

DEEPER BULBS ARE LARGER

Cody Coyotee Howard,^{1,*} Simon Attwood,[†] Carel Fourie,[‡] Andrew J. Hankey,[§] and Timothy S. Harvey^{||}

*Department of Plant Biology, Ecology, and Evolution, Oklahoma State University, Stillwater, Oklahoma, USA; [†]C.E. Moss Herbarium, School of Animal, Plant and Environmental Science, University of the Witwatersrand, Gauteng, South Africa; [‡]Department of Plant and Soil Sciences, University of Pretoria, Gauteng, South Africa; [§]Walter Sisulu National Botanical Garden, Gauteng, South Africa; and ^{||}Plante Novae, Thousand Oaks, California, USA

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Premise of research. Belowground bud placement generally offers plants protection from aboveground disturbances, such as frosts and fires. However, deeper bud placement requires more reliance on stored resources for emergence. The aim of this study is to examine the relationship between the size of an underground storage organ and its depth within the soil across taxa.

Methodology. We measured bulb diameter and bulb depth in the soil for 44 distinct species of Ledebouriinae (Scilloideae, Asparagaceae) found in Zambia and South Africa.

Pivotal results. Across species, we found that larger bulbs are positioned deeper in the soil. At the individual level within species, a positive relationship between bulb diameter and bulb depth was generally found, except for in a few instances where larger and smaller bulbs appeared to be found at similar depths.

Conclusions. Overall, our study suggests that deeper renewal bud positioning requires greater energetic costs (as indicated by larger bulbs) for emergence across species. Our within-species results could be interpreted as showing that older bulbous plants generally have larger, deeper bulbs. These characteristics are likely interrelated, where older plants have grown relatively larger bulbs that then allow for deeper bud placement, resulting in more protection from aboveground disturbances.

Keywords: Asparagaceae, bulbs, geophytes, Scilloideae, underground storage organs.

Online enhancements: appendix, supplemental data.

Introduction

Roots are important for resource acquisition and storage, but far greater plant organ diversity exists below the soil surface (Klimešová et al. 2020; Ottaviani et al. 2020). For example, renewal buds can be found on a variety of belowground shoot structures that protect meristems from aboveground disturbances, such as fire, grazing, and freezing temperatures (Vesk et al. 2004; Noy-Porat et al. 2013; Pausas et al. 2018; Hiers et al. 2021; Lubbe et al. 2021). Therefore, a positive relationship between bud depth and the amount of protection afforded may be assumed—the deeper, the better. However, the majority of belowground buds are located within the first 5 cm of soil (Vesk and Westoby 2004; Klimešová and Klimes 2007). This

suggests that deeper bud placement may come at a cost, which may include delayed emergence, reduced competitive ability, and/or a greater reliance on stored belowground resources for emergence (Ivany 1997; Lubbe and Henry 2019b; Ott et al. 2019; Chadha et al. 2022). Thus, bud depth likely depends upon whether an individual has the ability to offset these associated costs in a particular habitat (Spencer 1987; Klimes et al. 1993; Schnablová et al. 2021).

Plants with belowground buds are found across the plant phylogeny. This inherent lineage diversity alone contributes to wide variation in bud depth (Klimešová and Klimes 2007; O'Rourke 2014; Ott et al. 2019). Additionally, different belowground bud-bearing structures exist (i.e., bulb, corm, stem tuber, etc.), each of which show variation in vertical distribution in the soil (O'Rourke 2014; Ott et al. 2019). Many belowground structures that house buds are relatively enlarged (hereon referred to as underground storage organs [USOs]), and herbaceous plants with belowground buds and USOs are often referred to as geophytes (Raunkiaer 1934). USOs act as a site of resource allocation

¹ Author for correspondence; email: cody.howard@okstate.edu.

