\delta^{18}O$ values, we must understand the impact that each parameter has on the shell $\delta^{18}O$ value under a variety of environmental and climatic conditions at different spatial scales and for the taxa that are most abundant in the fossil record.

MATERIAL AND METHODS

Field sampling strategy

Modern land snails were collected from seven localities in the eastern continental United States (Fig. 2), including the following: (1) Fort George Island, Florida (30.410°N); (2) Norfolk Bluff, Arkansas (36.224°N); (3) Cedar Bog Preserve, Ohio (40.060°N); (4) Heritage Farm, Iowa (43.382°N); (5) Randeen Ridge, Minnesota (48.479°N); (6) Buffalo Lake, Manitoba (53.410°N); and (7) Goose Greek Road, Churchill, Manitoba (58.709°N) (Table 1; Supplementary Table 2). This transect spans a wide range in average annual temperatures (−6.5 to +21.2°C), precipitation amount (276 mm to 1271 mm), and weighted average annual precipitation $\delta^{18}O$ values (−17.5 to −3.0‰), while keeping average annual RH values relatively high (~69–76%). At each sampling site, snails were collected by hand for larger shells and litter sampling for smaller taxa from representative 100–1000 m^2 areas (Nekola, 2003). Soil litter sampling was primarily used as it provides the most complete assessment of site faunas (Oggier et al., 1998). As suggested by Emberton et al. (1996), collections were made at places of high micromollusk density, with a constant volume of soil litter of ~4 L being gathered at each site (Nekola, 2014).

Relevant climatic variables including mean annual temperature (MAT), precipitation amount (in millimeters), and average annual RH were gathered from data reported at the U.S. Climate Data website (www.usclimatedata.com) and the Canadian Climate Normals website (http://climate.weather.gc.ca/climate_normals/index_e.html). Oxygen isotope values of mean annual and monthly precipitation were obtained from the Online Isotopes in Precipitation Calculator of the Isoscapes website (http://wateriso.utah.edu/waterisotopes/pages/data_access/oipc.html) (Bowen, 2018). The calculated precipitation $\delta^{18}O$ values are derived from global data sets and equations presented and discussed in Bowen and Wilkinson (2002), Bowen and Revenaugh (2003), and Bowen et al. (2005).

Land snail species

Ideally, the same taxon would be collected at each site to minimize isotopic variability derived from variations in species-specific behavior, diet, resistance to dryness, mobility, and

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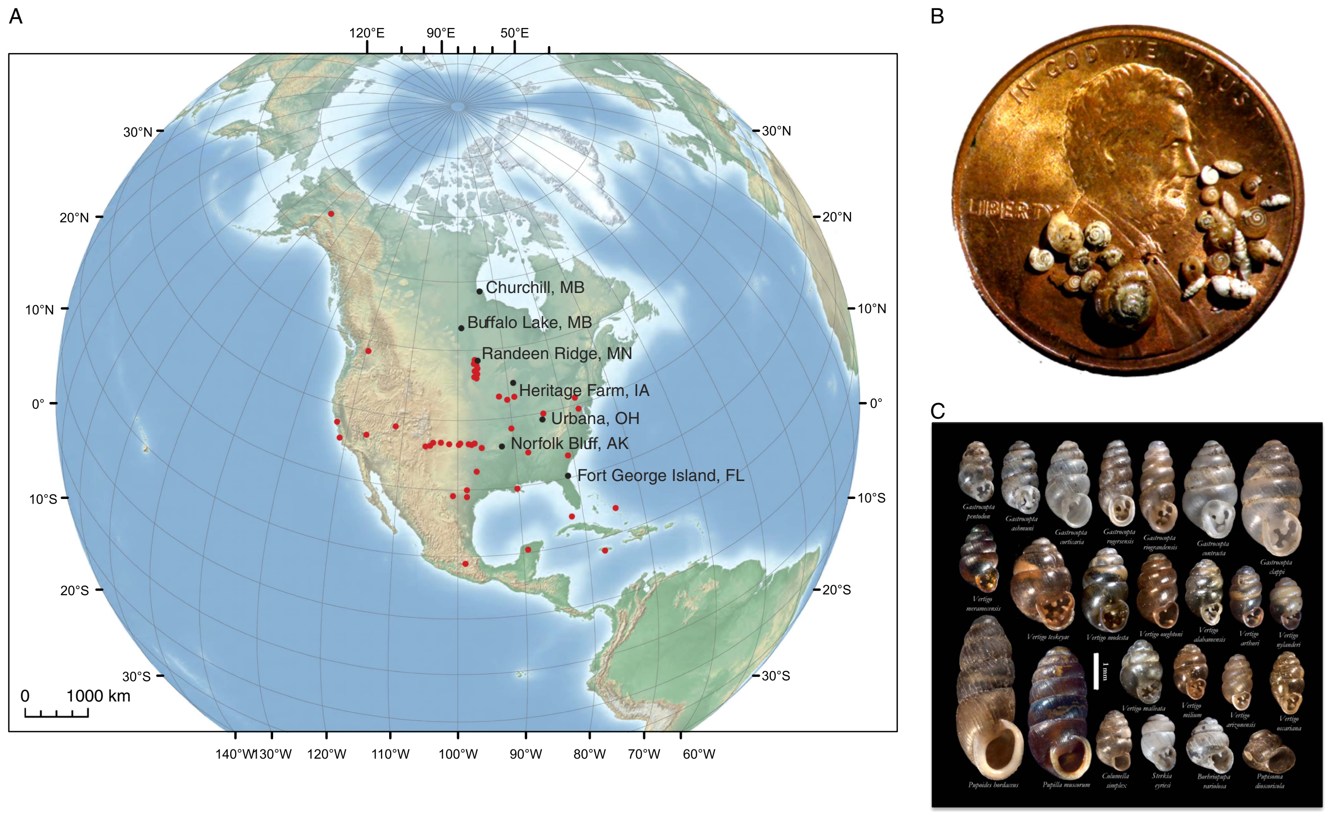

