"Heuweltjies" – the "Little Hills" of western South Africa

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10.1 "Heuweltjies"—the "Little Hills" of western South Africa

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Figure 10.1.2:
Western portion of South Africa with place names used in text. The pink-shaded areas represent the extent of the Succulent Karoo Biome within South Africa following Mucina, et al., 2006; the northern extension of this biome in southern Namibia is not represented. Names of cities and towns are in italicized, black serif font. Names of various physiographic regions are in dark red sans serif font. The Sandveld and Swartland regions are within the Fynbos Biome. Names of major rivers are in blue sans serif type. Note two separate rivers named "Olifants" in the Western Cape—one draining to the Atlantic Ocean, the other to the Indian Ocean.
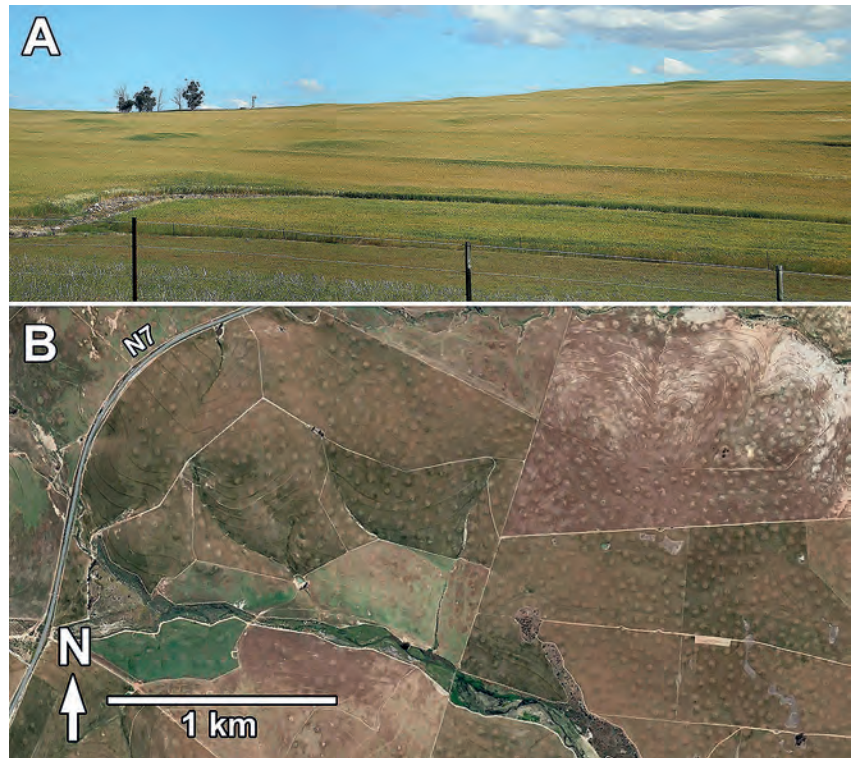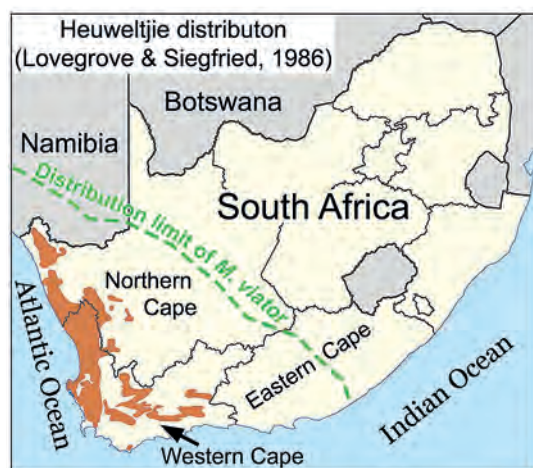
Introduction

What are heuweltjies and where are they found?

Heuweltjie, pronounced "hue-vil-kee," means "little hill" in Afrikaans. These low relief, circular, earthen mounds commonly range in diameter from 10–35 m, with heights of 0.5–2 m. They are a most unusual visual component of landscapes throughout the Succulent Karoo Biome of western-most South Africa, where in some places the mounds cover a quarter of the land surface (Fig. 10.1.1). Heuweltjies also occur in the drier portions of the Fynbos Biome (Rebelo et al., 2006) adjacent to the Succulent Karoo in the Western Cape, including the Sandveld near the Atlantic coast (Fig. 10.1.2 shows locations of principal place names used in the text). They occur throughout the Swartland farming region, 50–150 km north to northeast of Cape Town, which has been largely converted from the original renosterveld vegetation (a component of the Fynbos Biome) to cropland. Despite the long duration of intensive crop production in that region, the muted topographic bulges of heuweltjies persist in cultivated fields, densely dotting the agricultural landscape (Fig. 10.1.3). Heuweltjies occur over a wide range of annual precipitation, from areas receiving less than 100 mm annual average precipitation in the northwestern-most portions of South Africa (the Richtersveld) to regions receiving more than 400 mm in the southwestern portion of the Western Cape. Approximately 67,000 km^2 in western South Africa contain heuweltjies, principally located in the Northern Cape and Western Cape provinces (Lovegrove & Siegfried, 1986; Fig. 10.1.4).

Externally visible features of heuweltjies differ considerably from those of fairy circles of arid portions of Namibia:

- Heuweltjies, as the name implies, are raised mounds. However, fairy circles are either without vertical relief, or are very slightly concave due to deflation of sandy soil materials by the wind.
- Heuweltjies are in some places more densely vegetated than the areas surrounding them, but fairy circles lack permanent vegetation cover.
- Heuweltjies occur in diverse geological settings and landforms, including hillslopes underlain by different rock types (plutonic igneous, metamorphic, and sedimentary rocks) as well as deposits of aeolian sand and alluvium on valley floors and the wide, Atlantic coastal plain. Fairy circles, in contrast, generally occur only on sandy substrates primarily of aeolian origin.

Figure 10.1.3 A, B:
A: Terraced cropland in the Swartland planted to winter wheat; the darker green raised areas are heuweltjies. This region with warm climate coupled with a cool-season precipitation regime supports non-irrigated agriculture and is known as the "Breadbasket of South Africa." October, 2012.
B: Aerial view in the Swartland, 4 km northeast of Piketberg with the entire area occupied by cultivated lands and densely covered with regularly spaced heuweltjies. Average annual precipitation at Piketberg is 404 mm. Google Earth™ view, October 2010.
Latitudinal and longitudinal coordinates of center of view are -32.88266°, 18.79971°.

Figure 10.1.4:
The distribution of heuweltjies in South Africa (in brown, redrawn from Lovegrove & Siegfried (1986). The green dashed line extending from Namibia, southeast through the Eastern Cape represents the northern and eastern limits of the distribution of the southern harvester termite, *Microhodotermes viator* (boundary based on mapping of documented collections in Coaton & Sheasby, 1974). Heuweltjies occupy only a portion of the distribution range of this termite species.
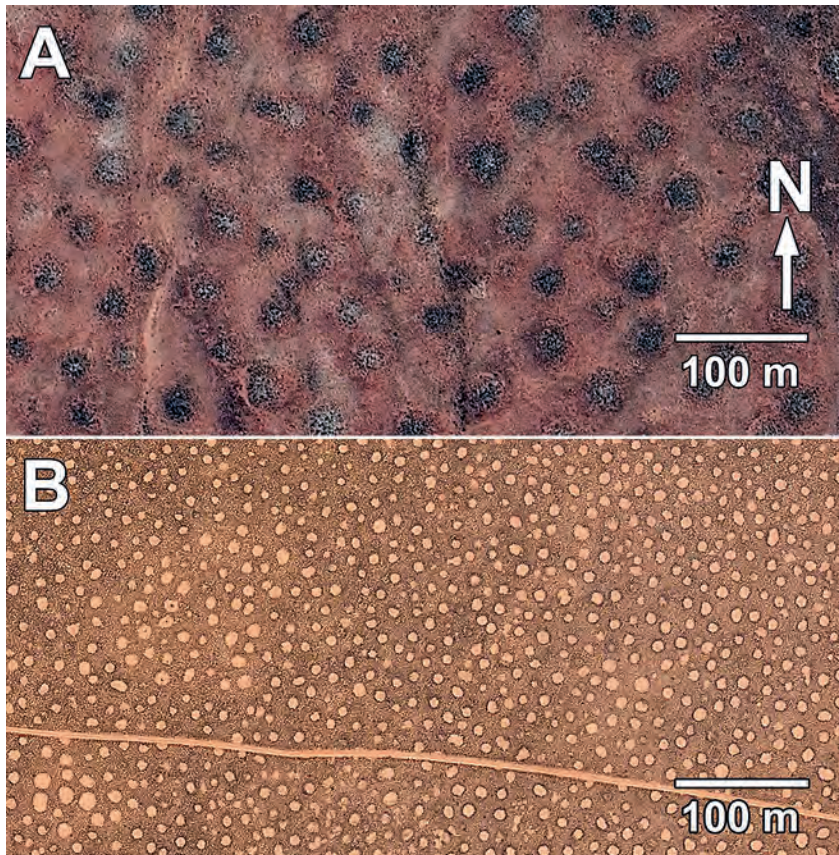
Figure 10.1.5 A, B:
Google Earth Pro ™ vertical aerial views of heuweltjies and fairy circles shown at identical scales.
A: Heuweltjies 54 km N-NW of Nuwerus, Western Cape, on stabilized Quaternary aeolian sand deposits. Denser vegetation gives the heuweltjies the dark, finely stippled appearance. Reddish-brown color of the soil surface is more apparent in off-mound areas with sparser vegetation. Center of view is -30.78637°, 18.78637°.
B: Fairy circles on aeolian sand deposits in northwestern Namibia, 29 km W-NW Sesfontein. The light-colored fairy circles lack vegetation; the darker surrounding matrix is vegetated. The linear feature cutting through the lower portion of the view is an unpaved road (Route D3707, leading east from Sesfontein). Center of view is -19.04269°, 13.35377°.