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(Ruiters 1995; Al-Tardeh et al. 2008; Diaz-Toribio and Putz 2021) that can be drawn upon during dormancy, during emergence, or after disturbance (Lapointe 2001; Werger and Huber 2006; Fidelis and Blanco 2014; de Moraes et al. 2016). It is hypothesized that the overall size of USOs is influenced by habitat (Ruiters et al. 1993; Procheş et al. 2005; Al-Tardeh et al. 2008; O'Rourke 2014; Mocko and Jones 2021) and may affect the ecology of geophytic plants (Lubbe and Henry 2019b; Lubbe et al. 2021; Mocko and Jones 2021). For example, larger below-ground organs are associated with plants that flower when photosynthesis is not optimal (e.g., cold temperatures) or severely limited (e.g., leaves are not present; Howard and Cellinese 2020; Harris et al. 2023). This is likely due to greater reliance on the resources stored in the USOs to fuel flowering since leaves cannot be fully relied upon to perform photosynthesis (Dafni et al. 1981; Dafni 1996). The depth within the soil column can also influence USO size/biomass, which has been found to have a negative relationship across a selection of South African geophytes (O'Rourke 2014). In the bulbous *Oxalis pes-caprae* L. (Oxalidaceae), individuals may sense depth and, in response, build larger USOs for later emergence if found deeper in the soil (Verdaguer et al. 2010). Although useful, maintaining the greater amounts of biomass in larger USOs may be difficult. In geophytic *Pelargonium* sect. *Hoarea* (Sweet) DC species, those with larger tubers were more negatively affected by chronic drought relative to those with smaller tubers (Mocko and Jones 2021). Additionally, monocot species with larger bulbs were overall associated with warmer, more thermally stable climates (Howard and Cellinese 2020), suggesting that maintaining larger USOs may be limited by the environment.

Geophytes are common features of seasonal habitats (Procheş et al. 2006; Cuéllar-Martínez and Sosa 2016; Howard et al. 2019). Within geophytes, bulbous plants (i.e., plants with true bulbs [e.g., onion]) are a unique geophytic morphology in that the majority of resources are stored in leaf tissue rather than stem or root tissue (Ruiters 1995; Al-Tardeh et al. 2008). The leaf tissue of bulbous plants can be composed of various leaf types, such as swollen scale leaves, protective scale leaves, sheathing scale leaves, or foliage-leaf-derived swollen leaf bases (Tribble et al. 2021). Bulbous taxa are overwhelmingly found within monocots, but bulb evolution has also occurred in *Oxalis* (eudicots; Oberlander et al. 2009). Also, the bulbous habit is fairly unique in that once the trait has evolved, it seems rarely lost (Howard et al. 2020). Furthermore, relative to other below-ground structures, bulbous plants generally have lower multiplication rates (i.e., ability to make genetically identical offsets) and renewal bud numbers (Herben and Klimešová 2020), which suggests that it is a “sit-and-stay” adaptation to the seasonal, high-light, and xeric habitats bulbous taxa commonly inhabit (Patterson and Givnish 2002; Howard et al. 2019; Klimešová and Herben 2024). For comparison, rhizomatous taxa tend to be more clonal, inhabit wetter environments, and have more buds (Grace 1993). Since bulbous taxa have relatively high resource storage capacity, have low bud bank number, and inhabit more seasonal habitats (Howard et al. 2019; Lubbe et al. 2021), deeper bud placement, which may require larger bulbs to fuel emergence, may be necessary to fully protect the limited number of meristems in often harsh environments. However, how bud depth and bulb size (diameter) correlate remains understudied across taxa.

Here, to investigate the relationship between bulb diameter and bulb depth in the soil, we collected data on both in *Ledebourinae* (Scilloideae, Asparagaceae) taxa across a section of northern Zambia and eastern South Africa (fig. 1a). We hypothesize that depth in the soil will influence bulb diameter. We predict that as bulb depth increases, bulbs will be larger (i.e., a positive relationship).

Material and Methods

Plant Collection and Measurement

Fieldwork was conducted in February 2023 in Zambia. Regions where *Ledebouria* Roth were known to be found based on previous fieldwork efforts were targeted. We also searched for *Ledebouria* in regions new to us to expand both species and geographic sampling for later studies. When individuals were encountered, prior to extraction with a 12-in, square-stem, flathead screwdriver, the location of the soil line on the leaves was noted so that measurements could be later taken at camp. Individual plants were then extracted, accessioned, and placed into a brown paper sandwich bag for transport. Once at camp, measurements were taken using a standard, 12-in/30-cm ruler. Measurements were taken by holding a ruler to the plant and noting the measurements in millimeters (mm) by eye. Measurements included (1) the diameter of the bulb at the widest point and (2) the distance from the lowermost bulb scale (i.e., the basal stem was excluded from measurement) to where the soil met the leaves (fig. 1b).