Figure 2. (A) Geographic locations of field-collected modern land snails from North America. Black dots depict new data presented in this study, and red dots represent data of modern snails from previously published work in North America. (B) General view of small land snails from North America on a penny as scale. (C) Detailed view of several species of *Gastrocopta*, a highly abundant genus found in modern settings and the fossil record across North America. Scale bar = 1 mm. Note that the majority of land snails used in this study are categorized as small taxa, with a shell length <10 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

perhaps vital effects (Yanes et al., 2017). However, in studies with a large spatial coverage, like the one presented here, this is not possible because the taxonomic composition of snail assemblages varies tremendously between the tropics and the Arctic. Thus, we collected and analyzed a variety of species encountered during our field sample collection, and focused on analyzing the smaller taxa of the assemblages collected. Twenty-two taxa were collected for isotopic analysis along the latitudinal transect, including *Anguispira alternata*, *Cochlicopa lubricella*, *Discus catskillensis*, *Euconulus fulvus*, *Gastrocopta contracta*, *Glyphyalinia umbilicata*, *Hawaiia minuscula*, *Helicina orbiculata tropica*, *Helicodiscus parallelus*, *Hendersonia occulta*, *Nesovitrea binneyana*, *Nesovitrea dalliana*, *Oxyloma verrilli*, *Polygyra lithica*, *Polygyra pustula*, *Pupilla muscorum*, *Pupoides albilabris*, *Rabdotus dealbatus*, *Succinea strigata*, *Succinea* sp., *Vallonia gracilicosta*, and *Vertigo modesta modesta* (Supplementary Table 1). Although these taxa exhibit significant differences in behavior, mobility, body size, and dietary habits and, consequently, will probably differ in oxygen isotope values (Yanes et al., 2017), we hypothesize that over broad spatial (latitudinal) scales, environmental variations will be large enough to overwhelm species-specific variations that can be significant at the microhabitat and habitat scales. Additionally, even though snails from low latitudes will likely exhibit longer active periods throughout the year than individuals from higher (colder) latitudes (Gaitán-Espitia and Nespolo, 2014), we further hypothesize that oxygen isotope shell data will reflect similar aspects of local environmental conditions.

Laboratory analyses

We analyzed a total of 112 entire shells with an average shell size of about 3 mm. Snail bodies were removed from the shells, which were then rinsed in deionized water and subjected to ultrasonication to remove organic and detrital contaminants. This procedure was repeated multiple times until all detritus adhering to the shell had been removed. Shell samples were also treated with 6% sodium hypochlorite (NaOCl) for 48 hours at room temperature to remove all remnants of adhering organic materials. Cleaned and treated shells were then crushed in an agate mortar and pestle and carefully homogenized. An aliquot of each pulverized shell (~150 μg) was then loaded into 12 mL Exetainer vials and analyzed at the stable isotope laboratory at the University of Northern Illinois where vials were flushed with helium, reacted with 100‰ phosphoric acid (H_3PO_4), and equilibrated at room temperature for 24 hours. They were then analyzed with a GasBench II and a MAT 253 stable isotope ratio mass spectrometer. Isotope measurements were calibrated using National Bureau of Standards (NBS)-19 and

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NBS-18 international standards. Results are described using δ notation relative to the international standard Pee Dee Belemnite. Analytical precision was ±0.1‰ for $\delta^{18}O$ and ±0.08‰ for $\delta^{13}C$ (1-sigma) based on the repeated measurements of NBS-19 and NBS-18 standards throughout a sequence.

Statistical analyses

All statistical analyses were performed using PAST 3.12 software (Hammer et al., 2001) considering statistical significance at $\alpha = 0.05$. Pearson correlation was conducted to assess the significance of monotonic relationships between two variables. Regression equations were computed to determine the slope and, therefore, the lapse rate of change of the dependent variable (shell $\delta^{18}O$) with respect to changes in relevant independent variables (i.e., latitude, longitude, altitude, meteoric precipitation $\delta^{18}O$, precipitation amount, air temperature, and RH; Tables 1 and 2). It should be noted that many of the examined variables are correlated with each other across the studied sampling sites. However, each environmental variable was compared with snail shell $\delta^{18}O$ separately and discussed in the text.

RESULTS

Transect from Florida to Manitoba (this study)

The oxygen isotope values of modern land snails from the sampled transect ranged from −9.5‰, for a *Vallonia gracilicosta* shell collected in Buffalo Lake, Manitoba, to +1.1‰, for a *Polygyra pustula* shell from Fort George Island, Florida, for the 112 individual shells analyzed (Supplementary Table 1). Average values for the seven sampling sites ranged from −1.3 ± 0.8‰ (n = 16) for the Fort George Island site in Florida (30.4°N) to −8.7 ± 0.5‰ (n = 13) for the Buffalo Lake site (53.4°N) in Manitoba (Table 1).

Average $\delta^{18}O$ values for each site decrease 0.3‰ for every 1° increase in latitude (Fig. 3A), which reflects the influence of both a decrease in precipitation $\delta^{18}O$ values and cooler air temperatures with increasing latitude. Shell $\delta^{18}O$ values did not show a relationship with altitude (Fig. 3B) likely because all samples were collected at sites below 400 m asl.

Latitude, precipitation $\delta^{18}O$, precipitation amount, and air temperature were all highly correlated with each other ($P << 0.01$), whereas RH, longitude, and elevation did not show correlations with each other or with other climate parameters ($P > 0.05$).

Shell $\delta^{18}O$ values increased at the rate of 0.5‰ for every 1‰ increase in average annual precipitation $\delta^{18}O$ values (Fig. 3C). This marked positive correlation ($R^2 = 0.89$; $P = 0.001$) suggests that 89% of the shell $\delta^{18}O$ variability can be explained by variations in precipitation $\delta^{18}O$ values alone. When considering climate data during snail active periods (i.e., activity during months with average air temperatures between 10°C and 27°C), shell $\delta^{18}O$ values increase at the rate of 0.7‰ for every 1‰ increase in snail "active period" precipitation $\delta^{18}O$ values (Fig. 3D). The relationship between both variables remained significant ($R^2 = 0.84$; $P = 0.004$). Shell $\delta^{18}O$ values increase by 0.3‰ for every 1°C increase in

Table 1. Site-average oxygen stable isotope values of land snails from North America and relevant instrument climate data. Geographic locations of these sites are indicated as black dots in Figure 2. m asl, meters above sea level; PDB, Pee Dee belemnite; RH, relative humidity; SMOW, standard mean ocean water.

