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RESEARCH ARTICLE

Geology constrains biomineralization expression and functional trait distribution in the Mountainsnails

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Abstract

Aim: Geographic variation in metabolic resources necessary for functional trait expression can set limits on species distributions. For species that need to produce and maintain biomineralized traits for survival, spatial variation in mineral macronutrients may constrain species distributions by limiting the expression of biomineralized traits. Here, we examine whether *Oreohelix* land snails that express heavily biomineralized shell ornaments are restricted to $CaCO_3$ rock regions, if they incorporate greater amounts of $CaCO_3$ rock carbon in their shell than less biomineralized smooth forms, and if ornamentation increases shell strength.

Location: Western United States.

Taxon: *Oreohelix* land snails.

Methods: We used random forest classification models at multiple spatial resolutions to evaluate the contribution of topographic, vegetation, climate, and geologic variables in predicting the presence of heavily biomineralized shell ornaments across the range of *Oreohelix*. We then measured and compared shell biometric variables, $^{14}C/^{12}C$ ratios, and peak force for fracture for ornamented and smooth forms from calcareous and non-calcareous substrates.

Results: Distance to $CaCO_3$ rock was the most important variable in all models and closer proximity to $CaCO_3$ rock was associated with greater probability of local ornamentation classification. Pairwise comparisons of $^{14}C/^{12}C$ ratios in closely occurring ornamented vs. smooth population pairs revealed ornamented forms incorporate greater $CaCO_3$ rock carbon than smooth forms. Ornamented types measured in this study were generally heavier and required greater peak force for fracture than smooth forms, except when comparing ornamented forms to smooth forms sampled from $CaCO_3$ rock.

Main Conclusions: Biomineralization expression, species distribution, and trait function appear to be constrained by mineral supply in a highly diverse group of land snails. This trait-environment relationship provides a basis for future investigations of $CaCO_3$ macronutrient constraints on shell form and species distribution in other terrestrial molluscs and has a direct impact on the management of *Oreohelix* species.

KEYWORDS

calcareous rock, ecophysiological constraint, functional biogeography, land snail, ornamentation, random forest, resource availability

1 | INTRODUCTION

Determining how trait expression affects the distribution of species is one of the central goals of functional biogeography (Violle et al., 2014). One class of functional traits that have considerable utility for improving our understanding of functional biogeography are ecophysiologically constrained (EPC) traits: traits whose expression is modulated by the availability of limiting metabolic resources (i.e. macronutrients) in the environment. Such EPC traits can provide a direct link between earth science, organismal ecology, and biogeography which can enable predictive functional biogeography on a global scale (e.g. Zanne et al., 2018). However, most groups with proposed EPC traits lack spatially resolved ecological, physiological, or phenomic data necessary to determine how trait-environment relationships vary in broad spatial contexts (Chown & Gaston, 2016; Iversen et al., 2022; Madliger et al., 2021). Furthermore, many ecophysiological relationships have only been discovered or proposed in the last few years (Reihart et al., 2021; Welti et al., 2019) and their utility for functional biogeographic inference is still being explored (Lynn et al., 2022). As the distribution and concentration of many metabolic resources necessary for various EPC traits are forecasted to change over the next century (Brahney et al., 2013; Hurd et al., 2019; Mahowald et al., 2017), there is a need to study ecophysiological relationships across species and spatial scales to understand how biodiversity may respond to future resource dynamics.

It is common for biogeographic studies of functional traits to employ correlative distribution models to understand trait-environment associations (e.g. Wijas et al., 2022), while approaches combining correlative distribution models with field measurement data are not as prevalent. The latter approach has considerable utility for the study of macronutrient-dependent EPC traits. Macronutrients from different sources can possess distinct chemical or radiological signatures that can be used to track the path from macronutrient source to trait expression (Goodfriend & Stipp, 1983). This physiological information can be leveraged with measures of trait function to assess how macronutrient availability affects trait expression and performance (Egge & Aksnes, 1992; Pančić et al., 2019; Grønning & Kiørboe, 2020). Correlative distribution models may then be considered jointly with measures of trait function and macronutrient dependence to determine whether EPC traits show evidence of being mechanistically linked to macronutrient availability across the landscape. Any revealed mechanistic relationships may then provide insight into how EPC traits vary with macronutrient availability across species which share similar physiological constraints (Tréguer et al., 2018).

One of the most diverse EPC groups are calcifying organisms which utilize environmental Ca^{2+} and HCO_3^- to produce $CaCO_3$ structures necessary for survival (Murdock, 2020). While calcifiers are broadly limited by the availability of minerals to produce their calcareous structures, there is considerable variation in the degree biomineralization expression is modulated by mineral availability within calcifying groups (Figuerola et al., 2021; Goodfriend, 1986). This variation is particularly pronounced among land snails which acquire minerals from various sources (i.e. soil, rock, metabolic) to produce $CaCO_3$ shells (Barker, 2004; Goodfriend, 1986). Individual studies of communities and clades have demonstrated contrasting patterns of shell biomineralization and mineral supply with some land snail groups expressing highly biomineralized or thick shells only in calcareous environments (e.g. calcareous rock habitats; Alonso et al., 1985; Teshima et al., 2003) while other species may express as thick shells as many calcareous resident species in anecdotally reported calcium deficient habitats (i.e. rainforests; Cowie & Robinson, 2003). Much of this variation is likely attributable to differences in mineral requirements as a result of ecological, physiological, and behavioural variation (Ohta & Saeki, 2020). However, an understudied potential contributor to spatial patterns of biomineralization is the degree that land snails access the available mineral resources in their habitat (Forman et al., 2021; Goodfriend, 1986). At calcareous rock sites, land snails can source as much as 33% of their shell carbon from 'dead carbon' in calcareous rock (Goodfriend & Stipp, 1983); however, dead carbon utilization is not uniform across calcareous rock resident species as many do not incorporate any dead carbon into their shells (Pigati et al., 2004, 2010). The ability of some species to utilize environmentally available minerals may result in lower costs of mineral acquisition compared to those species exclusively using metabolic carbon derived from their diet which may, in-turn, lower the cost for shell production and enable greater biomineralization expression. While the authors know of no energetic studies of shell formation in land snails to draw on, similar links between uptake costs and biomineralization output have been proposed in marine gastropods as higher fractions of metabolic carbon in the shell are associated with lower mineral availability and increased energetic costs of shell formation (Waldbusser et al., 2013; Baag & Mandal, 2022).