Later, in November 2023, fieldwork was conducted in South Africa to expand sampling of *Ledebouria* and close relatives. Bulb diameter and depth were measured for each individual collected, excluding those that were a grouping of offsets (i.e., many bulbs for one clone) since measurements would have been difficult for each single offset. Offsetting individuals were uncommon. When measuring, instead of with a ruler, a digital caliper was used to take measurements at the widest point on the bulb. To ensure measurements taken with a ruler in Zambia and measurements taken with a digital caliper in South Africa were statistically similar, 27 individuals had bulb diameter and depth measured first with a ruler and then by a caliper. These measurements were then used to ensure similarity across the two methods of measurement.

For the Zambian taxa, we identified or classified individuals into separate species based on morphology, habitat type, and/or geographic location. Unfortunately, none of the individuals were flowering, which made species identification difficult, except for *Ledebouria cordifolia* (Baker) Stedje & Thulin. This species characteristically has a single heart-shaped leaf that hugs the soil surface. Species delimitation within *Ledebouria*, and the *Ledebourinae* overall, remains complicated because of large variation across habitats as well as a dearth of knowledge on the diversity of the group across its range (Mwafongo et al. 2017; Howard et al. 2023). For all individuals, excluding *L. cordifolia*, morphologically distinguishable leaf and bulb characteristics and/or collection location were used in species delimitation. Based on extensive field research focusing on the *Ledebourinae* (Howard 2014; Howard et al. 2023) and our intimate familiarity with the group, we were able to confidently categorize most individuals/populations into different species,