• The average distance (center to center) between adjacent heuweltjies is typically 40–50 m, more than double the distance between neighboring fairy circles in Namibia (Fig. 10.1.5).

Despite the above contrasts, heuweltjies and fairy circles share a striking characteristic – their spatial overdispersion (i.e., non-random positioning, tending towards uniformity of spacing) (Lovegrove & Siegfried, 1989; Cramer & Midgley, 2015; Juergens et al., 2015; McAuliffe et al., 2019a; Fig. 10.1.5). Although the factors responsible for formation of both heuweltjies and fairy circles have been a topic of considerable debate, research published within the last decade provides substantial evidence for the role played by termites in the formation of both heuweltjies and fairy circles. Separate termite species are associated with the two features – the southern harvester termite (*Microhodotermes viator*) with heuweltjies, versus the sand termite (*Psammotermes allocerus*) with fairy circles of the Namib Desert region. The long-term presence of colonies of both species markedly alters the physical and biotic character of the landscapes they inhabit. This chapter reviews the current state of knowledge about heuweltjies, including:

• Biological and physical features
• Regional variation
• Occurrence of *M. viator* in areas lacking heuweltjies
• Their age
• Formation of heuweltjies
• Biodiversity and conservation

## Characteristics of heuweltjies

Biological and physical features

a) Occupation by termites

Abundant evidence demonstrates that colonies of *M. viator* occupy heuweltjies. Activity within the mound by the termites generates fresh accumulations of frass and soil dumps on the mound surface, whereas areas between mounds lack such accumulations (Moore & Picker, 1991; Milton et al., 1992). Detailed examinations of excavations and cross-sections through heuweltjies reveal features constructed by the termites, including tunnels and food storage chambers filled with small, cut plant stems (Moore & Picker, 1991; Francis et al., 2013), as well as large, centrally located spheroidal nests (Francis et al., 2021; Clarke et al., 2022; Fig. 10.1.6). The nests, or "hives" as they are sometimes called, may reach approximately 1 m diameter and are filled with closely set, subparallel layers of dark-colored carton composed of organic material. Individual colonies contain a single nest (Coaton, 1962; Coaton & Sheasby, 1974, Moore & Picker, 1991). Petrified remnants of entire nests impregnated with calcium carbonate or silica are also occasionally observed in cross-sections of mounds (Francis et al., 2021; Clarke et al., 2022; personal observations).

b) Soil characteristics

Soils of heuweltjies are enriched with nutrients and organic carbon. These fertile islands are generally surrounded by nutrient-poor, highly weathered soils, which are typical for most portions of western South Africa (Midgley & Musil, 1990; Milton et al., 1992; Booi, 2011; Kunz et al., 2012; Schmiedel et al., 2016). Mound soils also contain considerably higher concentrations of basic cations (Ca, Mg, Na, K) and have a higher pH than soils between mounds (Fig. 10.1.7; Midgley & Musil, 1990; Ellis, 2002, 2004; 1990, Petersen, 2008; Francis et al., 2012; Kunz et al., 2012; Midgley et al., 2012; Schmiedel et al. 2016;
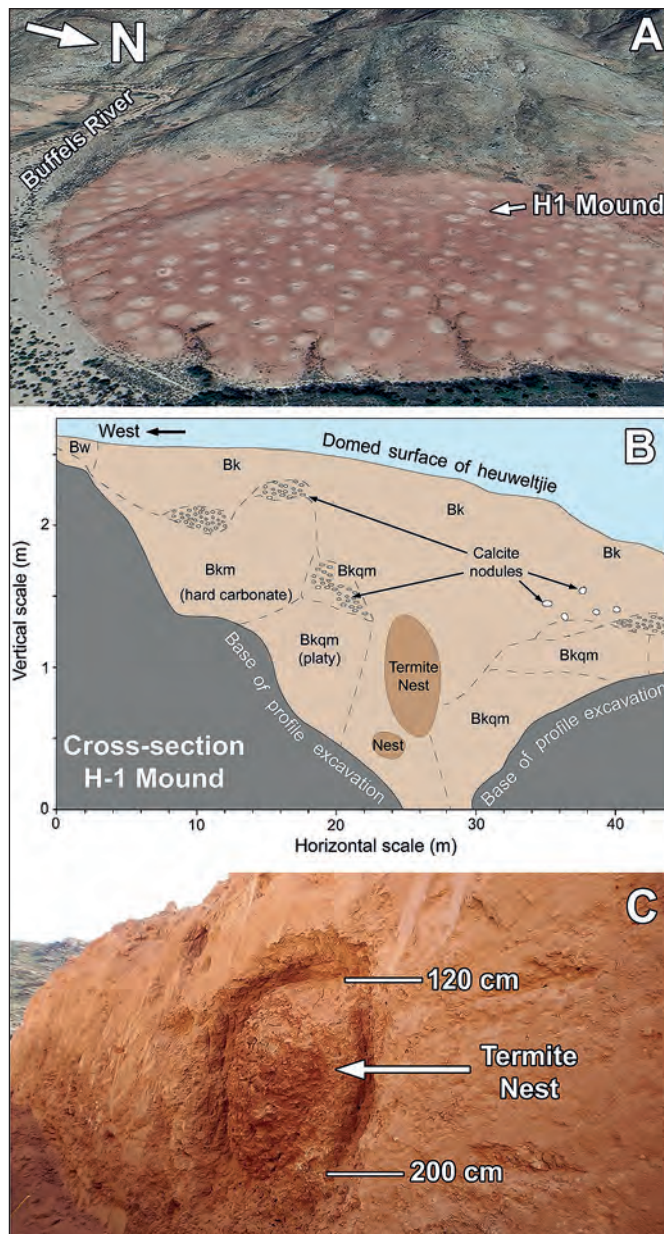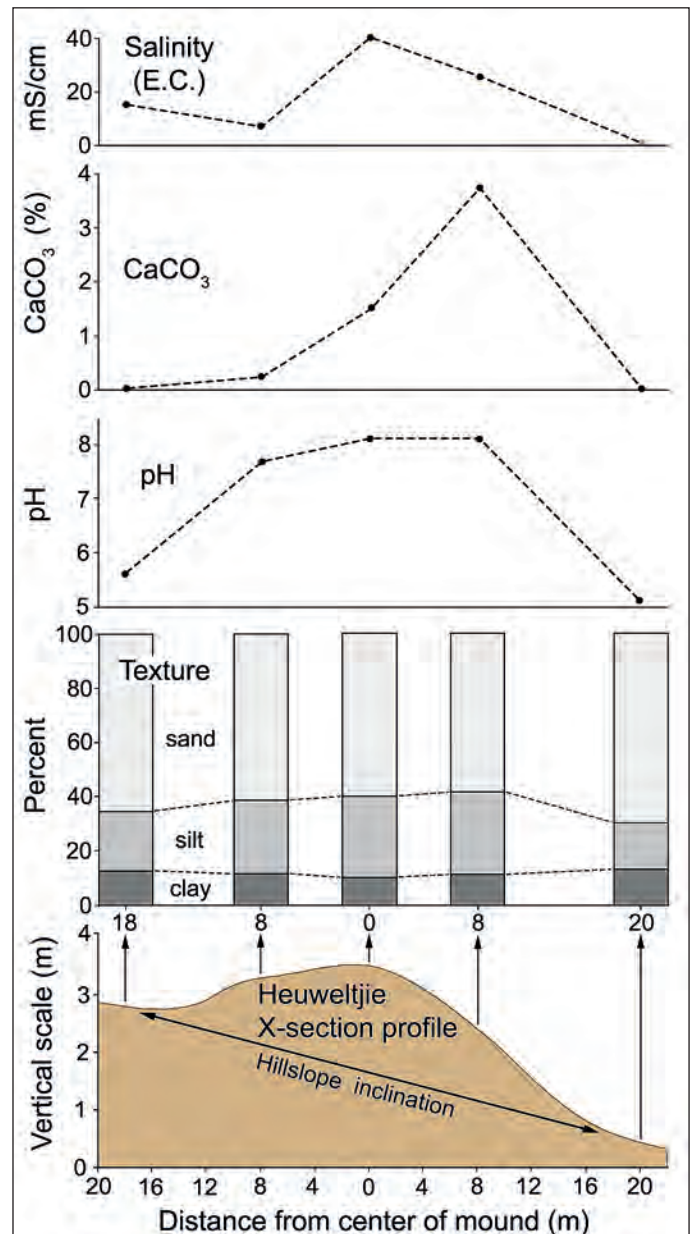
Figure 10.1.6 A–C:.
A: Google Earth™ oblique aerial view of sediment-covered pediment (reddish brown) at the base of low mountains, 8 km S-SE of the town of Buffelsrivier, Northern Cape, and location of soil investigations reported in Vermooten (2019), van Gend et al., (2021) Francis et al. (2021), and Clarke et al. (2022). Regularly spaced, light-colored heuweltjies ranging from 25-35 m diameter cover the pediment. One of the heuweltjies examined in those investigations (H1 mound) is indicated (-29.76654°, 17.63662). The distance across the pediment in this view is approximately 1 km.
B:Cross-section diagram of soil stratigraphy of the trenched H1 mound, redrawn from Francis et al. (2021) showing horizon designations (Bw, Bk, Bkm, etc.). Horizon designations include a specific capital letter indicating the master horizon (e.g., B), followed by lower case letters that designate particular subordinate characteristics within the master horizon. Subordinate designations included here are k – accumulation of pedogenic calcium carbonate, m – cementation, q – silica accumulation, and w – development of color or structure, but lacking accumulation of alluvial clay, calcium carbonate or other materials. Position of a large, centrally located nest of *M. viator* is shown in brown, and is pictured below in Fig. 5C.
C: Eastward view though the trenched H1 mound showing the large, egg-shaped nest of *M. viator.* Photograph courtesy of Michele Francis, Stellenbosch University.