Differences in biomineralization costs between sites could serve as a basis for adaptive divergence in land snails and should be reflected in the biogeographic distribution of their traits. Sites with abundant and accessible mineral resources may permit thickened or elaborate forms which may better resist shell crushing predators (Quensen & Woodruff, 1997) or be favourable along another selection axis (e.g. water retention; Giokas, 2008). Snails residing at sites with limited access to mineral resources may favour a metabolically optimal phenotype which balances selection for thicker shells with the energy required for mineral acquisition. Under this proposed process, the distribution of heavily biomineralized phenotypes are expected to be constrained to mineral rich habitats while moderate to weakly biomineralized phenotypes may occupy habitats ranging from low to high mineral resource availability. Heavily biomineralized phenotypes may also be expected to have a larger fraction of carbon derived from environmental sources than weakly biomineralized phenotypes on similar resource availability substrates, which would reflect greater demands or ability to access environmental resources by heavily biomineralized phenotypes. While untested, this hypothesis may help to explain the repeated convergent evolution of shell forms and restricted distribution of many calcareous rock endemic land snail species (Clements et al., 2006).

In this study, we test the hypothesis that mineral availability constrains biomineralization effort in the Mountainsnails (genus:*Oreohelix*) from western North America. *Oreohelix* is a diverse and calciphilous genus of land snails that inhabit semi-arid to mesic montane regions spanning from southern Canada to Northern Mexico (Pilsbry, 1939). Many *Oreohelix* species possess thickened shell ornaments and are products of recent and independent divergence from closely occurring smooth-formed species (Linscott et al., 2020). Given that ornamented *Oreohelix* appear to predominately reside on calcareous rock sites (Frest & Johannes, 1997) and that ornamentation evolution has happened repeatedly across the range of the genus (Linscott et al., 2020), ornamentation may represent a resource-constrained trait that may be primarily expressed on mineral-rich calcareous rock. We evaluate this hypothesis by integrating correlative distribution models of shell form with carbon isotope data, shell biometric variables, and measures of shell strength for ornamented and smooth shell types. We expect that ornamented forms will be heavier in terms of size-standardized mass than smooth formed species, require greater force to fracture the shell, be generally limited in distribution to calcareous rock sites, and incorporate greater dead carbon from calcareous rock than smooth formed species.

2 | MATERIALS AND METHODS

2.1 | Study area and observational data

Oreohelix presence data were assembled from a combination of opportunistic observation datasets and dedicated field surveys from across the Western United States of America (USA) (see Supplementary Table S1 for number of presence and absence records and Supplementary Figure S1 for maps of presence and absence records). Absence points were taken from surveys conducted by the authors, private surveys conducted by local experts, or government surveys. Species records were classified as ornamented or smooth based on the presence of a keel or ribs on the outer surface of the shell using photographs when available or species classification (see Supplementary Table S2 for ornamentation classifications of species). Occurrence points with greater than 500 m uncertainty or that were separated by a distance lower than our environmental raster resolution (i.e. duplicates that occur in the same pixel) were removed and the remaining filtered presence/absence data were used for analysis. The effect of predictors (see below) on ornamentation expression was assessed using a dataset composed only of *Oreohelix* presence locations so that any relationships between predictors and ornamentation expression are not confounded by associations with general *Oreohelix* presence or absence. Models created for projecting the distribution of morphologies across the Western USA used all presence and absence data.

2.2 | Environmental data

As land snails are often microhabitat specialists whose distribution may not be accurately captured using coarse resolution predictors, we evaluated ornamented and smooth *Oreohelix* species classification and distribution at predictor spatial resolutions ranging from fine to coarse (90 m^2–1 km^2; Table 2) across the continental USA (100–125 W° Longitude). We chose predictor variables known to be associated with land snail distribution, morphology, and/or physiology from other studies: compound topographic index, elevation, slope, heat load index, LANDSAT July mean surface temperature, global horizontal irradiance, height above nearest drainage, horizontal distance to nearest drainage, normalized difference vegetation index (NDVI), tree canopy cover, soil clay percent, soil pH, distance to developed area, and distance to $CaCO_3$ rock (Supplementary Table S3). We removed predictors that were highly correlated ($r < 0.75$) with each other across resolutions and kept the remaining variables for subsequent analysis. Predictor variables were projected and resampled from their native resolution to the desired analytical resolution (i.e. 90 m^2, 250 m^2, or 1 km^2) using bilinear interpolation in ArcGIS pro v.2.6.0 (see Supplementary Note S1 for more details). Sites of ornamented or smooth types were used as absences in the reciprocal class's species distribution model if the site was from a dedicated survey and if the reciprocal class (i.e. smooth vs. ornamented) was not found at the site.

2.3 | Classification and distribution models

We used random forest (RF) classification models to determine the relative importance of predictors for *Oreohelix* classification and to generate distributional models of the two morphologies. In brief, RF is a machine learning classification and regression approach that is capable of handling complex relationships between predictors by integrating classifications across a multitude of binary decision trees generated from random perturbations of the original dataset (Breiman, 2001). This method commonly outperforms other model types for ecological classification tasks (Cutler et al., 2007) and identifying relevant variables associated with different classes (Fox et al., 2017). We created RF models through the 'randomForest' v.4.6–10 package (Liaw & Wiener, 2002) in R v.3.6.3 (R Core Team, 2020). RF models were tuned to try two variables at each split (mtry = 2) after initial tuning using the 'rfTune' function (Liaw & Wiener, 2002). We chose to use a high number of decision trees (ntrees =3000) in our RF models as this increases reproducibility between model runs (Kopp & Allen, 2021; Liaw & Wiener, 2002). As class imbalance in datasets can have substantial effects on RF model outputs (Barbet-Massin et al., 2012), we sampled an equal number of localities from the minority and majority classes from the full dataset equal to the total localities of the minority class when constructing each decision tree. Variable importance of each predictor was assessed through mean decrease in accuracy (MDA) and significance of each variable was measured using the 'rfPermute' v2.5 package (Archer, 2016). 'rfPermute' generates null distributions of variable importance metrics for each predictor through permuting the response variable (Archer, 2016). We generated variable importance metric null distributions using 100 permutations of the dataset and measured significance according to an alpha threshold of 0.05. All variables were significant for either Gini node impurity or MDA in all classification models and were retained for distribution models. We then examined how all models performed with or without the distance to $CaCO_3$ rock predictor by comparing model accuracy using out-of-bag (OOB) error estimates reported directly from RF.