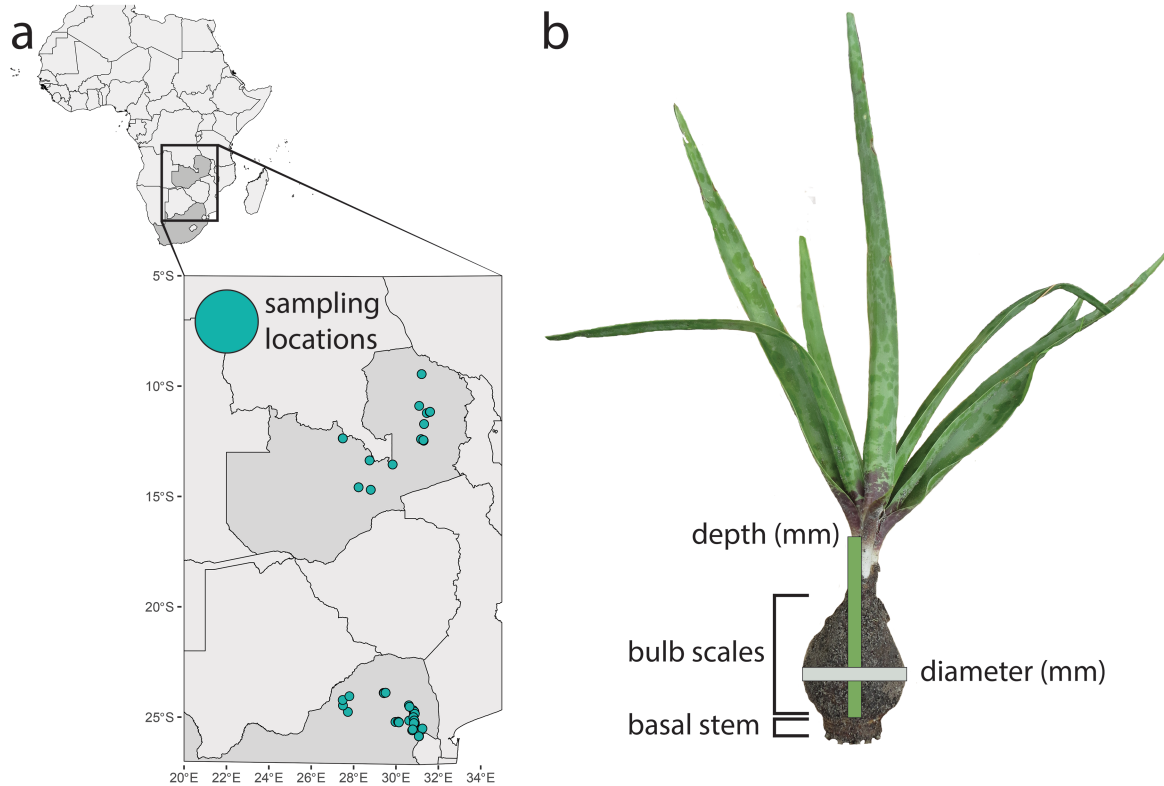


Fig. 1 Map showing sampling locations in Zambia (more northern country) and South Africa (a) and an example of the measurements taken for each individual plant dug up from the field (b). The individual in b is an undescribed *Ledebouria* species from Zambia (*Ledebouria* CCH254).

whether they are described to science or not. Fieldwork in South Africa was carried out in collaboration with a *Ledebouria* expert, A. J. Hankey (Hankey 2020, 2024), who determined species identity. See the appendix (available online) for distinguishing characteristics used for each undescribed taxon with five or more data points. Herbarium specimens for South African taxa have been deposited at the University of Pretoria (PRE), and associated voucher information is available upon request. Herbarium specimens for Zambian taxa remain in process.

Analyses

To ensure that measurements taken with a ruler and those with a caliper were similar, we ran a linear model in R version 4.2.1 for 27 individual measurements. Then, to test whether depth can explain bulb diameter, we calculated the mean bulb depth and diameter per species using the R package *dplyr* version 1.1.2. We calculated the mean values for all the species in the dataset (raw data) as well as for species with at least three and at least five data points. This was done to test the robustness of the data to sampling. Mean depth and mean diameter were natural log transformed to better meet the assumptions of the linear model. For all three datasets, we ran a generalized linear model in R. We used the `glm()` function with a Gaussian distribution and an identity link function with depth as the independent

variable and diameter as the dependent variable (diameter \sim depth). Then, for each species with at least five individual data points, we ran the same generalized linear model including each individual measurement.

To further test the robustness of the data, we performed a phylogenetic generalized least squares (PGLS) analysis on a subset of taxa using the `pgls` function found in the R package *caper* version 1.01 (Orme et al. 2013). Unfortunately, a fully sampled phylogeny is not currently possible for all taxa included in the present study, either due to being undescribed species or not being yet included in any phylogenetic studies on the group. The PGLS was performed using taxa with known phylogenetic information available (i.e., eight taxa with known tips in the phylogeny), as well as a random sampling of tips that had associated trait data randomly assigned. We performed this randomization procedure 1000 times, with each iteration maintaining the phylogenetic structure of the eight known taxa and the remaining taxa randomly selected and randomly assigned bulb diameter and bulb depth measurements from the data frame. The total number of taxa in the analysis always equaled the total number of taxa that had three or more data points (i.e., 35 taxa/tips). The phylogeny used in the analysis was that of Howard et al. (2023), which is a phylogenomic and biogeographic study of the *Ledebouria* species. Mean depth and mean diameter were natural log transformed in each randomized analysis. For each PGLS output, we recorded the slope, intercept, *P* value, adjusted r^2 , and

t value. All figures were created with R, then manually adjusted for sizing and visual aesthetic using Adobe Illustrator version 27.0.1.

Results

Measurements taken with a ruler and caliper were statistically significant for both bulb depth (adjusted $R^2 = 0.9985$, $df = 26$, $P < 2E-16$) and diameter (adjusted $R^2 = 0.9986$, $df = 26$, $P < 2E-16$). Therefore, all data for bulb depth and diameter were used in subsequent analyses regardless of method of measurement (i.e., ruler [Zambian taxa] vs. caliper [South African taxa]).

In total, 271 individuals were measured for both bulb diameter and bulb depth in the soil. Based on morphology, geographic location, and/or expert opinion, the dataset contained 44 different species, regardless of whether the species has previously been described. The raw data included four *Drimiopsis*, two *Resnova*, and 38 *Ledebouria* taxa. For this dataset the mean diameter was 24.1 mm (median = 19.0 mm; range = 6.7–64.3 mm), and the mean depth was 53.4 mm (median = 44.5 mm; range = 18.2–180.0 mm). A statistically significant, positive relationship (slope = 0.95) between depth and diameter was found ($t = 8.28$, $df = 43$, $P = 2.22E-10$; fig. 2a).