						Mean annual values				Snail active period values[c]		
Locality	Latitude (°N)	Longitude (°W)	Altitude (m asl)	n	Snail shell $\delta^{18}O$‰ (PDB)	T (°C)[a]	P (mm)[a]	Precipitation $\delta^{18}O$‰ (SMOW)[b]	RH (%)[a]	T (°C)[a]	P (mm)[a]	Precipitation $\delta^{18}O$‰ (SMOW)[b]
Fort George Island, Florida	30.4	81.4	1	16	−1.3 ± 0.8	21.2	1271	−3.0	72.1	21.2	1271	−3.0
Norfolk Bluff, Arkansas	36.2	92.3	183	6	−1.3 ± 1.2	15.8	1247	−5.5	69	19.5	937	−4.0
Cedar Bog Preserve, Ohio	40.0	83.8	330	21	−5.2 ± 1.3	10.2	1060	−8.0	70.4	17.4	708	−4.9
Heritage Farm, Iowa	43.4	91.8	350	12	−3.7 ± 0.6	8.8	876	−6.8	70.8	16.9	698	−5.4
Randeen Ridge, Minnesota	48.6	95.6	357	16	−5.8 ± 0.7	2.6	527	−11.7	72.4	15.7	379	−7.8
Buffalo Lake, Manitoba	53.4	99.3	243	13	−8.7 ± 0.5	0.6	361	−15.8	71	13.7	292	−11.3
Churchill, Manitoba	58.7	94.1	29	28	−7.6 ± 0.9	−6.5	276	−17.5	76.1	9.6	236	−12.6

[a]Data from U.S. Climate Data site (www.usclimatedata.com) and Canadian Climate Normals site (http://climate.weather.gc.ca/climate_normals/index_e.html).
[b]Data calculated from the Online Isotopes in Precipitation Calculator (http://wateriso.utah.edu/waterisotopes/pages/data_access/oipc.html).
[c]Snail active period values were calculated for months with mean air temperatures between 10°C and 27°C.

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Table 2. Site-average of published (1979–2018) oxygen stable isotope values of land snails from North America and relevant instrument climate data. Geographic locations of these sites are indicated as red dots in Figure 2. m asl, meters above sea level; PDB, Pee Dee belemnite; RH, relative humidity; SMOW, standard mean ocean water.

Locality	Latitude (°N)	Longitude (°W)	Altitude (m asl)	Snail shell δ^{18}O‰(PDB)		T (°C)	P (mm)	Precipitation δ^{18}O‰ (SMOW)[a]	RH (%)	Reference
McDaniel, OK	36.15	95.99	375	−2.2	±0.8	15.9	1039	−5.9	71.5	Balakrishnan et al. (2005b)
C.S. Ranch, NM	36.48	104.80	1940	−2.0	±0.0	9.6	452	−8.4	50	Balakrishnan et al. (2005b)
Chase, NM	36.55	104.92	2184	−2.5	±1.0	9.6	452	−8.6	50	Balakrishnan et al. (2005b)
Salt Fork, OK	36.64	97.59	320	−1.9	±0.3	13.8	895	−5.9	69.5	Balakrishnan et al. (2005b)
Hitch, OK	36.70	101.49	881	−1.8	±0.9	13.7	489	−6.4	69.5	Balakrishnan et al. (2005b)
Kubic, OK	36.71	97.09	353	−1.9	±0.7	14.9	886	−5.9	69.5	Balakrishnan et al. (2005b)
Skull Springs, OK	36.71	99.89	671	−1.6	±0.7	15.3	665	−6.4	69.5	Balakrishnan et al. (2005b)
Big Salt Plain, OK	36.74	98.14	482	−0.4	±0.8	14.8	829	−6.3	69.5	Balakrishnan et al. (2005b)
Burnham, OK	36.84	99.63	594	−1.1	±1.1	15.3	665	−6.2	69.5	Balakrishnan et al. (2005b)
Owensby, NM	36.90	104.44	2288	−2.0	±1.0	10.1	482	−9.0	51	Balakrishnan et al. (2005b)
Black Mesa, OK	36.93	103.00	1312	−2.2	±0.9	13.1	477	−7.1	69.5	Balakrishnan et al. (2005b)
San Salvador Island, Bahamas	24.00	74.47	10	−0.7	±0.8	25.0	669	−2.7	78	Baldini et al. (2007)
Del Rio, TX	29.36	100.90	296	−1.8	±1.1	21.4	496	−4.0	67	Goodfriend and Ellis (2002)
San Antonio, TX	29.42	98.48	202	−1.7	±1.0	20.4	836	−3.7	70.5	Goodfriend and Ellis (2002)
Rocky Creek, TX	30.25	98.53	413	−1.7	±1.8	21.2	1047	−4.3	71.5	Goodfriend and Ellis (2002)
Dallas, TX	32.77	96.80	139	−2.2	±0.9	18.0	1040	−4.3	71.5	Goodfriend and Ellis (2002)
Las Vegas, NV	36.93	116.45	2440	−2.6	±1.8	8.7	273	−14.2	36.0	Sharpe et al. (1994)
Barnesville, MN	46.72	96.29	345	−5.3	±0.7	2.6	527	−10.4	72.4	Yanes et al. (2017)
Bluestem Prairie, MN	46.85	96.48	298	−6.0	±1.2	2.6	527	−10.4	72.4	Yanes et al. (2017)
Callaway, MN	47.07	95.92	386	−4.6	±1.4	2.6	527	−11.0	72.4	Yanes et al. (2017)
Waubun, MN	47.17	95.92	384	−6.5	±1.1	2.6	527	−11.1	72.4	Yanes et al. (2017)
Eastlund, MN	47.44	95.78	391	−6.3	±1.2	2.6	527	−11.3	72.4	Yanes et al. (2017)
Huot Forest, MN	47.87	96.42	293	−5.9	±1.1	2.6	527	−10.9	72.4	Yanes et al. (2017)
Oak Ridge, MN	48.15	96.36	341	−5.8	±0.8	2.6	527	−11.0	72.4	Yanes et al. (2017)
Strathcona, MN	48.53	96.23	343	−5.3	±0.7	2.6	527	−11.3	72.4	Yanes et al. (2017)
Halma Swamp, MN	48.66	96.67	293	−6.3	±0.8	2.6	527	−11.1	72.4	Yanes et al. (2017)
Beaches, MN	48.84	96.43	305	−6.1	±0.6	2.6	527	−11.4	72.4	Yanes et al. (2017)
San Salvador, Bahamas	24.00	74.47	10	−0.4	±0.5	25.0	669	−2.7	78	Yanes (2015)
Fairbanks, AK	64.83	147.72	136	−10.8	±0.5	−2.5	275	−18.7	65	Yanes (2015)
Mexico City, Mexico	19.40	99.12	2167	−5.1		25.0	1185	−9.0	74.7	Yapp (1979)
Yucatan, Mexico	20.70	89.08	11	−2.1	±1.3	25.0	1185	−3.2	74.7	Yapp (1979)
New Orleans, LA	29.95	90.07	1	−0.9		20.9	1613	−3.5	77	Yapp (1979)
Orangeburg, SC	33.48	80.85	75	−1.1	±0.6	17.2	1193	−4.4	68.5	Yapp (1979)
Taos, NM	36.40	105.57	1922	−0.3		8.4	313	−9.2	50	Yapp (1979)
Sevier, UT	38.79	111.33	1997	−2.02		6.7	201	−14.2	50	Yapp (1979)
Clermont, OH	39.08	84.18	297	−2.4		12.6	1073	−7.6	75.5	Yapp (1979)
Mineral Point, WI	42.85	90.18	256	−3.3		7.4	968	−6.8	78	Yapp (1979)
Jefferson, WI	43.00	88.80	323	−2.1	±0.3	8.4	867	−7.4	78	Yapp (1979)