It is often difficult to interpret directly how complex machine learning methods generate classifications from predictor values (i.e. they seemingly act as a 'black box'). To determine how predictors contribute to RF model classification, we used local interpretable model-agnostic explanation (LIME). LIME is a post-hoc interpretation method that fits a simpler local surrogate model that is of lesser complexity but greater interpretability for a limited area of the n-dimensional space defined by the predictor variables (Ribeiro et al., 2016; Ryo et al., 2021). Through LIME, we can examine how our RF models used predictors to generate class predictions at a given locality and evaluate whether different predictors change in importance across the diverse areas that *Oreohelix* occupy (Ryo et al., 2021). LIME was applied across sites spanning subregions of *Oreohelix* ornamentation presence and absence (Rocky Mountain North, Great Basin, and Southwest USA) on RF models that included the distance from $CaCO_3$ predictor. We used the 'explain' function in the 'lime' v.0.5.3 package, selecting the top five features with the highest weights and the remaining parameters on default settings (Ribeiro et al., 2016). We then generated loess smoothed partial dependence plots of distance to $CaCO_3$ rock for each model to examine whether resolution of this variable affected predicted model outputs using the R packages 'pdp' v.0.7.0 and 'ggpubr' v.0.6.0 (Greenwell, 2017; Kassambara & Kassambara, 2020).

Finally, we created distribution models using RF for both morphologies using all available presence and absence data and the same predictor variables as previous RF analyses. No pseudo-absence selection or background sampling was included for any model. RF distribution models used the same model parameters as the RF classification models (i.e. mtry, ntree, and class balanced sampling). RF distributional models were evaluated using OOB error estimates. Variable importance and significance for RF distributional models were assessed using MDA and 'rfPermute' (Archer, 2016).

2.4 | Radioisotope data and analysis

We conducted ^{14}C dating to determine the proportion of dead carbon used for shell formation in *Oreohelix*. One recently dead adult shell was selected for ^{14}C dating from 30 sites which span across *Oreohelix*'s range. We sampled 9 $CaCO_3$ rock and non-$CaCO_3$ pairs across 18 sites which occur in relatively close geographic proximity to each other (median distance: 2.82 km; range: 0.057–41.57 km). The remaining samples were chosen to capture geographic extremes of *Oreohelix*'s range ($n=6$) or for being smooth forms residing on calcareous rock ($n=6$). All snail shells were washed in deionized water repeatedly to ensure they were free of detritus and then dried in an oven overnight at ~70°C. Small shell fragments weighing approximately 0.015 g were then sampled from the far outer lip of each specimen to avoid ontogenetic bias in dead carbon incorporation (Forman et al., 2021). Fragments were shipped to Woods Hole Oceanographic Institution for sample weight standardization and ^{14}C dating using accelerator mass spectrometry on their MICADAS system (Synal et al., 2007). Fraction modern (F_m) was calculated for each sample by the Woods Hole Oceanographic Institution and represents the $^{14}C/^{12}C$ ratio in modern carbon corrected for isotopic fractionation and fossil fuel release of ^{14}C into the atmosphere (Supplementary Material Table S4). Calcareous rock has little to no ^{14}C due to radioactive decay and results in lower F_m ratios in proportion to its incorporation into snail shells (Goodfriend & Stipp, 1983). F_m may also be higher than 1.0 in land snails if land snails are consuming dead vegetation which was living during periods of higher atmospheric ^{14}C (Hua & Barbetti, 2004; Pigati et al., 2004). As organic sampling of detritus was not currently compatible with the MICADAS dating system at Woods Hole Oceanographic Institution and was not sampled during our field work, we were not able to compensate for this effect directly by measuring F_m for site detritus. However, pairwise sampling may mitigate this effect as these sites were chosen based on their close geographic proximity to each other and similar climatic conditions, which should be reflected in the decomposition rates and F_m of detritus at the semi-arid sites *Oreohelix* occupies (Cortez, 1998). We compared F_m across ornamented and smooth morphologies and calcareous and non-calcareous rock using a Welch's *t*-test and paired *t*-test in R (R Core Team, 2020).

2.5 | Shell biometric variables and crushing resistance

To measure differences in biomineralization effort in *Oreohelix*, we measured various shell biometric variables (e.g. mass, shell length, shell height; Supplementary Table S5) of ornamented and smooth snails. We measured shell biometric variables from five species of the *O. strigosa* species complex (*O. strigosa* sp. $n=25$, *O. strigosa goniogyra* $n=33$, *O. idahoensis* $n=18$, *O. haydeni hesperia* $n=33$) which represent all major ornamentation types within *Oreohelix* (smooth, commarginal ribs, antimarginal ribs, and keel; Supplementary Figure S3). We split *O. strigosa goniogyra* into smooth ($n=18$) and keeled ($n=15$) categories as this subspecies expresses keels on calcareous rock outcrops and a smooth rounded morphology elsewhere. Live adult and subadult snails were collected from May to July 2020 throughout the lower Salmon and Snake River drainages, ID, USA. Snails were euthanized by drowning in 5% EtOH for 24 h, then flash-boiled. Soft tissue was removed from the shell and the shells were left to dry for at least 48 h. After the drying period, we measured shell biometric variables using a mass scale (Mettle Toledo: AL104) and digital callipers (Mitutoyo ABS Digimatic Callipers: Model CD-6 ASX).

Shell integrity is a necessary function of the shell for land snail survival (Barker, 2004). Peak compressive force is closely linked to shell integrity (Barker, 2004) and generally increases per unit shell mass (Quensen & Woodruff, 1997). As ornamentation has been shown to increase shell strength in other land snail groups (Boettger, 1932; Quensen & Woodruff, 1997), ornamentation expression may lead to greater shell strength in *Oreohelix*. To investigate whether ornamentation is increasing shell strength in *Oreohelix*, we measured the peak force needed to fracture the shell laterally as this form of crushing allowed for consistent load placement across different shell shapes and ornamentation types. Shells were placed on a flat metallic surface and crushed laterally on the whorl just after the aperture using a Mark-10 Force Gauge (Model M5-100) and associated test stand (Model ES20). We recorded the peak compression force (N) required to break the shell. All variables were then log transformed and analysed using a one-way ANCOVA and a post-hoc pairwise comparison of estimated marginal means using the 'rstatix' v.0.7.2 package (Kassambara, 2020) to compare the differences between the mean mass of all ornamented types after controlling for shell height and width as covariates and evaluated significance at an alpha level of 0.05 after using a Bonferroni correction for multiple comparisons (Supplementary Tables S6 and S7). This same analysis was then repeated to compare shell strength among all ornamented types using shell mass as a covariate.