The dataset that included taxa with at least three data points had 35 species: three *Drimiopsis*, two *Resnova*, and 30 *Ledebouria*. For this dataset the mean diameter was 20.3 mm (median = 16.2 mm; range = 6.6–49.9 mm), and the mean depth was

45.2 mm (median = 38.4 mm; range = 18.2–105.0 mm). A statistically significant, positive relationship (slope = 0.94) between depth and diameter was found ($t = 6.47$, $df = 34$, $P = 2.41E-7$; fig. 2b).

The dataset that kept taxa with at least five data points had 20 species: one *Drimiopsis*, one *Resnova*, and 18 *Ledebouria*. In this dataset the mean diameter was 21.9 mm (median = 17.8 mm; range = 9.1–50.0 mm), and the mean depth was 45.5 mm (median = 43.5 mm; range = 22.6–72.8 mm). A statistically significant, positive relationship (slope = 1.16) between depth and diameter was found ($t = 5.55$, $df = 19$, $P = 2.89E-5$; fig. 2c).

Bulb depth and bulb diameter were found to be significantly positive across all 1000 PGLS analyses performed on the dataset containing taxa with three or more data points (fig. 3). This pattern was held even when we repeated the 1000 iterations several different times with different starting seeds (data not shown). For the final PGLS analysis, the mean slope was 0.955 (range = 0.613–1.238), the mean intercept was -0.682 (range = -1.765 – 0.677), and the mean adjusted r^2 was 0.553 (range = 0.250–0.732). Overall, these results suggest that the patterns with and without phylogeny are similar (i.e., significant positive relationship; figs. 2, 3).

When analyzing the individual measurements for each species that had at least five data points, we found that 17 of the 20 species had overall positive slopes for the relationship between bulb diameter and bulb depth in the soil, but only seven of these were statistically significant (fig. 4a–4c, 4i, 4l, 4o, 4r; table A1 [available