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Table 2. (*Continued*)

Locality	Latitude (°N)	Longitude (°W)	Altitude (m asl)	Snail shell $\delta^{18}O$‰(PDB)		T (°C)	P (mm)	Precipitation $\delta^{18}O$‰ (SMOW)[a]	RH (%)	Reference
Menominee, WI	45.02	88.73	168	–4.3		4.8	742	–9.5	75.5	Yapp (1979)
Lower Grand Coulee, WA	48.68	119.68	1900	–5.8		7.9	318	–16.8	80.5	Yapp (1979)
Santeetlah Creek, NC	35.34	83.84	710	–1.5	0.7	13.9	1387	–6.7	76	Yanes et al. (2018)
Santeetlah Creek, NC	35.34	83.84	800	–1.8	1.2	13.1	1387	–6.9	76	Yanes et al. (2018)
Santeetlah Creek, NC	35.34	83.84	845	–1.4	0.5	12.6	1387	–7.0	76	Yanes et al. (2018)
Santeetlah Creek, NC	35.34	83.84	910	–1.9	0.8	12.0	1387	–7.1	76	Yanes et al. (2018)
Santeetlah Creek, NC	35.34	83.84	1010	–2.1	0.7	11.1	1387	–7.3	76	Yanes et al. (2018)
Santeetlah Creek, NC	35.34	83.84	1135	–1.8	0.8	9.9	1387	–7.6	76	Yanes et al. (2018)
Santeetlah Creek, NC	35.34	83.84	1310	–2.0	0.8	8.2	1387	–8.0	76	Yanes et al. (2018)
Santeetlah Creek, NC	35.34	83.84	1620	–2.1	0.8	5.3	1387	–8.7	76	Yanes et al. (2018)
Jamaica	18.13	77.27	333	–0.3	±0.6	29.0	1800	–4.4	74.8	Zaarur et al. (2011)
Stock Island, FL	24.54	81.74	1	–1.6		25.4	1010	–2.6	75	Zaarur et al. (2011)
Florence, AL	34.82	87.66	167	–1.1		15.7	1437	–5.0	75	Zaarur et al. (2011)
San Simeon, CA	35.64	121.19	70	–0.6	±0.1	15.5	734	–6.2	72.5	Zaarur et al. (2011)
Palo Alto, CA	37.74	122.24	10	0.8	±0.5	14.7	411	–7.4	76	Zaarur et al. (2011)
St. Louis, MO	38.63	90.20	140	–2.1		12.9	1095	–6.5	75.5	Zaarur et al. (2011)
Washington, D.C.	39.50	77.05	20	–2.9		13.2	1036	–7.0	66	Zaarur et al. (2011)
Philadelphia, PA	41.23	77.18	335	–1.5		11.1	884	–9.5	67.5	Zaarur et al. (2011)
East Saginaw, MI	43.23	84.70	260	–3.6		8.4	867	–9.0	76	Zaarur et al. (2011)

[a]Data calculated from the Online Isotopes in Precipitation Calculator (http://wateriso.utah.edu/waterisotopes/pages/data_access/oipc.html).

MAT (Fig. 3E). Both variables are strongly correlated ($R^2 = 0.83$; $P = 0.005$). Snail shell $\delta^{18}O$ values are also significantly correlated with snail active period temperature ($R^2 = 0.77$; $P = 0.009$), increasing by 0.7‰ for every 1°C increase in snail active period temperature (Fig. 3F). Site-averaged land snail $\delta^{18}O$ values increase by 1‰ for every 100 mm increase in precipitation amount (Fig. 3G and H). In contrast to a previous study conducted in North America (Yapp, 1979), no relationship was observed between the oxygen isotope offset ($\mathbf{\Delta}^{18}O$) of the calculated $\delta^{18}O$ snail body fluid and average annual precipitation $\delta^{18}O$ in isotopic equilibrium with the reciprocal of average annual RH (Fig. 3I and J), possibly because the high average annual RH values from all sites sampled in this study (all above 70%). All of these bivariate relationships remained statistically significant when only minute (<5 mm) taxa were considered.

Transect from Jamaica to Alaska (combined published work)

The monotonic relationships identified previously continue and are significant when combining our shell $\delta^{18}O$ values, which ranged from Florida to Manitoba, with previously published data from North America and the Caribbean, which span from Jamaica to Fairbanks, Alaska (Table 2, Fig. 4). Combining these data sets allows us to incorporate a much larger and contrasting range of habitats (from semiarid to wet woodlands), altitudes (from 1 to 2800 m asl), and snail species (from minute to very large species with variable ecologies and behaviors). In this larger data set, correlations between variables remain in many instances significant but display greater scatter (Fig. 4).

When all shell oxygen isotopic data are considered, shell $\delta^{18}O$ values decline 0.2‰ for every 1° increase in latitude (Fig. 4A and B), increase 0.5–0.6‰ for every 1‰ increase in average annual precipitation $\delta^{18}O$ value (Fig. 4C and D), and increase 0.2–0.3‰ for every 1°C increase in MAT (Fig. 4E and F). These bivariate relationships are all significant (see the R^2 and P values reported in Fig. 4). The only correlation that is no longer significant is the one between shell $\delta^{18}O$ values and annual precipitation amount (Fig. 4G and H). Finally, as before, no significant relationship was documented between the oxygen isotope offset ($\mathbf{\Delta}^{18}O$) of the calculated snail body fluid $\delta^{18}O$ and the average annual precipitation $\delta^{18}O$ with respect to the reciprocal of average annual RH (Fig. 4I and J).

DISCUSSION

Relationship between shell $\delta^{18}O$ values and instrument climate data

Land snail shell $\delta^{18}O$ values yielded significant and comparable best-fit linear regression equations when compared against both average annual climate data and expected snail active period climate data (Figs. 3 and 4)—that is, when air temperature is between 10 and 27°C, and RH is >70%. For simplicity, and to facilitate direct comparison with similar snail calibration studies elsewhere, the subsequent discussion focuses on average annual climate data.