3 | RESULTS

3.1 | Model performance

RF classification and distributional models including the distance to $CaCO_3$ predictor consistently had lower OOB error estimates than those omitting this variable (Table 1). RF classification and distribution models showed a general trend of decreasing OOB error estimates with greater variable resolution (Table 1). Ornamented and smooth distribution models had lower OOB error estimates when including distance to $CaCO_3$ rock (Table 1).

3.2 | Variable importance and partial dependence plots

For all dataset resolutions and models of ornamented *Oreohelix* expression (i.e. classification or distribution models), distance from $CaCO_3$ rock was the most important predictor for classification and ornamented/smooth form presence (Table 2, Figures 1 and 2; Supplementary Table S8). This pattern was consistent across permutations of the RF model (Table 2). Partial dependence plots of the RF ornamentation classification model showed a declining ornamentation probability with greater distance from $CaCO_3$ rock but a reduction in the slope of decline as resolution increased (Figure 3). Ornamented distributional model partial dependence plots mirrored the classification model plots with decreasing ornamentation probability as distance to $CaCO_3$ rock increased (Figure 3). Distance from $CaCO_3$ rock variable importance declined with decreasing resolution but remained the most important variable for classification models and for predicting ornamented/smooth presence in all distribution models (Table 2).

Distance to $CaCO_3$ rock was also the most important variable for distribution models of smooth *Oreohelix* (Supplementary Table S8). Smooth *Oreohelix* partial dependence plots indicated that smooth form classification probability increased with increasing distance to $CaCO_3$ rock but increased with closer proximity to $CaCO_3$ rock for distributional models (Figure 3). However, this relationship was relatively minimal compared to ornamented species distribution models.

TABLE 2 Mean decrease in accuracy variable importance for RF classification models at different predictor resolutions. Predictors in bold are the most important predictors for that classification set.

	Variable importance		
Predictor	90 m^2	250 m^2	1 km^2
Soil pH	34.34	39.09	20.36
Soil clay content	34.30	30.96	20.76
Horizontal distance to nearest drainage	27.17	23.15	15.21
Height above nearest drainage	36.62	30.17	22.95
Compound topographic index	24.56	8.36	21.92
Global horizontal irradiance	39.11	27.00	6.47
Heat load index	38.73	36.51	25.40
Slope	40.22	26.45	30.82
Elevation	46.59	38.77	27.32
Normalized difference vegetation index	47.33	38.60	35.06
July mean land surface temperature	60.21	51.59	41.85
Distance to developed area	45.08	37.71	26.46
Distance to calcareous rock	**94.02**	**88.96**	**68.74**

TABLE 1 OOB error estimates for models at different predictor resolutions. Left values include the distance to $CaCO_3$ rock predictor and the right with that predictor removed.

	Out-of-bag error (%)		
Model	90 m^2	250 m^2	1 km^2
RF classification	17.03 / 19.29	17.60 / 20.64	18.00 / 20.90
RF ornamented distribution	13.72 / 15.69	14.64 / 17.36	14.94 / 18.56
RF smooth distribution	19.69 / 21.33	20.06 / 22.03	21.84 / 22.80

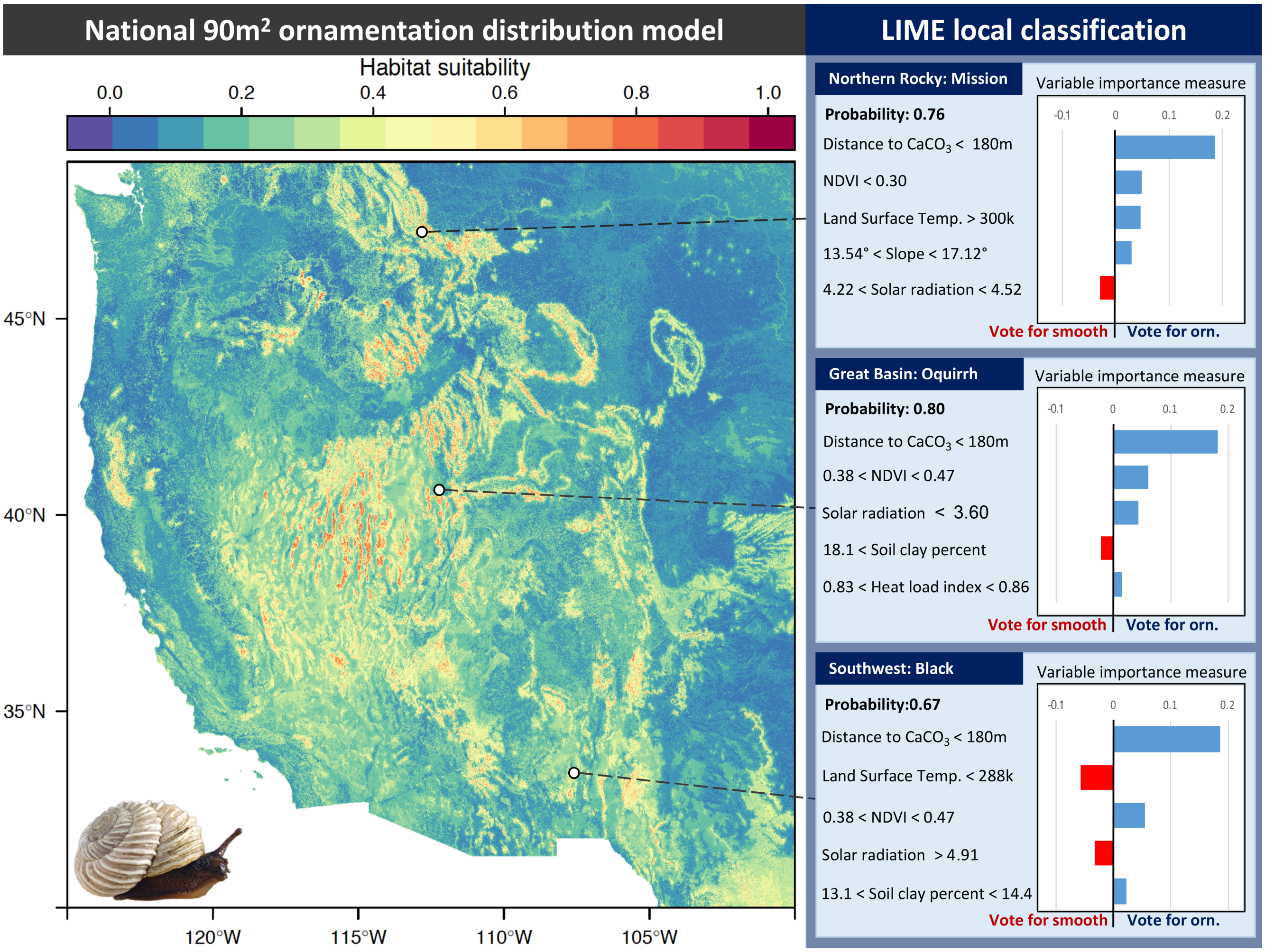

FIGURE 1 Ornamented RF distributional model at 90 m^2 resolution and LIME local classifications for mountain ranges within the Rocky Mountain North, Great Basin, and Southwest regions. Local probability and variable importance metrics are derived from the ornamented vs. smooth classification model. Figure layout inspired by Ryo et al. (2021). Photo credit: *O. idahoensis*, Richard A. Salsbury.