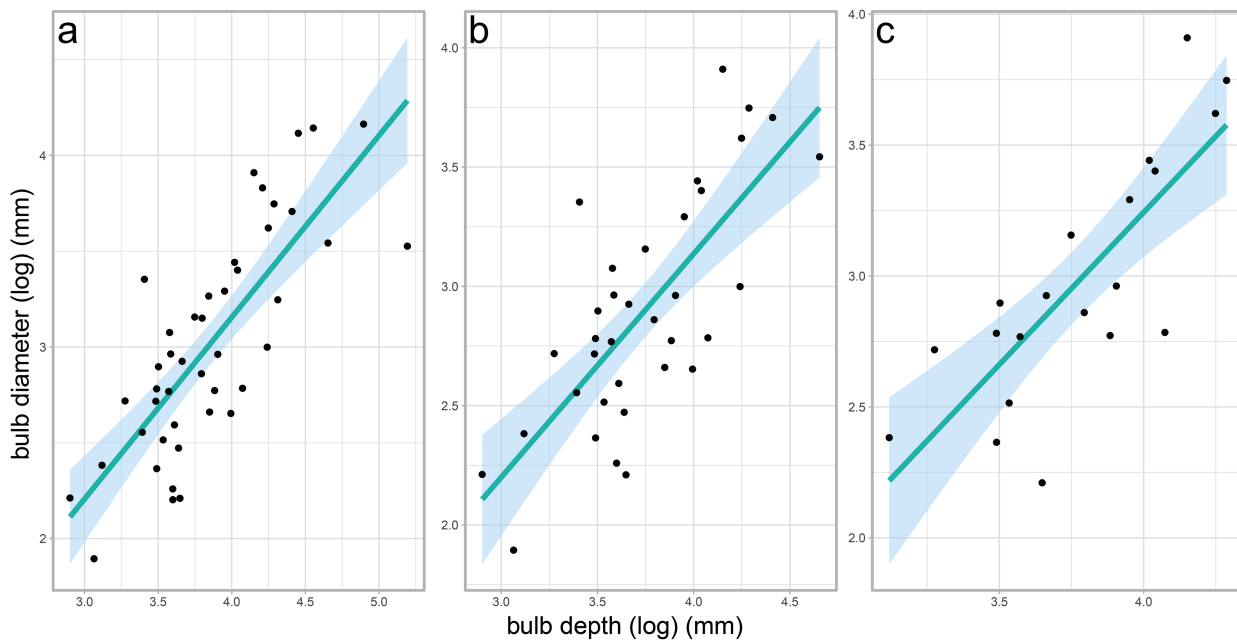


Fig. 2 Larger bulbs are found deeper in the soil across species. Plots show the relationship between the natural log of bulb diameter and bulb depth for all species with data (a), species with three or more data points (b), and species with five or more data points (c). Axis scales in each plot differ from one another. Plots were made using ggplot2 version 3.4.2 (Wickham 2016).

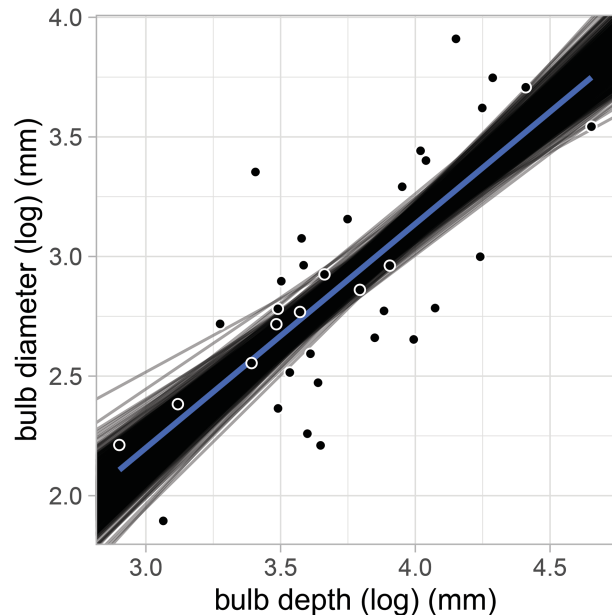


Fig. 3 When correcting for phylogeny, a positive relationship between bulb diameter and bulb depth remains. The plot shows the relationship between the natural log of bulb diameter and bulb depth using a semirandomization procedure for performing a phylogenetic generalized least squares (PGLS) analysis. The data points and blue line correspond to the slope and intercept for species with three or more data points without phylogenetic correction, and the gray lines in the background show the slope and intercept from the results of 1000 semirandomized PGLS analyses. All analyses returned statistically significant results. The plot was made using ggplot2 version 3.4.2 (Wickham 2016).

online]). Three species had nonsignificant, negative slopes for bulb diameter and bulb depth in the soil (fig. 4j, 4k, 4n; table A1).

Discussion

Overall, we found a positive relationship between bulb diameter and bulb depth in the soil across taxa. These results therefore support our hypothesis and prediction. This result provides evidence that emergence from deeper depths in the soil likely requires larger USOs. Furthermore, we found that for individuals within a species, a positive trend remains (either statistically significant or not), except for in a few species. Our findings offer insights into future research questions pertaining to the ecology and morphology of bulbous plants that remain to be investigated.

Deeper buds and therefore deeper bulbs in the soil are attached to overall larger bulbs, and larger bulbs indicate a greater potential resource pool (Ruiters 1995; Al-Tardeh et al. 2008; Bartušková et al. 2022). These larger amounts of stored energy are likely necessary for shoot emergence from greater depth in the soil. In doing so, greater protection from aboveground disturbances (e.g., frost, fires, herbivores) is afforded to the plants (Lubbe and Henry 2019a, 2019b; Bartušková et al. 2022). In addition to larger bulbs, emerging from deeper in the soil could be further facilitated by species' specific traits. For example, it is hypothesized that the formation of tunnels made by previous years'

growth assists emergence in bulbous *Oxalis* species (Oberlander et al. 2009). Furthermore, many geophytic plants have evolved leaf shapes that efficiently plow through the soil (e.g., spear-shaped leaves; Salisbury 1916). Lastly, it has been found that many species preform buds in the current growing season that aid in rapid emergence and maximum resource capture at the start of the next growing season before other competing plants have sprouted (Schnablová et al. 2021). In addition to depth, these characteristics should be measured across taxa and incorporated into future studies.