Figure 10.1.7:
Soil characteristics from five soil profiles distributed across the width of a 32 m-wide heuweltjie south of Soebatsfontein, Northern Cape, from Petersen (2008). The cross-section profile is redrawn from Figure 155, p. 197, and the plotted data are values listed in Table 5, p. 197 of that work.
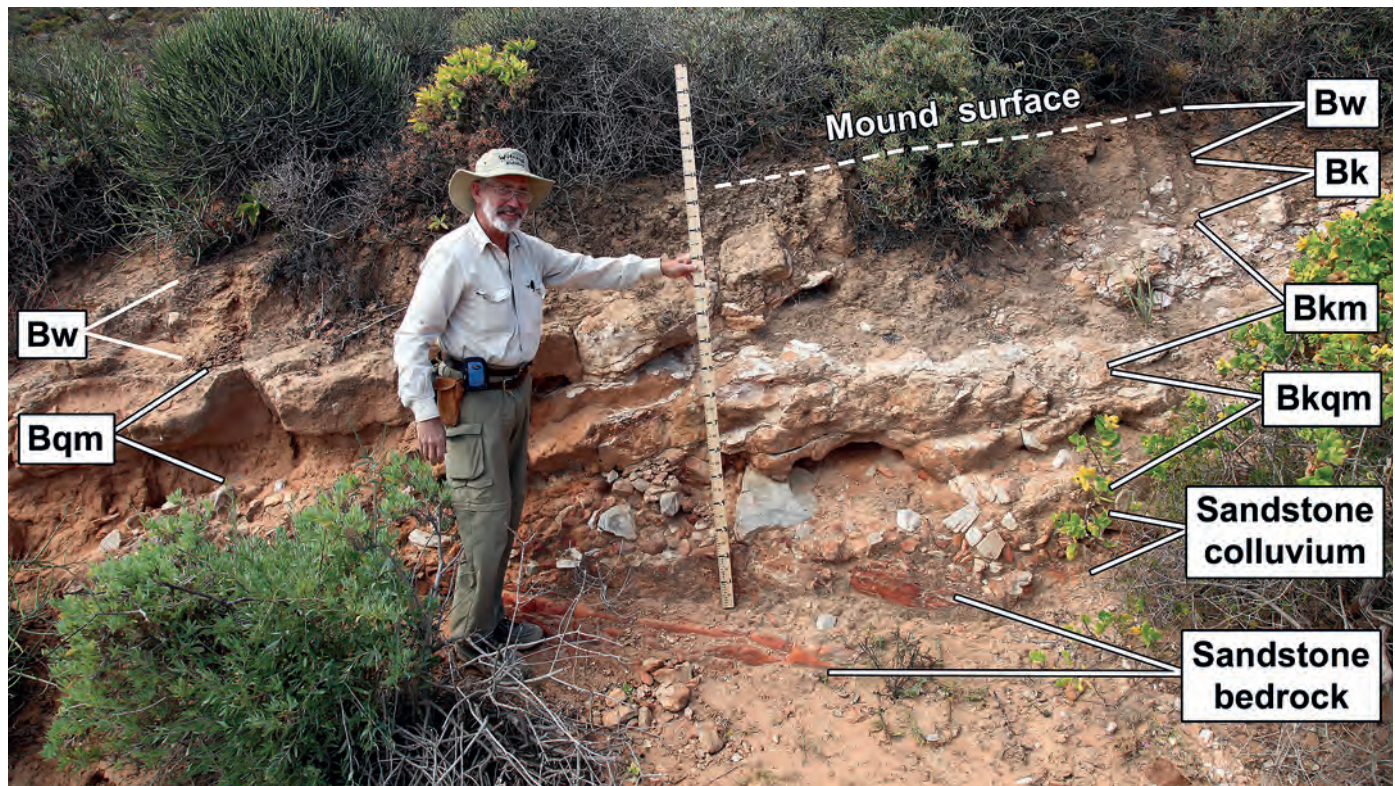
Figure 10.1.8:
Jeremy Midgley, Univ. of Cape Town (center) discussing the origin of cemented pedogenic carbonate exposed in a heuweltjie bisected by roadway excavation. The upper surface of the mound to the left of Midgley is covered by vegetation. The white material beneath the brown, fine-grained soil is cemented calcium carbonate, a *petrocalcic soil horizon*. 8 km E of Worcester, South Africa (-33.62501°, 19.53503°); 19 October 2012.

Clarke et al., 2022). Substantial accumulations of calcium carbonate ($CaCO_3$) in the form of thick, cemented layers (petrocalcic soil horizons or calcrete, designated as Bkm horizons in soil profile descriptions), are often present beneath the surface (Fig. 10.1.8). Heuweltjies also frequently contain massive, silica-cemented soil horizons (petroduric horizons or duripans, labeled "Bqm" horizons in soil profile descriptions; Ellis, 2002; Francis et al. 2012; 2013; Fig. 10.1.9). In addition to the formation of carbonate- and silica-cemented horizons, heuweltjie soils typically have considerably higher salinity than surrounding soils (Fig. 10.1.7; Petersen, 2008; McAuliffe et al, 2014, 2019a; van Gend et al., 2021; Clarke et al., 2022), and the contrast in salinity between on-mound and off-mound soils increases with decreasing average rainfall of various regions (Booi, 2011). In some of the more arid regions, extremely high soil salinity at deeper levels of the soil of heuweltjies can potentially inhibit vegetation if those layers are exposed at the surface by erosion (Petersen, 2008; McAuliffe et al., 2014).