All other predictors significantly contributed to classification or distributional models measured through MDA or Gini node impurity. The top three predictors changed across models and included distance to CaCO$_3$ rock, NDVI, LANDSAT July mean surface temperature, and elevation (Table 2) for ornamentation or smooth form distributional or classification models. Variables important for classification models were generally also important in smooth form and ornamented distribution models (Supplementary Material Table S8).

Local classification of *Oreohelix* sites by LIME (Figures 1 and 2) revealed that distance to CaCO$_3$ rock is the most important variable for local classification of *Oreohelix* sites and that decreased distance leads to greater probability of ornamentation classification across subregions. Ornamentation also appeared to be mildly associated with warmer surface temperatures, moderate solar radiation, and less claylike soils at local sites, though these contributed relatively little to local classification compared to distance to CaCO$_3$ rock.

3.3 | Dead carbon incorporation

There was considerable variation in F$_m$ values across the 30 sampled sites (0.78–1.27) indicating differences in dead carbon utilization and/or F$_m$ of site detritus (Figure 4). Ornamented form on calcareous rock had significantly lower F$_m$ than smooth forms either on calcareous rock (*p*-value = 0.044, t-statistic = −2.372, df = 8.067), or off calcareous rock (*p*-value = 0.003, t-statistic = −3.3794, df = 18.267). Calcareous rock vs. non-calcareous F$_m$ differences were significantly different in our pairwise dataset which included eight ornamented-smooth pairings and a single comparison between calcareous and non-calcareous smooth forms (*p*-value = 0.004; t-statistic = −3.9931, df = 8).

3.4 | Shell biometric variables and shell strength

Size standardized mass was significantly greater for all ornamented types when compared to smooth forms residing on

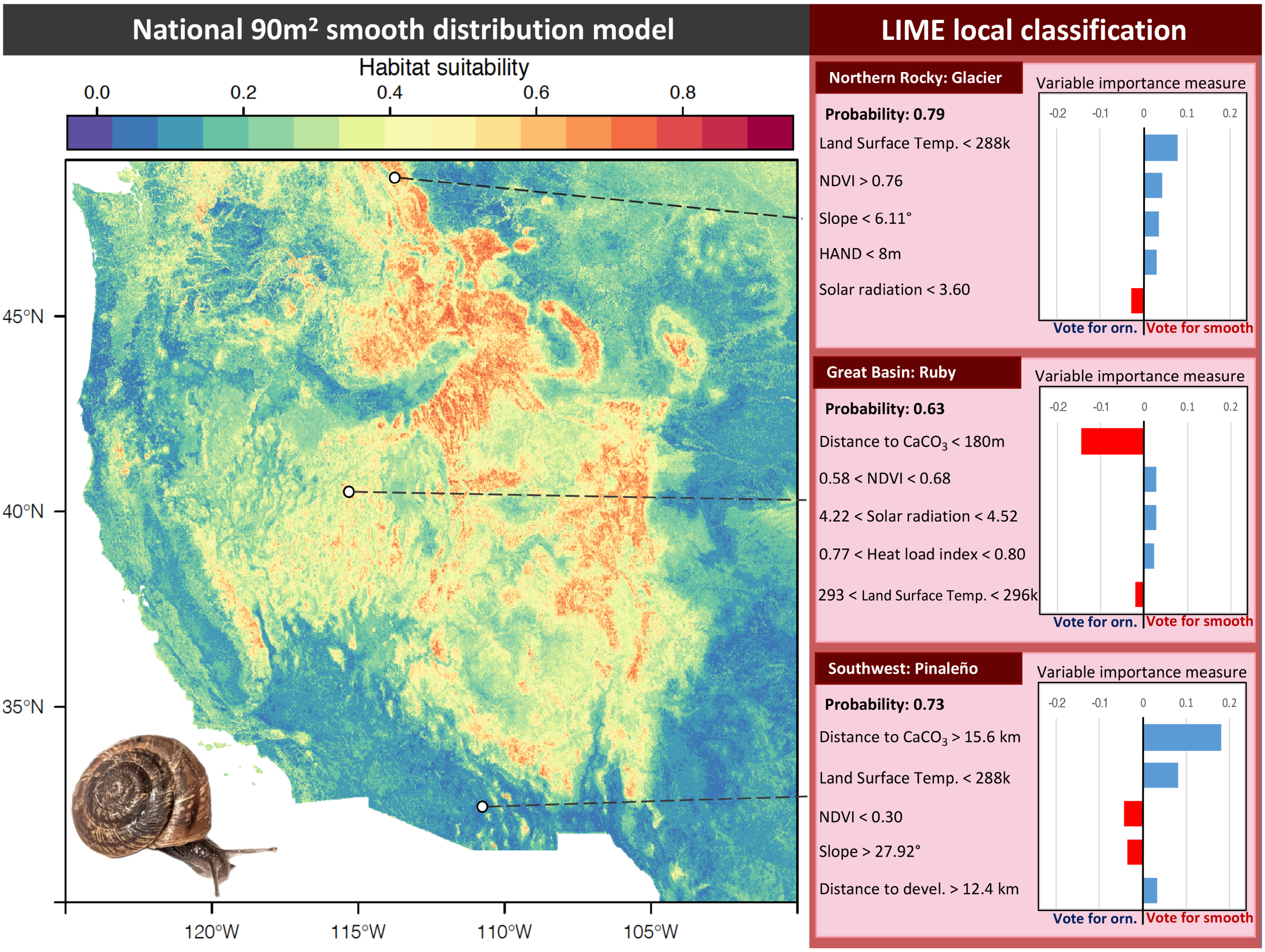

FIGURE 2 Smooth RF distributional model at 90 m^2 resolution and LIME local classifications for mountain ranges within the Rocky Mountain North, Great Basin, and Southwest regions. Local probability and variable importance metrics are derived from the ornamentation vs. smooth classification RF model. Photo credit: *O. grahamensis* Jeff Sorenson, CC BY SA 4.0.