For species that had at least five data points, at the individual level, we found that many show a positive relationship between bulb diameter and bulb depth in the soil, either statistically significant (fig. 4a–4c, 4i, 4l, 4o, 4r) or not (fig. 4d–4h, 4m, 4p, 4q, 4s, 4t). For the within-species patterns, we hypothesize that we are capturing the age of the individual plants. Geophytic plants can adjust the positioning of their renewal buds over time (e.g., as they age; Pütz 1993; Maun 1998; Pütz and Sukkau 2002; Tessier 2012; Klimešová et al. 2017; Qian et al. 2017), and older bulbous plants have larger bulbs that are positioned deeper in the soil (Pütz 1993, 1996; Pütz and Sukkau 2002). Anecdotally, younger individuals (as indicated by leaf characters being thinner and more elongated relative to adult plants) of *Ledebouriinae* are generally shallower in the soil (C. C. Howard, personal observation). It is probable that at the individual level, plant age, bulb diameter, and bulb depth are interrelated. For example, the longer an individual persists in the environment (i.e., the older it gets), the more it can grow and develop a larger bulb. Surviving year after year then gives it time to burrow itself deeper into the soil through, for example, contractile roots (Pütz 2002). The deeper placement then offers more protection from aboveground disturbances for the individual. Some support for the potential relationship between plant age and bulb diameter can be seen in two species that have an overall negative relationship between bulb diameter and bulb depth, albeit not statistically significant (fig. 4k, 4n). For these species (*Ledebouria noritica* [fig. 4k] and *Ledebouria* aff. *galpinii* [fig. 4n]), soil composition and habitat preferences may be partly the cause for larger, shallower bulbs since both are sheet rock specialists. Here, larger bulbs may be less deep because as the plants grow and develop larger bulbs, the wider diameter of the bulb pushes the individual shallower in what little soil exists on top of the rock. Whether these species pull themselves deeper if given the opportunity remains unknown. Interestingly, there is another species that showed an overall negative slope, *Ledebouria mokobulaneensis* (fig. 4j), which is a montane grassland species in a habitat with relatively long, cold winters. Why individuals of this taxon would have shallower, larger bulbs is not immediately apparent. This result may simply reflect our sample size, or there could be other traits that provide protection to the plant rather than depth (e.g., tunics that insulate the bulb). More in-depth *in situ* observations and measurements should be made for this species as well as additional species from across the *Ledebouriinae* distribution.

The patterns we observed allow us to generate several hypotheses that should be tested in not only *Ledebouriinae* taxa but bulbous species in general. For example, species collected in Zambia had overall deeper bulbs than those found in South Africa (fig. A1 [available online]). There are several variables that could explain this pattern, such as drought season duration, temperature, or habitat. Additionally, a range of bulb