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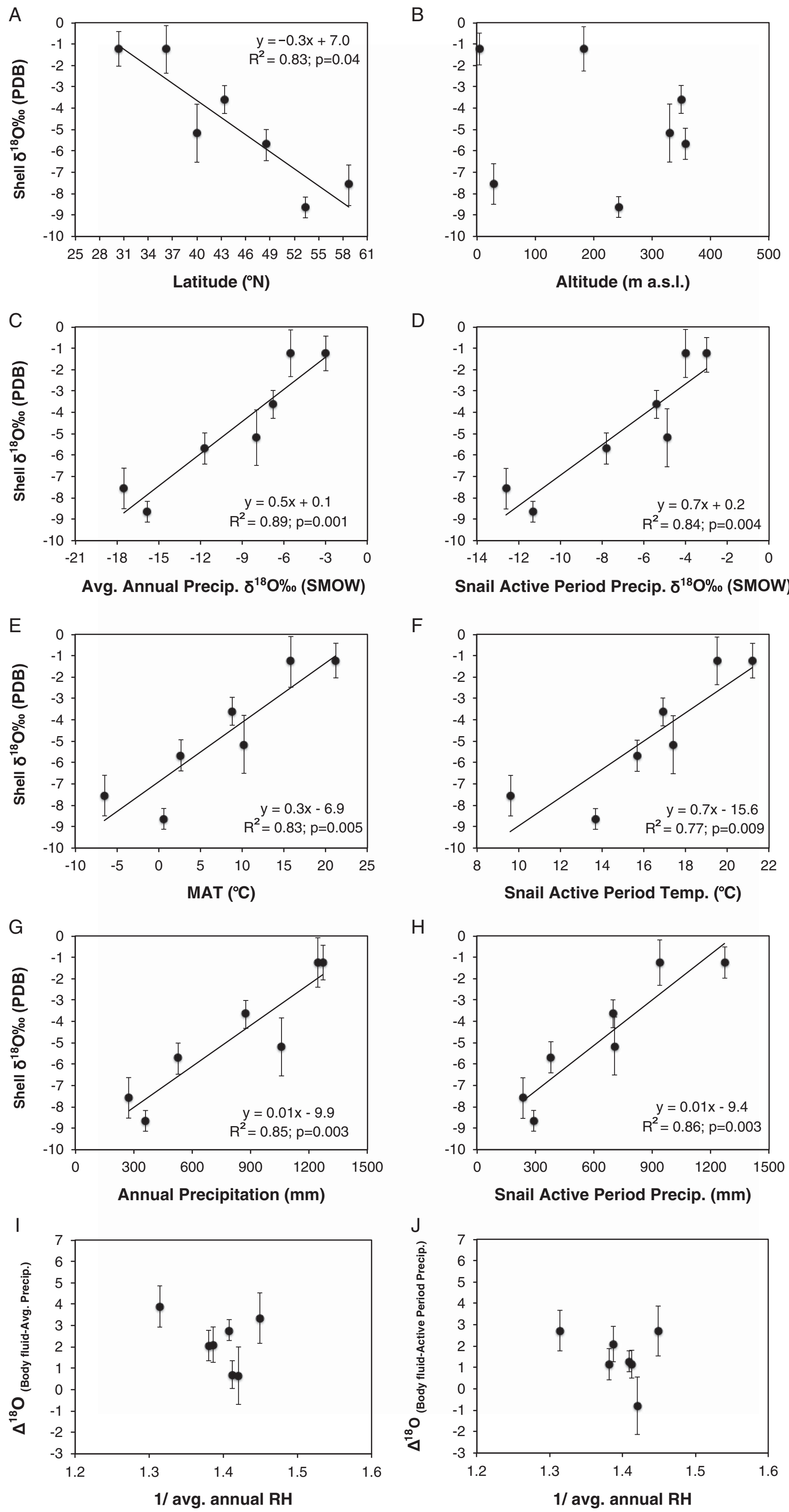

Figure 3. (A–J) Bivariate relationships between site-average shell $\delta^{18}O$ values and relevant instrument climate parameters from this study using all land snail taxa combined. m asl, meters above sea level; MAT, mean annual temperature; PDB, Pee Dee belemnite; RH, relative humidity; SMOW, standard mean ocean water.

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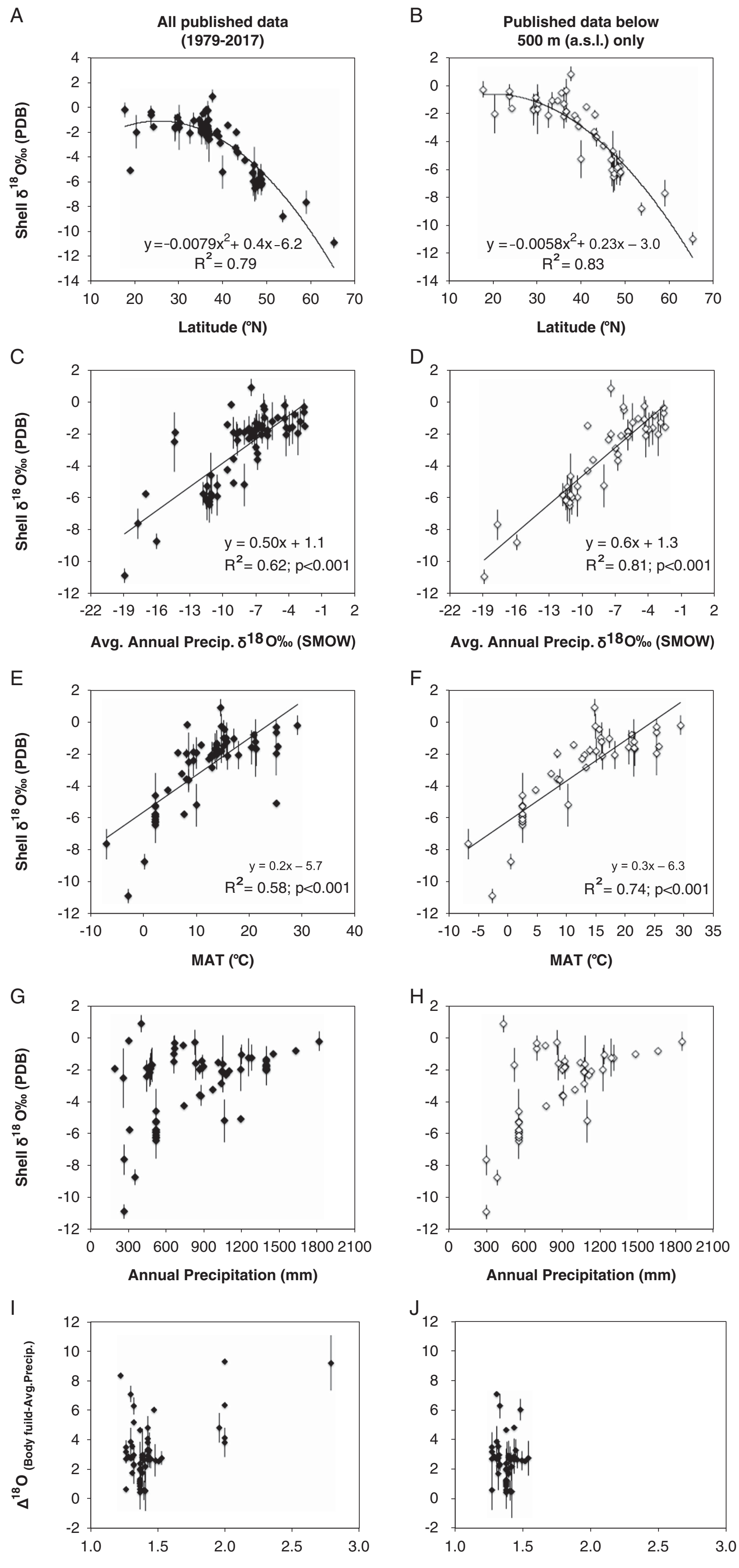