In the upland settings in arid and semi-arid environments where heuweltjies occur, the considerable depth to the water table (> 30 m; Musekiwa & Majola, 2011) rules out groundwater as the source of the $CaCO_3$ contained within the pet-

rocalcic soil horizons of mounds. Additionally, the downward variation of increasingly soluble minerals in the mounds indicates that calcite and gypsum in the mounds is not a precipitate formed by evaporative wicking of saline groundwater to the surface (Clarke et al., 2022). Nearly the entire region where heuweltjies occur is underlain by non-calcareous bedrock from which very little calcium can be derived by weathering. Soderberg & Compton (2007) determined that atmospheric inputs, largely by the washout of aeolian materials by precipitation, are the principal source of soil calcium in the region. Those exogenous inputs, broadcast uniformly over the landscape, are extracted by plants and are used or stored in plant tissues, often as calcium oxalates (Midgley & Musil, 1990, Williams, 1979; Milton et al., 1994). Harvest and transport of plant materials by *M. viator* generate a net transfer of calcium and other elements to the area of the central nest from the surrounding area, inexorably leading to the localized accumulation of those materials over time (Ellis, 2002; Francis & Poch, 2019; McAuliffe et al., 2019a). In the soil environment, calcium oxalates weather to $CaCO_3$, through the action of oxalate-metabolizing (oxalotrophic) fungi and bacteria (Garvie, 2003, 2005; Braissant et al., 2002), in a process called the oxalate-carbonate pathway (Verrechia et al., 2006). Oxalotrophic bacteria

Figure 10.1.9:
Cross-section through a 30 m diameter heuweltjie bisected in a roadcut excavation. The right side of the image is located to the left of the mound's center. The hillslope surface surrounding the mound is mantled by angular sandstone colluvium over sandstone bedrock. Stratigraphically, the heuweltjie is superimposed on top of the same colluvium and underlying bedrock, indicating the fine-grained materials of the mound *accumulated* on top of the original hillslope surface at that location. The significance of this stratigraphic positioning of the mounds is discussed in the section titled "Formation of heuweltjies*".* With time, those fine-grained materials have subsequently been altered pedogenically, including formation of the silica-cemented Bqm horizon. Towards the center of the mound, the Bqm horizon transitions to a Bkqm horizon that also contains cemented $CaCO_3$. The Bkm horizon above the Bkqm horizon lacks silica cementation. Fine-grained, non-cemented horizons near the mound surface contain $CaCO_3$ in the lower portion (Bk), but lack it nearer the surface (Bw). The location is a west-facing hillslope 6 km east of the confluence of the Doring and Olifants rivers, 14 km S-SE of Klawer, Western Cape; Figure 15 shows additional views of the surrounding hillslope environment (-31.88114°, 18.70586°).Pictured is the author; photo by Sam Jack, 16 October 2016.

have been identified from the guts of fungus-cultivating termites (*Odontotermes*) (Suryavansi et al., 2016). *Microhodotermes viator* does not cultivate fungus gardens, but rather directly consumes plant material. Nevertheless, oxalotrophic bacteria have also been identified from the hindgut of *M. viator* (Rohland, 2010). However, Francis & Poch (2019) provided evidence that most of the chemical transformation of calcium oxalates to $CaCO_3$ may not occur within the digestive tracts of *M. viator*. Rather, the consumption and digestion of plant materials by the termites, followed at least in part by consumption of termite fecal materials by minute orobatid mites, produces very finely digested materials. The transformation of calcium oxalates contained in those materials to $CaCO_3$ eventually occurs within the soil environment. Similarly, the accumulation of soluble salts

is a consequence of the net transfer of materials from surrounding areas to the central location of colonies by the termites and the accumulation of salts in the vicinity of the colony focus is a time-dependent process (McAuliffe et al., 2019a). The enrichment of soils around termite colonies with $CaCO_3$ and soluble salts is a widespread phenomenon that occurs throughout the world (Lobry de Bruyn & Conacher, 1990).

Soils of heuweltjies typically have higher silt or combined silt + clay contents than surrounding soils (Fig. 10.1.7; Midgley & Musil, 1990; Milton et al., 1992; Petersen, 2008; Booi, 2011; Cramer et al., 2012; Kunz et al., 2012; McAuliffe et al., 2019b; Vermooten, 2019). The texture of heuweltjie soils, particularly high silt content, has implications regarding processes of mound

Figure 10.1.10 A–G
Contrasts in diameters of heuweltjies and extent of coverage of the land surface by the mounds in different locations. The white horizontal scale bar in each image is 100 m.
A – 16 km W of Steinkopf, Northern Cape (-29.26147°, 17.57059°)
**B** – 8 km S-SE of Buffelsriver, Northern Cape (-29.76733°, 17.60463°)
C – 18 km S-SW of Soebatsfontein, Northern Cape (-30.27644°, 17.54464°)
D – Strip-cropped wheat fields, 8 km W of Graafwater, Western Cape (-32.14314°, 18.51908°)
E – Agricultural fields 5 km SE of Piketberg, Western Cape (-32.92560°, 18.79721°)
F – 19 km S-SW of Laingsburg, Western Cape. In this area, heuweltjies range between 8-15 m diameter and cover 3% of the land surface (McAuliffe et al., 2014) (-33.35485°, 20.79855°)
G – Tierberg Long-Term Ecological Research site, 23 km E-NE of Prince Albert, Western Cape (-33.17377°, 22.27160°).Heuweltjies average 13 m diameter and cover 3.2% of land surface (Milton et al., 1992).
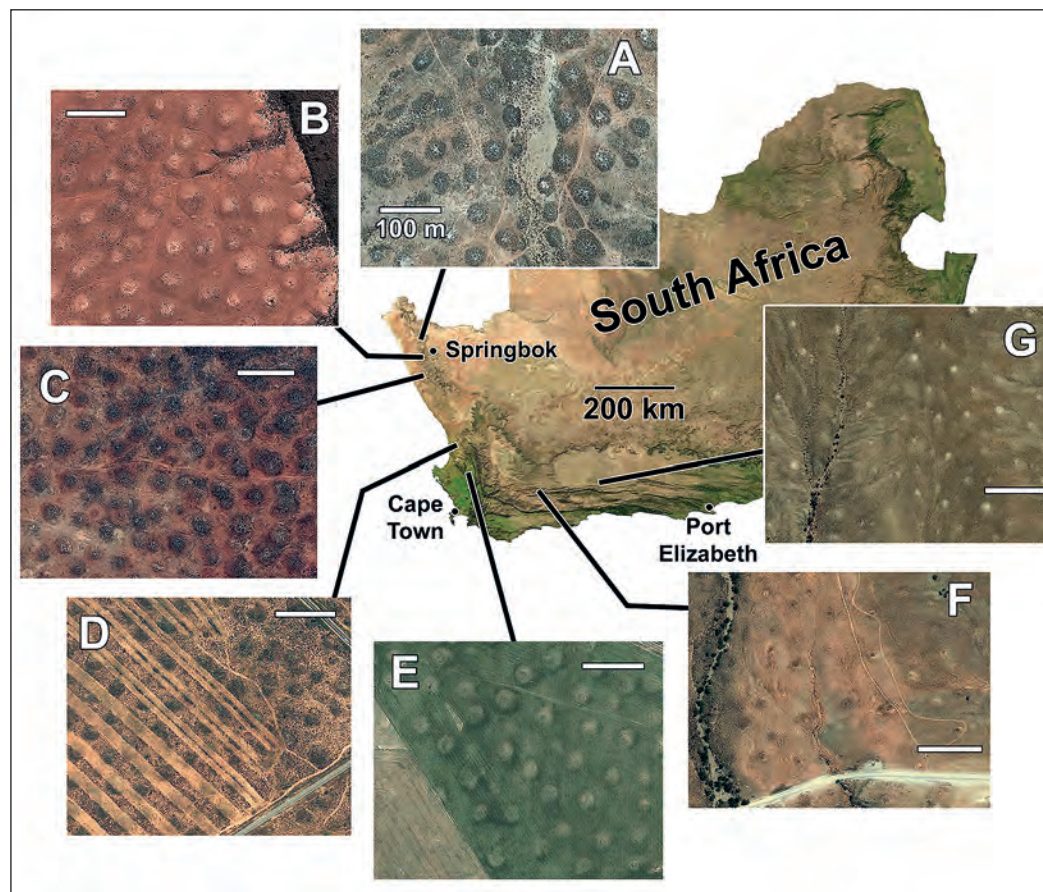
formation, discussed later. Despite the finer texture, unless they are compacted by livestock or other disturbances, soils of heuweltjies absorb precipitation more readily than surrounding areas (Dean, 1992). Abundant macropores created by termite tunnels likely enhance the infiltration and downward percolation of water. The finer texture and higher organic matter content give mound soils higher water-holding capacity than surrounding soils, and soil water contents in heuweltjies are generally higher and persist longer into dry seasons than in surrounding soils (Midgley & Musil, 1990; Booi, 2011).