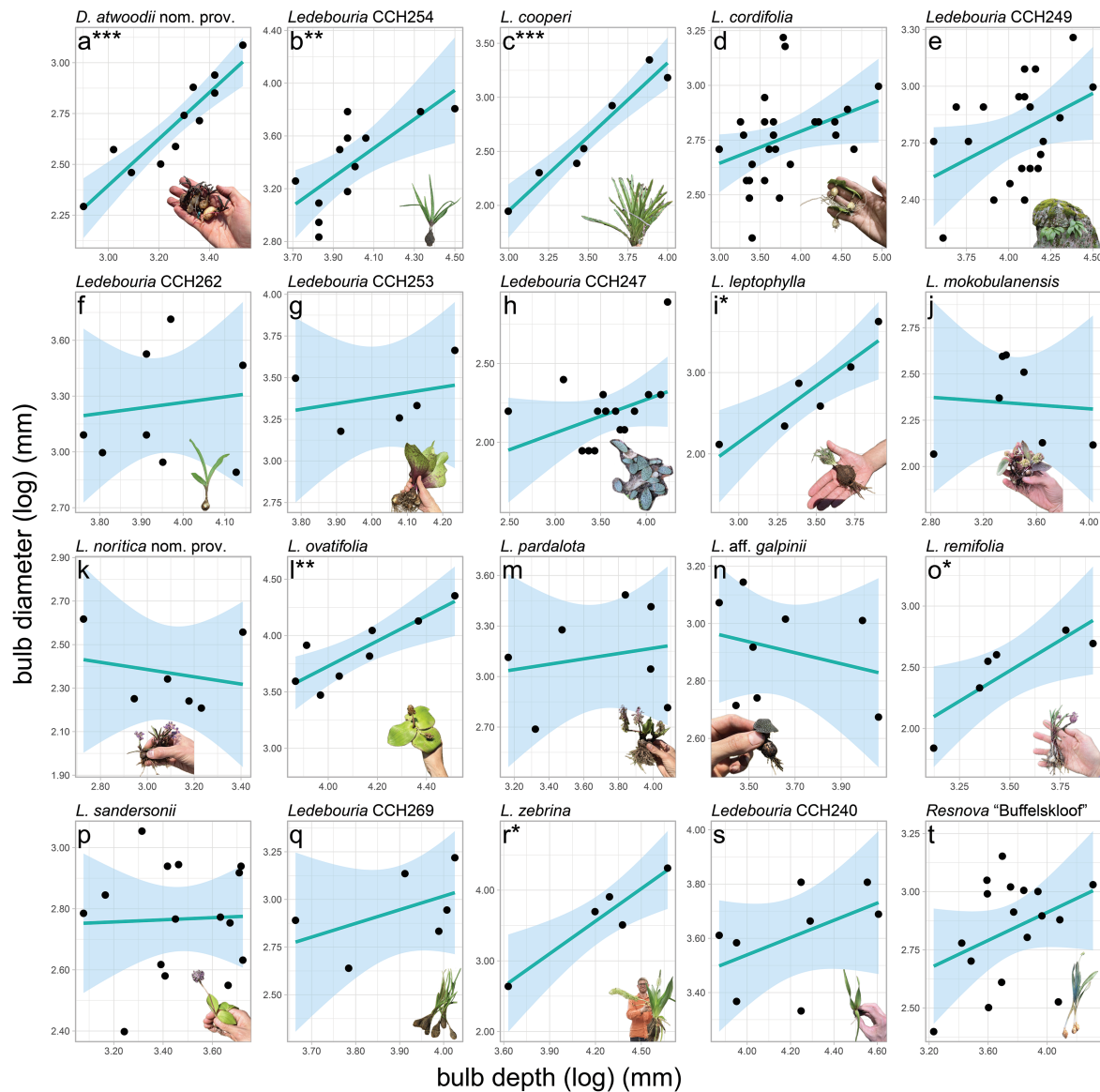


Fig. 4 Within species, larger bulbs generally tend to be deeper, with a few exceptions. Plots show the relationship between the natural log of bulb diameter and bulb depth for species that had five or more individuals measured for both traits. Species without specific epithets (i.e., those with collection numbers) are undescribed taxa that are morphologically distinct from known species within the Ledebouriinae (see the appendix for more information). Collection numbers are example specimen numbers and do not indicate every collection of the species located. Plots with asterisks indicate statistical significance (** $0 < P < 0.001$; * $0.001 < P < 0.01$; * $0.01 < P < 0.05$). Inset images show examples of individual plants from the field. Axis scales for each plot differ from one another. Plots were made using ggplot2 version 3.4.2 (Wickham 2016).

diameters were found across the Ledebouriinae species examined, but the morphological composition of the different bulbs and their sizes remains unknown. Across taxa, bulb diameter can vary by differences in the number and thickness of bulb scales (i.e., fleshy leaves) as well as the overall shape of the scales (Rees 1968, 1972; Speta 1984; Gordanić et al. 2021). Therefore, a logical next step would be to examine and incorporate data on the internal morphological bulb composition across Ledebouriinae taxa in addition to the position in and properties of the soil. Furthermore, examining and gathering similar

data from species found across the independent evolutions of the bulbous habit (Patterson and Givnish 2002; Howard et al. 2019) would greatly expand our understanding of the relationship between bulbous plant morphology and ecology. For example, some bulbous species make one relatively large bulb scale (e.g., some *Allium*), whereas others make relatively thinner scales in greater number (e.g., Amaryllidaceae; Irmisch 1850; Rees 1972). The ecological influences shaping the evolution of these different morphologies are still obscure, many of which have independently evolved. The bulbous habit offers us fantastic

opportunities to understand the drivers of convergent evolution and the functional significance of variations in seemingly similar morphologies.

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