Figure 4. (A–J) Bivariate relationship between site-average land snail shell $\delta^{18}O$ and relevant instrument climate parameters from all published snail work in North America, including the new data presented in Figure 3. Left column includes all snail data, whereas right column shows data from below 400 m asl only. m asl, meters above sea level; MAT, mean annual temperature; PDB, Pee Dee belemnite; RH, relative humidity; SMOW, standard mean ocean water.

Data from our new latitudinal transect (between 30°N and 58°N) suggest that shell $\delta^{18}O$ values strongly correlate with average annual precipitation $\delta^{18}O$ (Fig. 3C). We obtained the following linear regression equation for our sites from Florida to Manitoba (between 30°N and 58°N) (Fig. 3C):

$$\delta^{18}O_{shell} = 0.5\,(\pm 0.08) \times \delta^{18}O_{precip.} - 0.1\,(\pm 0.9). \quad \text{(Eq.1)}$$

This equation is comparable to that obtained from the limited data reported by the only other large coarse-scale study in North America by Yapp (1979) for sites with RH >70%:

$$\delta^{18}O_{shell} = 0.43\,(\pm 0.12) \times \delta^{18}O_{precip.} - 0.4\,(\pm 0.8). \quad \text{(Eq.2)}$$

The relationship was similar when all published data from North America and the Caribbean (between 18°N and 64°N) are combined (Fig. 4C):

$$\delta^{18}O_{shell} = 0.5\,(\pm 0.05) \times \delta^{18}O_{precip.} - 1.1\,(\pm 0.5). \quad \text{(Eq.3)}$$

The slopes of these regression equations for North America are comparable to those obtained from modern land snails collected in other regions of the world, including central Europe (Lécolle, 1985), the Italian Peninsula (Zanchetta et al., 2005), and Libya (Prendergast et al., 2015), which range between 0.5 and 0.8.

From these equations, we can infer that at broad spatial scales (1) land snail shell $\delta^{18}O$ values primarily track variations in meteoric precipitation $\delta^{18}O$ and (2) shell $\delta^{18}O$ values increase at a lapse rate of 0.5‰ for every 1‰ increase in average annual precipitation $\delta^{18}O$ values (Fig. 3C and D; Fig. 4C and D). The slight differences with respect to other calibration studies from different regions of the world suggest that the relationship between the $\delta^{18}O$ values of shell and average annual precipitation may be region specific, as previously proposed (Prendergast et al., 2015), and also may vary with the spatial scale and range of environments considered. In future studies in North America, the scientific community will be able to collect more data from underinvestigated regions and test the applicability of these equations (Eqs. 1 and 2). New data from different locales will reveal the presence or absence of correlations between shell $\delta^{18}O$ and environmental variables noted herein. It is likely that additional data from high altitude and extreme environments are needed to generate equations that can be applied at the global scale.

On average, the calculated body fluid $\delta^{18}O$ values in isotopic equilibrium with water $\delta^{18}O$ values using the equation by Grossman and Ku (1986) are 0.6–3.8‰ higher than observed average annual precipitation $\delta^{18}O$ values per site (Fig. 3I and J). This offset is consistent with the majority of previous studies and suggests that snail shell aragonite is likely formed from snail body fluid that has undergone some evaporation (Yapp, 1979; Goodfriend et al., 1989; Balakrishnan and Yapp, 2004; Prendergast et al., 2015).

Our data also show that land snail shell $\delta^{18}O$ values also increase by 0.3‰ for every 1°C increase in average annual temperature (Fig. 3E). This lapse rate matches well with the known relationships between temperature and precipitation $\delta^{18}O$, and the effect of temperature on oxygen isotope fractionation between aragonite and water. For example, precipitation $\delta^{18}O$ values decrease, on average, 0.58‰ for every 1°C decrease of temperature (Rozanski et al., 1993). In contrast, the equilibrium $\delta^{18}O$ values of aragonite increase ~0.23‰ for every 1°C decrease in temperature (Grossman and Ku, 1986). Together, therefore, this should result in a 0.35‰ increase in the land snail shell $\delta^{18}O$ values for every 1°C increase in temperature (Balakrishnan et al., 2005b), a value that is similar to that observed in our study (see Fig. 3E).

We found that the relationship between shell $\delta^{18}O$ values and average annual temperature was similar when considering only small taxa as well as when we included all taxa regardless of body size. However, the rate increases to 0.7‰ for every 1°C increase in temperature when considering snail active period temperatures rather than average annual temperatures (Fig. 3F). These matching patterns illustrate that despite the complexities inherent to interpreting snail shell oxygen isotope data sets, it is clear that shell $\delta^{18}O$ values increase with increasing precipitation $\delta^{18}O$ values and increasing air temperatures. Thus, at broad spatial scales, higher shell $\delta^{18}O$ values could be interpreted as representing higher precipitation $\delta^{18}O$ values and warmer temperatures, whereas lower shell $\delta^{18}O$ values should generally depict lower precipitation $\delta^{18}O$ values and cooler conditions, although species-specific variations should probably be considered at the habitat and microhabitat scales (Yanes et al., 2017).