Regional variation

a) Dimensions

Heuweltjies vary considerably in size from region to region. The mounds are considerably larger (both diameter and height), and the proportion of the land surface covered by the mounds is greater, in the broad Atlantic coastal plain region within 50–80 km of the coast compared to more inland locations (McAuliffe et al., 2014; Fig. 10.1.10). In portions of the coastal plain, heu-

weltjies commonly attain diameters of 30 m or more and heights of 1–2 m, and there can be a more than 20-fold difference in the average volume of individual mounds in this region from those of more inland locations (Fig. 10.1.11; McAuliffe et al., 2014). Cramer & Midgley (2015) arrived at similar conclusions through quantitative analyses of satellite imagery throughout the entire geographic range of heuweltjies—heuweltjies achieved largest diameters and occupied the largest portion of the landscape in the western coastal region. Additional analyses by Cramer et al. (2017) indicated that heuweltjies also cover a larger fraction of the landscape in areas near large rivers (Fig. 10.1.2). That relationship is readily observed in the Northern Cape along the middle to upper reaches of the Buffels River west of Springbok (Fig. 10.1.10B; Clarke et al., 2022), and in the Western Cape, along the Olifants River in the vicinity of Vredendal south to Clanwilliam, the middle reaches of the Berg River in the Swartland farming region area north from Malmesbury to the northeast of Piketberg, the Breede River valley from the vicinity of Worcester southeast to Robertson, and the 20 x 70 km-wide intermountain basin that contains the cities of

Figure 10.1.11 A–C:
Contrasts in diameters and heights of heuweltjies in various locations.
A: Heuweltjie bisected by roadway 8.5 km W of Graafwater, Western Cape with diameter of 34 m and height of 2.45 m. This is in the Sandveld region, much of which has been converted to both irrigated and non-irrigated crop production. The landscape beyond the fence, including the mound has been cleared of vegetation for non-irrigated, strip-cropped wheat cultivation (-32.14764°, 18.51436°). 1 November 2012.
B: Heuweltjie with dense cover of pink-flowering *Mesembryanthemum* (= *Psilocaulon*) *junceum* (Aizoaceae), 19 km S-SW of Laingsburg, Western Province. Surrounding vegetation is dominated by *Pteronia pallens* (Asteraceae). Mound diameter = 13 m. Note fine-grained texture of mound soil (-33.35558°, 20.80033°). 14 November 2012.
**C:** Heuweltjie lacking vertical relief, Wolwekraal Private Nature Reserve near Prince Albert, Western Cape. The 6.5 x 5.0 m circular possesses distinct vegetation, dominated by *Lampanthus unifloris, Malephora crassa*, and *Phyllobolus defoliata* (Aizoaceae), and two members of the Amaranthaceae: *Caroxylon aphyllum* (= *Salsola aphylla*), and *Atriplex lindleyi*, a non-native species from Australia. The surrounding area is dominated by *Ruschia spinosa, Mesembryanthemum noctiflorum* (Aizoaceae) and *Pteronia pallens. Microhodotermes viator* workers were observed and collected within the patch, actively expelling frass onto the soil surface. Long-term presence of the termites imparts a distinct signature on soil characteristics. Soil within patch has a salt content nearly 20x that of the surrounding area (4,340 vs. 231 ppm), and the presence of the halophytic *C. aphyllum* is a response to the greater salinity. Soil $CaCO_3$ content is also higher within the patch (6.33% vs. 0.26%) (-33.18314°, 22.03020°). Plant species list was recorded by M. Timm Hoffman. 7 October 2016.
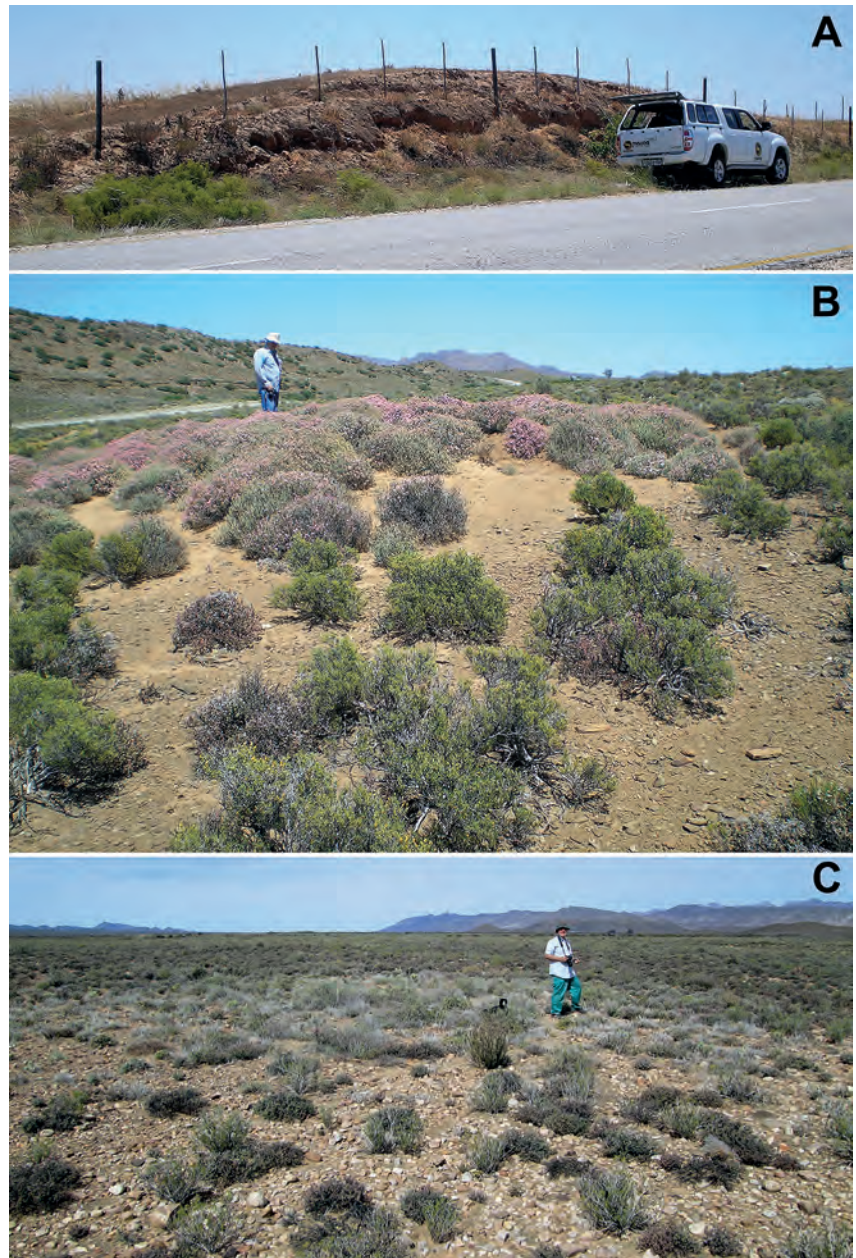
Calitzdorp and Oudtshoorn and the confluence of the Olifants and Gamka Rivers. The larger size of mounds and proportion of the land surface they occupy in these areas contrast strongly with many inland areas, including portions of the Little Karoo to the east in the smaller basins of the Cape Fold mountains, where diameters of heuweltjies typically are 15 m or less and heights rarely exceed 0.5 m (Fig. 10.1.11B, C). Whereas heuweltjies commonly cover a quarter or more of the land surface in areas throughout the western coastal region (McAuliffe et al., 2014; Schmiedel et al., 2016, Fig. 10.1.10A-D), heuweltjies in parts of the Little Karoo frequently cover less than