non-calcareous rock (Figure 5, Supplementary Table S6). Size standardized mass was also greater for smooth calcareous rock populations compared to non-calcareous rock smooth populations (Figure 5, Supplementary Table S6). Mass standardized shell strength was greater for all ornamented types than smooth forms except when comparing smooth forms that were calcareous rock residents to commarginal ornaments (Figure 5, Supplementary Material Appendix II, Table S6). These results are consistent with previous studies documenting increased shell strength along the axis of ornamentation expression (Johnson, 2021; Posilović & Bajraktarević, 2010) as shell strength during lateral crushing was higher for keeled and antimarginal shell forms which have greater shell thickness along the axis of crushing compared to smooth or commarginal ornaments.

4 | DISCUSSION

By incorporating trait distribution models, measures of dead carbon utilization, and phenotypic data of ornamented and smooth *Oreohelix*, we obtained evidence that calcareous rock mineral availability is an ecophysiological constraint on biomineralization effort in *Oreohelix*. Our results also show that ornamented forms are generally associated with greater biomineralization effort, are limited in distribution to calcareous rock, and incorporate larger amounts of dead carbon from calcareous rock than smooth formed *Oreohelix*. In the following sections, we discuss differences in biomineralization effort and trait function between shell types, how mineral availability may constrain shell form expression, place our findings in context with previous studies of EPC associated trait expression, and how our results may inform land snail conservation.

4.1 | Biomineralization effort and shell function of Oreohelix

All ornamented forms, except keeled morphologies, were found to have greater size standardized shell mass compared to smooth forms sampled from calcareous rock or non-calcareous rock,

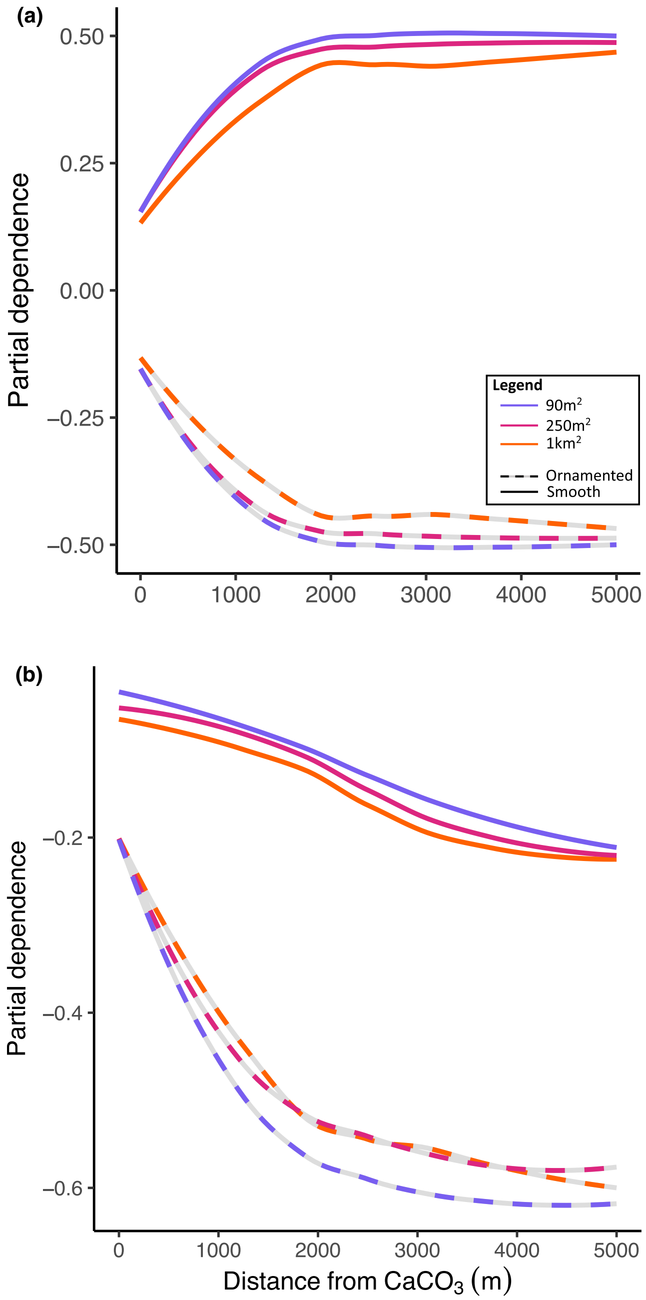

FIGURE 3 Loess smoothed partial dependence plot of distance to $CaCO_3$ rock for classification (a) and distribution models (b) at 90 m^2, 250 m^2, and 1 km^2 predictor resolutions. Negative values indicate classification probability of the focal class decreases and vice versa for positive values.

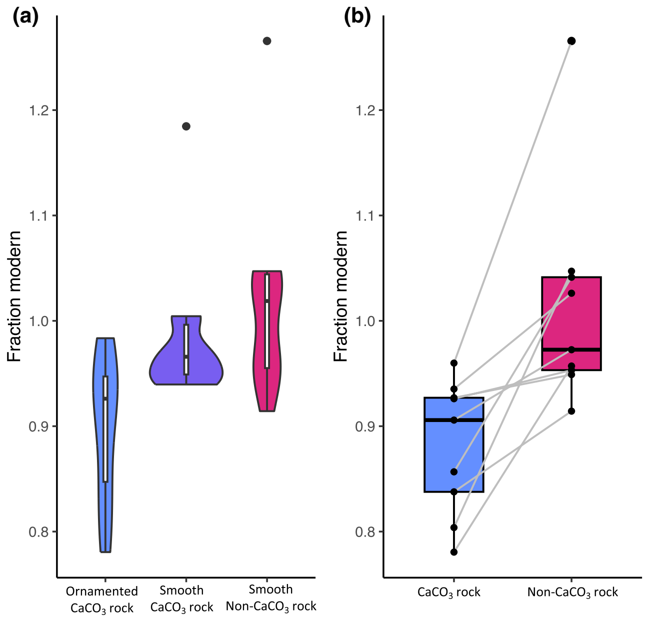

FIGURE 4 Violin and box plots of *Oreohelix* radiocarbon samples. (a) Violin and box plots F_m for ornamented and smooth *Oreohelix* split apart by calcareous rock residence. (b) Pairwise boxplot of F_m for closely occurring calcareous and non-calcareous rock pairs. F_m represents the $^{14}C/^{12}C$ ratio in modern carbon corrected for isotopic fractionation and fossil fuel release of ^{14}C into the atmosphere. Lower Fm ratios indicate greater incorporation of calcareous rock into shell carbonate.