The evaporative steady-state flux balance model by Balakrishnan and Yapp (2004) suggests that shell $\delta^{18}O$ values should decrease by 0.4‰ for every 1% increase in RH if all other climatic parameters stay constant. Our data (Fig. 3I and J), as well as combined published data (Fig. 4I and J), did not show a conclusive relationship between the isotopic offset of snail body fluid $\delta^{18}O$ and average annual precipitation $\delta^{18}O$ against the reciprocal of average annual RH. Further research is still needed to effectively assess the effects of RH variations on land snail shell $\delta^{18}O$ values across species, biomes, and spatial scales. We hypothesize that at high elevations characterized by extremely cold and dry conditions, where absolute humidity is low, as well as in desert environments, RH will play an important role in determining shell $\delta^{18}O$ values (see Fig. 5) (see also Yanes et al., 2009).

Figure 5 summarizes the theoretical relationship between average annual precipitation $\delta^{18}O$ and land snail shell $\delta^{18}O$ along the total range of continental environments. Our predictions suggest that at coarse scale, multiple species of land snails growing shells in tundra, taiga, temperate forest, and grassland biomes should primarily record ^{18}O-enriched body fluid $\delta^{18}O$ values in isotopic equilibrium with average annual precipitation $\delta^{18}O$ values (Fig. 5). However, in environments with extreme dryness (e.g., deserts, high elevations) or that are extremely cold (e.g., polar latitudes, high elevations), we expect that shell $\delta^{18}O$ values will be higher than predicted relative to the relationship of shell and precipitation $\delta^{18}O$ values at other biomes with milder environmental conditions

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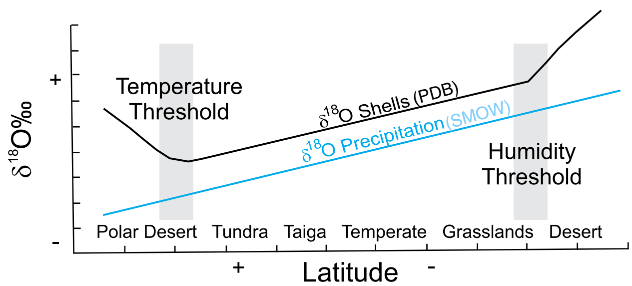

Figure 5. (color online) Theoretical relationship between $\delta^{18}O$ values of land snail shell carbonate and major continental biomes. The relation between shell $\delta^{18}O$ values and latitude is predicted to be nonlinear in cold (average $T < 0°C$) and relatively dry (average $RH < 50\%$) regions. PDB, Pee Dee belemnite; RH, relative humidity; SMOW, standard mean ocean water.

(Fig. 5). These hypotheses should be tested in future snail research investigations.

Processes driving snail shell $\delta^{18}O$ spatial patterns

Bowen and Wilkinson (2002) evaluated global patterns of meteoric precipitation $\delta^{18}O$ values using empirical and theoretical data and found that variations in global precipitation $\delta^{18}O$ values versus latitude are best explained by variations of air temperature following a Rayleigh fractionation process between liquid water and water vapor (Dansgaard, 1964). Thus, the relationship between global precipitation $\delta^{18}O$ values and latitude for low-altitude stations (<200 m asl) was best described by a second-order polynomial equation (Eq. 4) depicting the nonlinear relationship between latitude and temperature, which, in turn, is amplified by the negative relationship between annual precipitation amount and precipitation $\delta^{18}O$ values in the tropics (Rozanski et al., 1993; Bowen and Wilkinson, 2002).

$$\delta^{18}O_{\text{global precip.}} = -0.0051\,(\text{Latitude})^2 + 0.1805(\text{Latitude}) - 5.247 \qquad (\text{Eq.4})$$

When this global meteoric precipitation $\delta^{18}O$ equation (Eq. 4) is compared with the equation obtained from all low-altitude published snail shell $\delta^{18}O$ values in North America along latitude (Eq. 5), we can observe a strong match between both data sets at the considered spatial scale (Fig. 6).

$$\delta^{18}O_{\text{shell}} = -0.0056(\text{Latitude})^2 + 0.2178(\text{Latitude}) - 2.737 \qquad (\text{Eq.5})$$

The striking match between global meteoric precipitation and snail shell $\delta^{18}O$ values along latitude further reinforces that multitaxa land snail shells can be used as paleoprecipitation $\delta^{18}O$ proxies at large spatial scale, at least for low altitude (<400 m asl) settings. Additional research along elevation gradients, desert and polar regions (Fig. 5), and areas with strong water vapor masses transport need additional research to further examine factors and mechanisms controlling snail shell $\delta^{18}O$ values (see also Bowen and Wilkinson, 2002).

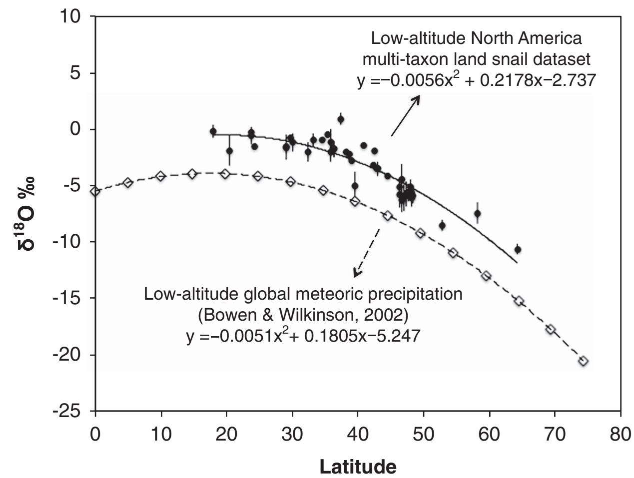

Figure 6. Comparison between $\delta^{18}O$ values of global meteoric precipitation by Bowen and Wilkinson (2002) (in SMOW scale) and published multitaxon land snail shells from North America from low-altitude (<400 m) settings along latitude (in PDB scale). Note that both proxies show a remarkably similar distribution of $\delta^{18}O$ values as a function of latitude, reinforcing that low-altitude land snail shell $\delta^{18}O$ values mimic variations in meteoric precipitation $\delta^{18}O$ values. PDB, Pee Dee belemnite; SMOW, standard mean ocean water.

Interpreting glacial land snail shell $\delta^{18}O$ values

Oxygen isotope values of land snails have been used to infer climate conditions during the last glacial maximum (Kehrwald et al., 2010; Yanes et al., 2011b, 2013; Nash et al., 2018) and Younger Dryas (Yanes et al., 2012). Many of these studies have documented significantly higher shell $\delta^{18}O$ values than expected from present-day regression equations between mean annual meteoric precipitation $\delta^{18}O$ and shell $\delta^{18}O$ values. The effects of considerably low humidity during glacial times (as shown in Fig. 5) on shell $\delta^{18}O$ values and/or the impact of higher glacial seawater $\delta^{18}O$ values on meteoric precipitation $\delta^{18}O$ values have been proposed to explain these relationships (e.g., Yanes et al., 2011b). Accordingly, additional research on modern settings characterized by extremely cold and/or arid environments (e.g., high-elevation sites, deserts, high-latitude areas, etc.) may help to elucidate environmental controls on glacial or stadial snail shell $\delta^{18}O$ values in future paleoclimatic studies in North America.