5% of the land surface (Milton et al., 1992; Fig. 10.1.10F, G). In some of those areas, heuweltjies do not accurately reflect the literal translation of the Afrikaans word for "little hills" because their surfaces are level with the surrounding landscape. Nevertheless, they are typically referred to as "heuweltjies" due to the contrasting vegetation cover of those patches (Fig. 10.1.11C). Despite this considerable variation in size of heuweltjies of different regions, heuweltjies throughout typically have an average, minimal center-to-center nearest neighbor distance in the range of 40-60 m (Fig. 10.1.10; Lovegrove & Siegfried, 1989; McAuliffe et al., 2014; Cramer & Midgley, 2015).
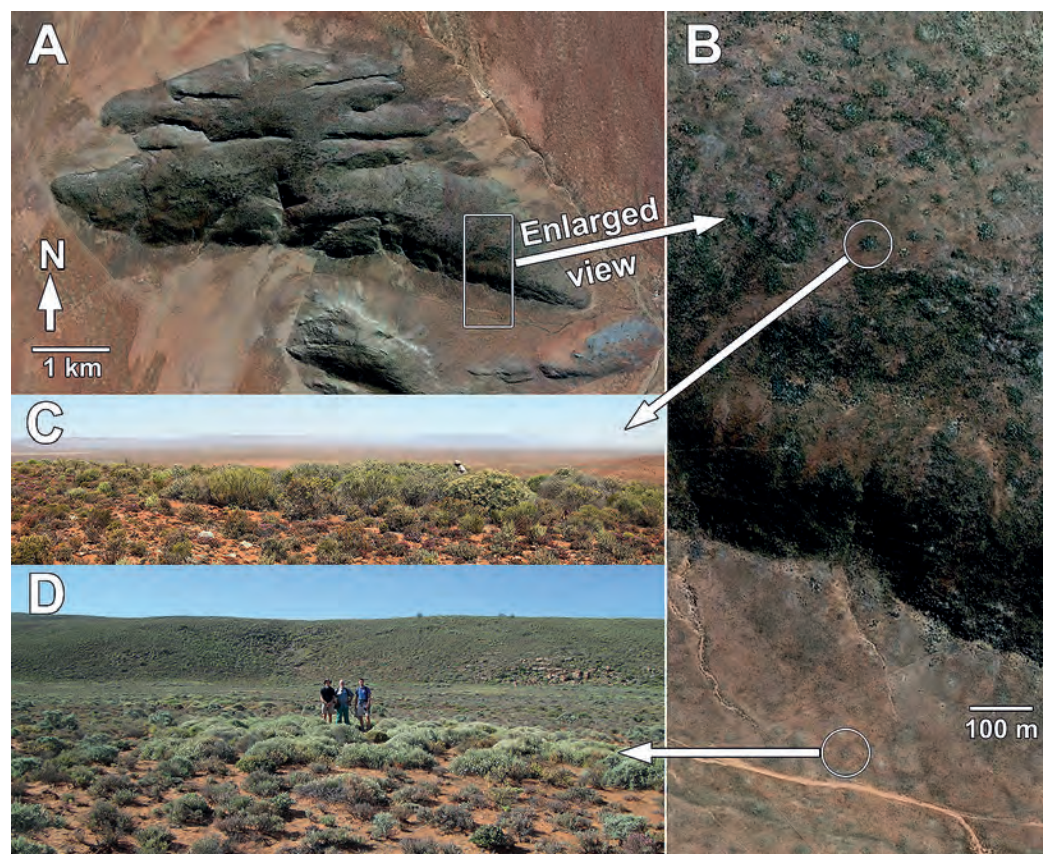
Figure 10.1.12 A–D:
A: Grootklip se berg, a low, granitic inselberg with ~ 100 m elevation relief above a wide expanse of Quaternary aeolian sand deposits. The entire inselberg has been fenced since the 1960s to prevent livestock access and poisoning by consumption of toxic plants including *Tylecodon* sp. (M. Timm Hoffman, personal communication with landowner). Sharp linear fenceline boundary visible in lower center. Google Earth™ imagery.
B: Enlarged Google Earth™ view showing locations of individual heuweltjies on upper surface of inselberg (top circle) and aeolian sand deposits at base.
C: Panoramic photo of heuweltjie with dense plant canopy cover (95% of soil surface cover) aver-aging 1.2 m height. Author (height 1.83 m) standing within vegetation of mound. Dominant species are *Stoebaria frutescens, Euphorbia mauritanica,* and *Lycium* sp. Surrounding vegetation averages 20-30 cm height with < 50% cover. Mound height estimated at 90 cm and fine-textured soil (0–10 cm depth) had lower sand content but higher silt content (sand = 69%, silt = 25%, clay = 7%) than the ad-jacent, off-mound soil (sand = 81%, silt = 12%, clay = 7%). (-30.83629°, 18.84232°). 20 October 2016.
D: Heuweltjie on basin floor with 30 cm vertical relief above surrounding soils. Fresh frass of *M. viator* was present of the surface. 60% canopy cover dominated by an unidentified *Mesembryanthe-mum* (*Psilocaulon*) species. The hillslope in the background is the south flank of Grootklip se berg (-30.84359°, 18.84261°).

b) Vegetation

Vegetation cover of heuweltjies varies. In more mesic regions, mounds are typically more dense-ly vegetated than the area immediately surround-ing them. However, in the more arid portions of the Succulent Karoo, the opposite is the norm—vegetation on the mounds is often considerably sparser than the surrounding area and, in some cases, the mounds are barren or nearly so. In either case, heuweltjies stand out visually be-cause of the vegetation contrast. The following discusses vegetation cover of heuweltjies in more mesic environments, followed by consideration of causes of the scant vegetation cover in more arid settings.

Given sufficient precipitation, the higher fertility and more favorable soil moisture conditions of heuweltjies promote growth of taller and denser vegetation. Plant species composition on the mounds differs substantially from that of the sur-

rounding area, usually with little overlap in species compositions. The greater productivity of heuweltjies (plant height and total canopy cover) is apparent in areas that have been spared a long history of heavy use for livestock production, either due to their remoteness or inaccessibility, or the exclusion of livestock by fencing. The species composition inhabiting heuweltjies varies considerably across the region. Throughout much of the Succulent Karoo, dense cover of succulent-leaved shrubs in the family Aizoaceae (e.g., *Mesembryanthemum, Drosanthemum*) frequently dominate mound vegetation (Figs. 10.1.11B, 10.1.12). In the *Robertson Karoo* (Mucina et al., 2006) near Worcester, the non-succulent shrub *Pteronia incana* (Asteraceae) often predominates, giving the mounds their distinct, ashen gray-green color that contrasts strongly with the surrounding, dark green vegetation dominated by *P. paniculata* (Fig. 10.1.13). In the Succulent Karoo, other species that frequently occur on heuweltjies include the succulents *Euphorbia mauritanica* (Euphoriaceae), *Tylecodon paniculatus* (Crassulaceae), and *Aloe microstigma* (Asphodelaceae). Non-succulent shrubs frequently include *Lycium* spp. (Solanaceae), *Rhus* (= *Searsia*) *undulata*, *Asparagus* spp. and others. In areas of even greater precipitation in the Fynbos Biome, for example the *Sandveld* coastal region in the area inland from Lamberts Bay to south of Elands Bay, the landscape has widely been converted to crop agriculture. However, remnants of the original vegetation remain, and non-succulent, woody shrubs up to 1.5 m tall predominate on heuweltjies, with shorter, sparser vegetation cover between mounds (Fig. 10.1.14). Heuweltjies in transition zones between typical vegetation of the Succulent Karoo vegetation and denser fynbos vegetation can have extremely diverse floral assemblages (Fig. 10.1.15). Quantitative descriptions and analyses of the contrast between vegetation of heuweltjies and adjacent off-mound areas have been reported from several individual sites or within limited areas (Knight et al., 1989, Armstrong & Siegfried, 1999; Midgley & Musil, 1990; Kunz et al., 2012). Swanepoel (2021) presented vegetation results collected from ten sites across a much more extensive region, from the Little Karoo region in the eastern portion of the Western Cape, westward to include sites in fynbos vegetation, and then north to the Vanrhynsdorp area in the Succulent Karoo. Collectively, these studies show that although the predominant plant species occupying heuweltjies vary geo-

graphically, the strong contrast between vegetation composition of mounds and adjacent areas off-mound in any one place is maintained.
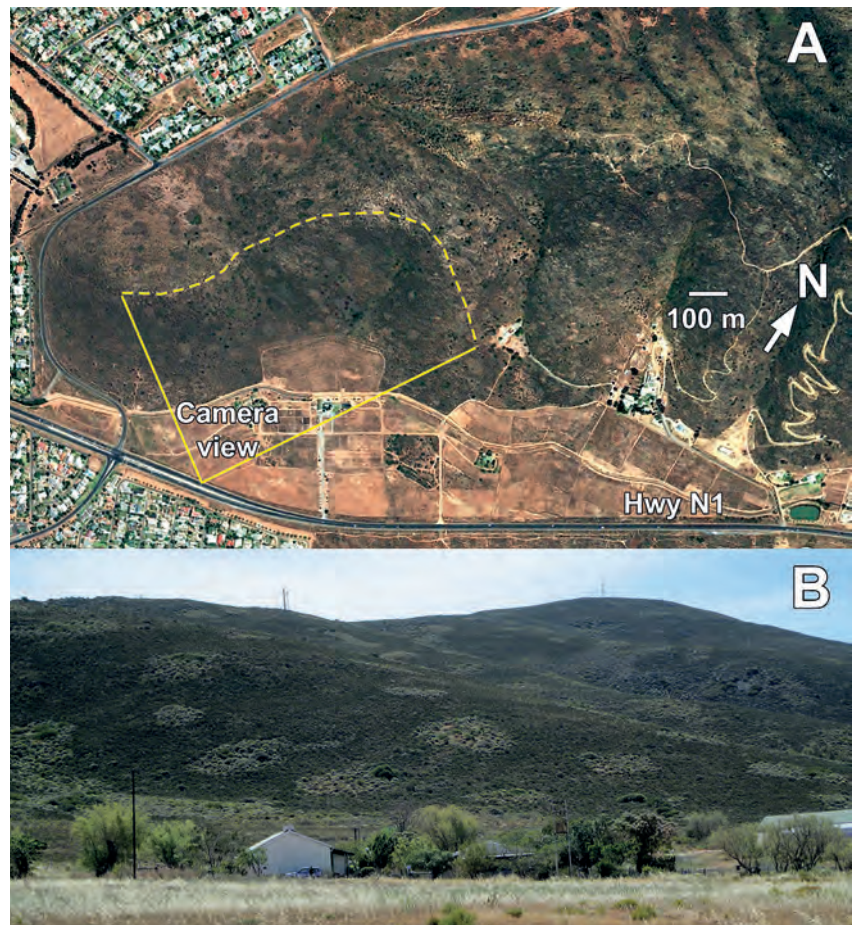
Livestock, particularly sheep, tend to graze the vegetation of heuweltjies more heavily than surrounding areas (Armstrong & Siegfried, 1990), probably attracted by the higher forage quality of mound vegetation, including greater average nitrogen content (Kunz et al., 2012). Comparison of how pastoral livestock production impacts vegetation of a site in the Succulent Karoo using a fence-line contrast demonstrated significant declines in cover of succulent-leaved shrubs under heavier grazing (Hanke et al., 2014). Esler et al. (2006) noted that under heavy grazing pressure, heuweltjies are the first to be denuded. Consequently, a long history of livestock production has greatly altered the vegetation of heuweltjies (Kunz et al., 2012; Schmiedel et al., 2016). Rahlao et al. (2008) documented that at a site near Worcester receiving 269 mm mean average precipitation (MAP), long-term rest from grazing (67 years) led to the recovery of denser and taller vegetation on heuweltjies. However, in an area with only 130 mm MAP, vegetation recovery following disturbance