indicating that most ornamented shells were thicker and required more material to produce than a smooth form of the same size. Ornamented forms were also generally stronger per unit mass when crushed laterally, which suggests that ornamentation has a distinct functional benefit whose importance remains to be assessed in natural populations. Many *Oreohelix* populations have noticeable frequencies of repair scars from shell breakage (Frest & Johannes, 1997; Pilsbry, 1939), which indicates crushing by rock talus or predation may be a substantial agent of selection for some members of this group. Other functional benefits of ornamentation expression that have been identified in other semi-arid land snail groups, such as increased convective cooling and water retention (Giokas, 2008), may also be at play in *Oreohelix* given the contribution of solar radiation and summer mean surface temperature to ornamentation classification. Differences in the form of reinforcement with ornamentation (e.g. lateral reinforcement: antimarginal ribs and keels; vertical reinforcement: commarginal ribs) and shape (i.e. keeled forms being flat) may also indicate site-specific selective pressures for different forms of crushing. When taken in the context of the spatial patterns of ornamentation expression identified in this study, ornamentation in *Oreohelix* appears to generally represent a resource-constrained trait which may be a response to a variety of selective pressures.

4.2 | Mineral availability and ornamentation expression

Across all models and spatial resolutions (90 m^2–1 km^2), ornamentation was associated with proximity to $CaCO_3$ rock and that distance to $CaCO_3$ rock was the most important variable for either classification or distributional models. Previous spatial studies of land snail ornamentation and geology have either found no association with geology (Welter-Schultes, 2010) or only anecdotally reported a preponderance of keeled forms at karst sites (Alonso et al., 1985;

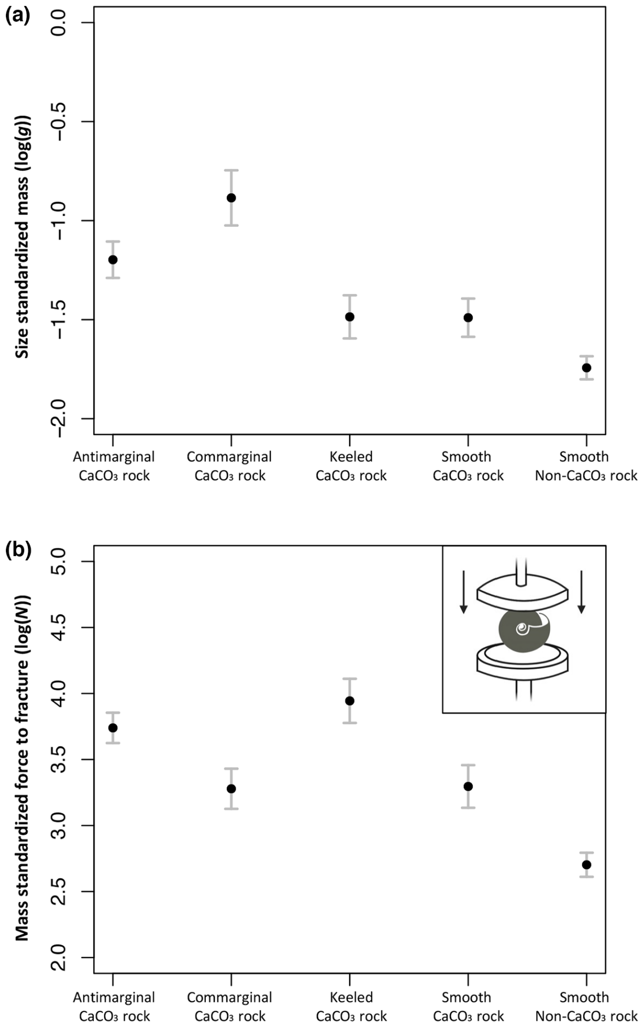

FIGURE 5 Biometric and shell crushing measurements for major ornamented types. (a) Mean and 95% confidence intervals of size standardized shell mass after the effects of shell height/width were removed. (b) Mean and 95% confidence intervals of mass standardized peak force at fracture of lateral crushing for after the effect of shell mass was removed. Inset depicts orientation of shell and direction of load applied during crushing.

Goodfriend, 1986; Teshima et al., 2003). In *Oreohelix*, ornamented forms can be of a variety of shell shapes and are all commonly associated with $CaCO_3$ rock sites (median distance to $CaCO_3$ rock = 0 m for ornamented forms in our 90 m^2 dataset, Supplementary Table S9). This pattern indicates an association of ornamentation with other qualities of $CaCO_3$ rock sites across Western North America besides topography.

In this study, we found that calcareous rock residents had lower F_m than non-$CaCO_3$ rock resident *Oreohelix* and that ornamented forms from calcareous rock sites had significantly lower F_m than calcareous rock resident smooth forms (Figure 4). As site detritus generated post-1955 can only upwardly bias F_m in shell carbonate (Pigati et al., 2010) and our results show a consistent decrease of F_m between sister pairs of ornamented and smooth forms as well as between smooth and ornamented calcareous rock resident species, we interpret our data as showing greater usage of dead carbon in ornamented snails on calcareous rock. We cannot rule out the alternative that there is consistently higher F_m of detritus at smooth form sites which masks dead carbon incorporation; however, it is unlikely given our number of samples, sampling design, and that our samples come from different regions of North America.

Given the increased amounts of dead carbon incorporation and generally greater biomineralization effort of calcareous rock endemic *Oreohelix*, we conclude that calcareous rock mineral availability generally constrains biomineralization effort in *Oreohelix*. Although, as we did not sample radiocarbon data for soil, calcareous rock, and detritus, we cannot determine whether dead carbon incorporation is through indirect assimilation of dead carbon from secondary sources like soil or detritus or through direct assimilation of calcareous rock (Forman et al., 2021). We believe this oversight does not affect our main conclusions as *Oreohelix* are incorporating greater dead carbon and increasing biomineralization effort at calcareous rock sites and either mineral uptake pathway would result in increased mineral availability.