FUTURE LAND SNAIL RESEARCH DIRECTIONS IN NORTH AMERICA

The review presented here has allowed us to identify some areas of investigation in land snail oxygen isotope research throughout North America and to propose some future directions in land snail studies.

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Spatial sampling deficiencies: Overall, there have been a reasonably large number of snail oxygen isotope studies conducted in eastern North America, covering middle latitudes (~30–58°N) and relatively humid environments (average RH >69%) (see Fig. 2A). In contrast, fewer studies have been conducted in the drier environments of the central and western United States (Fig. 2A). Tropical (<30°N) and high (>65°N) latitudes are still minimally surveyed, and future studies are necessary to assess the main climatic controls on snail shell $\delta^{18}O$ values for individuals living under more marginal or extreme environmental conditions (see hypotheses in Fig. 5). Sampling at high latitudes is especially important if fossil shells are to be used to infer past glacial or stadial environmental conditions, as these fauna are mostly restricted to high latitudes today.

Altitudinal gradient studies: The majority of published snail oxygen isotope data from North America have focused on areas of low elevation, generally below 400 m asl (see Table 2). Altitudinal gradients remain to be further investigated and can help to test the effects of decreasing air temperatures with increasing elevation on snail shell $\delta^{18}O$ values. This could be particularly useful to better interpret the oxygen isotope values of Pleistocene snail shells recovered from sites across North America, as the highest elevation sites may be able to act as analogs to glacial conditions in middle latitudes.

Time-series analysis: The bulk of the published work has focused on entire shell isotope analysis regardless of snail shell size or longevity, whereas time-series analysis along shell growth direction has been explored in just a few published studies so far (Supplementary Table 1). Entire shell analyses are probably the best approach for small snail species (<10 mm in shell length), as they are short lived and their shells are too small and thin to efficiently conduct high-resolution intrashell analyses. However, medium to large snail shells (>10 mm) from species that have lived longer lives (1 or more years), could also be further tested and investigated to measure seasonal variations along snail life span. Furthermore, intrashell isotope values of snail shells have the potential to offer relevant information about the season of land snail harvest when studying archaeological land snail shells (Yanes and Fernandez-Lopez-de-Pablo, 2017), much like marine shell midden research.

Laboratory-controlled experiments: growing snails under controlled conditions to monitor shell $\delta^{18}O$ values remain to be undertaken. Although four published studies have grown snails in the laboratory, these studies focused on carbon isotope values and snail diet. Future controlled experiments should attempt to monitor and quantify the effects of variations of water $\delta^{18}O$ values, RH, and ambient temperature on land snail shell $\delta^{18}O$ values.

Clumped isotopes: Thus far, three studies have measured clumped isotopes in land snail shells (Supplementary Table 1). These studies, although informative, suggest that additional research should be pursued because the combination of clumped isotopes and oxygen isotopes in land snail shells could provide more informed details about the environmental conditions at which snails grew their shells. Published clumped-isotope studies suggest that some snails appear to grow at warmer temperatures than environmental air temperatures, which also challenges the idea of land snails being fully ectothermic. This kind of research will be useful not only for paleoenvironmental investigations, but also to better understand land snail ecology, physiology, and behavior.

Multitaxon data sets: We have found that published studies sometimes focus on a single taxon, whereas others combine data from multiple species, especially in broader spatiotemporal-scale studies. A recent study by our research group (Yanes et al., 2017) showed that different taxa of small land snails living at the same sites in northwestern Minnesota (USA) exhibited significantly different shell $\delta^{18}O$ values. This likely reflects some combination of differing snail species ecologies, mobility habits, and/or microhabitat preferences. These results suggest that similar studies of modern snails should be undertaken for different regions and species of the world to assess the utility and potential limitations of multitaxa data sets. The data presented here, however, suggest that large spatial-scale studies may combine multiple species for paleoenvironmental reconstructions, but only if environmental variations are large enough to overwhelm species-specific variations that are significant at local or regional scales.

Quaternary continental paleoclimate studies: In mainland North America, isotopic studies involving ancient land snail shells have been conducted at archaeological sites (Yapp, 1979; Goodfriend and Ellis, 2000; Balakrishnan et al., 2005a; Paul and Mauldin, 2013), whereas the Quaternary fossil record of land snails has not been generally used for paleoclimatic reconstructions (but see Nash et al., 2018). This is surprising considering the vast abundance and accessibility of Quaternary shells preserved in loess, wetland, alluvial, colluvial, and fluvial deposits throughout North America (e.g., Pigati et al., 2004, 2010, 2013; Rech et al., 2012; Nash et al., 2018). Our calibration study presented here suggests that land snails from North America primarily track the oxygen isotope signature of the average annual precipitation in a predictive near-linear fashion, although we acknowledge that there is a significant scatter from snail data sets because of the influence of other parameters such as temperature, RH, water vapor, and variations in snail mobility habits and behavior. Nevertheless, fossil shells across North America may be an invaluable continental proxy to make semiquantitative inferences of precipitation $\delta^{18}O$ values during the Quaternary.

CONCLUSION

Land snail shells collected from a large range of middle latitude (30–58°N) sites across eastern North America exhibit $\delta^{18}O$ values that show a strong positive correlation with both meteoric precipitation $\delta^{18}O$ values and air temperature. Shell $\delta^{18}O$ increases at a lapse rate of 0.5–0.7‰ for every 1‰ increase in precipitation $\delta^{18}O$, and 0.3–0.7‰ per 1°C increase in temperature (for both average annual and active period values). These relations persist when solely minute species (<5 mm) are included, as well as when all snail taxa are considered, regardless of their body size, ecology, and ethology. Other environmental factors, such as RH or precipitation amount, seem to play only minor roles at coarse spatial scales. Accordingly, middle-latitude shell $\delta^{18}O$ values of small to minute species should be reliable semiquantitative proxies for precipitation $\delta^{18}O$ in mainland North America. Future investigations of land snail shells should include additional modern calibration studies in low and high latitudes, desert and cold environments, and along altitudinal gradients to gain a better understanding of the isotope systematics for snails living in extreme environments, which could reasonably resemble glacial or stadial scenarios and can help us to better interpret glacial shell $\delta^{18}O$ values extracted from the Quaternary fossil record of North America.

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SUPPLEMENTARY MATERIAL

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