Figure 10.1.13 A, B: Hillslopes dotted with heuweltjies at the Worcester Veld Reserve on the northeast side of Worcester, Western Cape Province. **A:** Aerial view showing camera field of view from north side of Highway N1. Vestiges of heuweltjies in cleared area to left of Hwy N1 label indicate that occurrence of the mounds originally extended to the valley floor. January 2010 Google Earth imagery. **B:** Hillslopes dotted with regularly spaced heuweltjies dominated by light gray-green canopies of *Pteronia incana.* Surrounding, off-mound areas are dominated by *P. paniculata* (camera position approx. -33.62574°, 19.46674°). 2 October 2016.

Figure 10.1.14 A, B:
A: Heuweltjies in dry fynbos vegetation (Namaqualand Sandveld), 5.3 km N of Graafwater, Western Cape. Much of this area has been cleared for dryland wheat cropping (pictured) or for center-pivot irrigated fields. Bright green, circular patches in field on right show original locations of heuweltjies. The area between the cultivated fields on the left and right has not been cleared, and taller and denser vegetation cover persists on some heuweltjies. White arrow indicates the position of a heuweltjie partially cut by excavation of the roadway and shown below in B.
B: View toward south showing heuweltjie with 2.5 m vertical relief above the surrounding area. Mound vegetation is dominated by non-succulent woody shrubs including bird-dispersed *Rhus undulata.* Adjacent off-mound vegetation includes *Willendowia incurvata* (Restionaceae) and *Ehrharta thunbergii* (Poaceae) (-32.10923°, 18.59394°). 5 November 2016.

is slow, and vegetation cover on heuweltjies remains diminished long after heavy use by livestock ceases (Schmiedel et al., 2016).

Although vegetation on heuweltjies in regions with very limited rainfall is more susceptible to long-lasting reductions of cover and altered species compositions, environmental factors unrelated to land use history are apparently involved in the most arid portions (< 100 mm average) of the Succulent Karoo. At a site with MAP = 73 mm in the Richtersveld region of northwestern-most South Africa (Fig. 10.1.16), Petersen (2008) examined a series of aerial photos taken from 1938 through 2004, observed no change in appearance of the mounds over that time span, and concluded that the barrenness of heuweltjies across the site was due to soil conditions unfavorable to plants (e.g., high salinity), and not the impacts of animal grazing or other disturbance.

The effects of climate on the condition of heuweltjies is demonstrated by a comparison of north-facing (towards the equator) versus south-facing hillslopes in the same area. The contrast in solar radiation (insolation) received as a function of hillslope aspect exerts a strong control over vegetation through both direct physiological effects on plants (e.g. differences in transpiration and water use), and the rate of direct evaporative losses of soil water (Burnett et al., 2008; Gutiérrez-Jurado et al., 2013). The linkage between insolation, soil moisture, and plant responses greatly influences erosive processes on hillslopes in semi-arid regions, with greater erosion frequently occurring on those facing the equator (Persico et al., 2022; McAuliffe et al., 2022). These relationships can be observed on hillslopes in some parts of western South Africa, where heuweltjies on the more mesic, south-facing hillslopes are densely vegetated, thereby inhibiting erosion. Those on the more arid, northern xeric exposures, however, have greatly diminished vegetation cover, or in some cases, are nearly completely barren and exhibit substantial, ongoing erosion (Fig. 10.1.17).

c) Spacing and density

The regular spacing of heuweltjies is attributed to strong, intraspecific, territorial interactions between members of neighboring termite colonies. Colonies of other termite genera (e.g., *Macrotermes, Odontotermes*) also tend toward
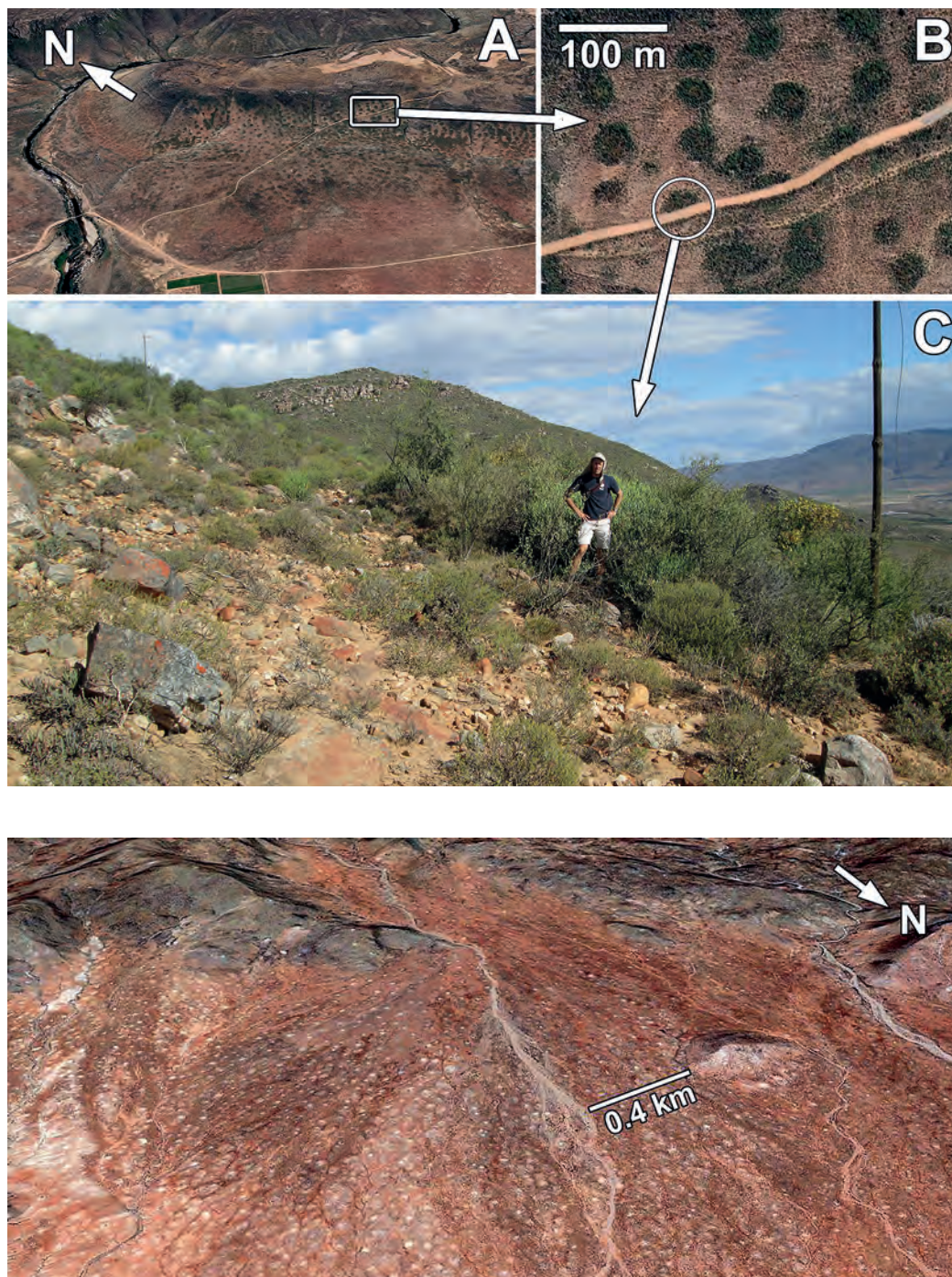
Figure 10.1.15 A, B:
A: Oblique angle Google Earth™ view of hillslopes 4-6 km east of the confluence of the Doring and Olifant rivers, Northern Cape. The Doring River is on the left side of view, and the distance in the foreground from left to right is approximately 3 km. Hillslopes are covered with heuweltjies from near the steep escarpment to the valley floor. Mounds on steeper slopes are densely vegetated, but vegetation cover diminishes with closer proximity to the valley floor due to clearing for crops and other agricultural uses. The white rectangle indicates enlarged view in B.
B: Enlarged Google Earth™ vertical view of densely vegetated heuweltjies on upper portions of slope. The circled mound is bisected by the road (see soil profile information in Fig. 10.1.9).
C: Contrasts in canopy cover between densely vegetated heuweltjie and adjacent area. The mound consists of ~ 1 m of fine-grained materials deposited on top of coarse sandstone colluvium and bedrock. The number of perennial plant species recorded on the heuweltjie (30) greatly exceeded that from the adjacent off-mound area (16) (plant species list recorded by Sam Jack, pictured (-31.88114°, 18.70586°). 16 October 2016.