Like other dispersal limited calcicole species such as edaphically specialized plants, ornamented *Oreohelix* are generally constrained in distribution to calcareous rock outcrops (Rajakaruna, 2018). However, unlike many calcicole plants which must develop morphological and physiological adaptations to tolerate high mineral concentrations in these environments (Rajakaruna, 2018), *Oreohelix* appears to have a physiology favourable for exploiting the excess mineral availability at these sites. The difference between calcareous rock acting as a filter vs. a source is likely a contributor for major differences in the distribution of generalist smooth form species in *Oreohelix* and generalist sister species of edaphically specialized plants. Generalist smooth-formed *Oreohelix* occupy and likely are more prone to colonize calcareous rock than generalist plants which are unlikely to be able to tolerate mineral rich substrates (Corlett & Tomlinson, 2020). Similarly, it may be expected that the process of edaphic specialization in land snails may be wholly different from classic examples of edaphic specialization in plants (Linscott et al., 2022). For example, secondary contact and competition between $CaCO_3$ specialist and generalist *Oreohelix* species may be more frequent than plant $CaCO_3$ specialist-generalists pairs due to favourable conditions for generalist smooth formed *Oreohelix* species at calcareous outcrops. Comparative studies across communities and clades of calcareous rock endemics may unravel the diverse roles this mineral resource can have on shaping morphological evolution and functional biogeography of EPC species.

While it is probable that similar EPC-shell form relationships exist in other land snail groups, differences in land snail physiology, morphology, and environmental conditions within species distributions may limit the applicability of our approach to other systems. For example, ornamentation expression, which is generally associated with greater biomineralization effort in *Oreohelix*, does not always represent an increased investment in biomineralization in other land snail groups such as *Albinaria* (Giokas, 2008). Species which can produce shell ornaments by redistributing shell material rather than increasing biomineralization effort may not require access to sites with higher mineral availability (Welter-Schultes, 2010). Similarly, strong selection for heavily biomineralized or ornamented forms (e.g. due to predation or insolation) may result in increases in biomineralization effort without higher levels of $CaCO_3$ availability, though this may require increased energy assimilation or reduced shell growth rate (Bourdeau, 2010).

Differences in body size may also alter expected relationships between mineral availability and biomineralization effort as it appears on a gross scale large land snail species incorporate greater amounts of dead carbon than smaller land snail species, which may indicate that smaller sized species have lower mineral requirements relative to their body size than large land snail species (Pigati et al., 2010). Size variation within species also plays a role in environmental mineral uptake as species who utilize dead carbon in shell construction have larger fractions of dead carbon early in life which declines with age (Forman et al., 2021). Parallel ontogenetic trends in environmental carbon utilization are found within marine and freshwater molluscs which also show decreasing fractions of environmental carbon over the lifetime of an individual (Lorrain et al., 2004; Waldbusser et al., 2013), which may suggest that the contribution of environmental carbon scales at a slower rate compared to the mineral requirements necessary for shell formation over time (Lorrain et al., 2004). Under such an allometric relationship, small land snail species that can utilize environmental carbon would be expected to have the greatest biomineralization effort relative to their size and very large land snail species may be expected to only achieve meagre increases in biomineralization effort if they can access environmental carbon. Large land snail species, like *Oreohelix*, may be expected to only produce shell ornaments which require greater biomineralization effort in environments rich in mineral resources while small land snail species may be expected to express shell ornaments across a broader range of mineral availabilities. Broad functional biogeographic studies of biomineralized traits (i.e. ornamentation or shell thickness) in the context of mineral availability and size may shed light whether there exists a shared allometric relationship between mineral uptake and biomineralization effort across gastropods.

Other considerations for applying our approach to other land snail groups or species which rely on $CaCO_3$ for trait expression is that $CaCO_3$ can be deposited through various mechanisms such as aeolian deposition (Oerter & Amundson, 2016), sea spray (Whipkey et al., 2000), or biotic processes (Cailleau et al., 2011; Hotopp, 2002) which require in situ field measurements and greater effort to interpolate and project spatially than the geologic maps used here. Species may also be specialized to meet their $CaCO_3$ requirements through either dietary (Fournié & Chétail, 1984), soil (Charrier et al., 2013; Forman et al., 2021), or dissolved carbonate rock/shell absorption (Appleton & Heeg, 1999; Kado, 1960) which may vary in relative availability across sites. As many of the aforementioned mineral sources can more rapidly change in mineral availability than calcareous rock outcrops (i.e. soil and detritus), or depend on other species that may be affected by anthropogenic disturbance and climate change (Cailleau et al., 2011; Hotopp, 2002; Nation, 2007), species which depend on these labile mineral resources may be more vulnerable to local environmental disturbance and climate change. Future functional biogeographic studies of land snails should focus on determining how $CaCO_3$ dynamics influence biomineralization expression across ecosystems and clades so that we can determine how mineral supply contributes to the habitat requirements and morphological evolution of land snail species.

4.3 | Calcareous rock and land snail conservation

Almost a quarter of IUCN Red List land snail species with near threatened or higher threat assessments appear to reside primarily or exclusively on calcareous substrates (371 of 1460 species; IUCN 2021). The narrow range of many ornamented *Oreohelix* and ongoing threats of road and industrial development have contributed to the listing of nearly all ranked ornamented *Oreohelix* species and subspecies (Supplementary Table S2) as imperilled (G2 or S2 rank) or critically imperilled (G1 or S1 rank; Linscott et al., 2020, NatureServe 2021) by NatureServe and local state governments. The apparent exclusivity of ornamented *Oreohelix* to $CaCO_3$ rock areas and slight association of smooth *Oreohelix* to $CaCO_3$ rock areas has immediate applications for conservation agencies as ornamented *Oreohelix* populations likely require access to $CaCO_3$ rock to persist. Conservation plans of ornamented *Oreohelix* and other large, ornamented snails should consider the habitat requirements identified in this study to better balance the requirements of these species with societal demands for carbonate rock.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and scripts are available on dryad (10.5061/dryad.0k6djhb40).

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BIOSKETCHES

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Author contributions: T. Mason Linscott and Christine E. Parent conceived the ideas. T. Mason Linscott and Nicole K. Recla conducted fieldwork and collected experimental data. T. Mason Linscott analyzed the data with support from Nicole K. Recla and Christine E. Parent. T. Mason Linscott led the writing with assistance from Nicole K. Recla and Christine E. Parent. Christine E. Parent supervised the project and facilitated funding for Nicole K. Recla and T. Mason Linscott.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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