Figure 10.1.16: Google Earth™ oblique aerial view containing the 1 km x 1 km BIOTA *Koeroegap Vlakte Biodiversity Observatory* in the Richtersveld where soils were investigated by Petersen (2008). The white spots distributed across the reddish fan deposits are heuweltjies, largely barren of perennial plant cover; their light coloration is due to the abundance of soil carbonates. The site is located 17 km SE of the small town of Sendelingsdrift on the Orange River. The coordinates for the peak of the small hill to the direct right of the scale bar are -28.22508°, 17.02641°.

regular spacing (e.g., Grohmann et al., 2010; Pringle et al., 2010; Mujinya et al., 2014), and studies have documented agonistic interactions between workers of different colonies, but not among members of the same colony (compilation of studies in Kaib et al., 2002). There is also evidence for these kinds of interactions in *M. viator* (Coaton, 1958: p. 32; Muna, 2013).

Using heuweltjies and resident colonies of *M. viator* as an example, Laurie (2002) considered costs and benefits of resource transport by a
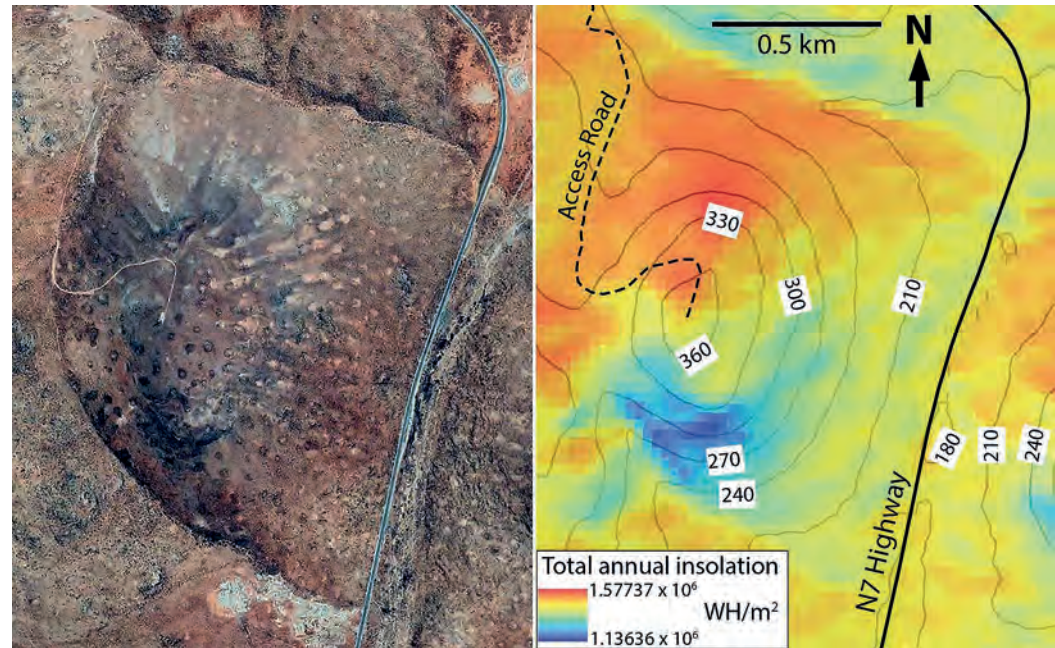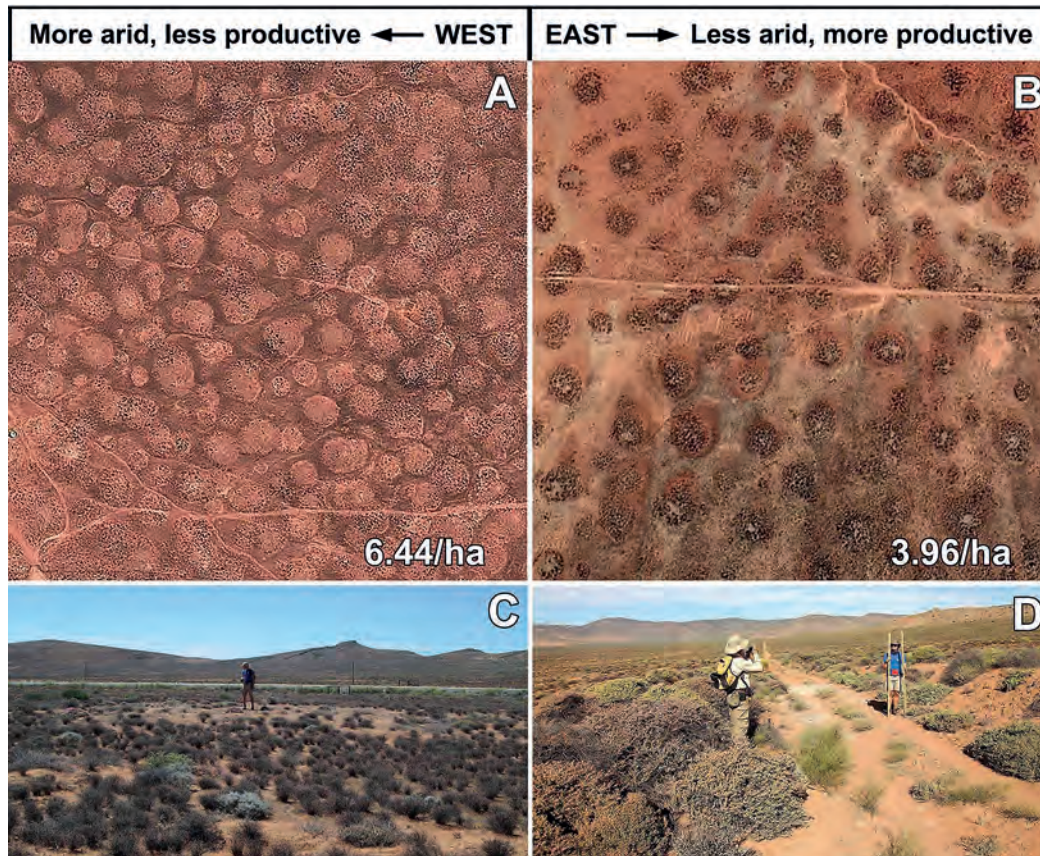
Figure 10.1.17:
Left – Google Earth™ view (October, 2018 image) of small hill with 150 m vertical relief located to the west side of the N7 highway, 30 km N-NW of Bitterfontein. Topographic map on right (countour intervals in meters) of the same area showing contrasts in total annual insolation on north- versus south-facing portions of hillslopes. Condition of heuweltjies on north-facing (towards equator) and south-facing hillslopes differ greatly due to strong topoclimatic contrasts. Light-colored spots on northern and northeastern aspects are heuweltjies lacking substantial vegetation cover. Linear streaking below many of the mounds are washes of light-colored, fine-grained sediments eroded from the mounds. In contrast, the dark spots of the same size on south-facing slopes of similar slope inclinations are heuweltjies protected from erosion by dense vegetation cover. (summit of hill = -30.80162°, 18.11082°).
Right – insolation modified by topographic shading was modeled using the Esri ArcGIS Pro *Area Solar Radiation tool*. Elevation data is from the Shuttle Radar Topography Mission (SRTM), with a grid spacing of 1 arc second (~ 30 m) (Farr & Kobrik, 2000). Topographic and insolation map layers created by Lyman Persico, Whitman College.

colony in a model of the factors responsible for the regular spacing of colonies and the size of their foraging areas. In that model, if transport costs increase at a higher power of foraging distance than do benefits (harvested food material), a unimodal maximum surplus of harvested energy exists (S^*) that defines the optimum foraging radius of the colony (R^*). This model predicts that R^* declines with increasing productivity (Laurie, 2002, p. 144, testable prediction #4). In other words, more productive environments should contain higher densities of heuweltjies.

Throughout the geographic range of heuweltjies, nearest neighbor distance between mounds averages slightly over 40 m, and mean density is approximately 3 ha^{-1} (Cramer & Midgley, 2015). Evidence for an increase in heuweltjie density and a decrease in mean nearest neighbor distance as a function of increasing productivity predicted by Laurie's (2002) model is equivocal. Picker et al. (2007) described a positive relationship between mound density and mean annual precipitation (MAP) for areas experiencing up to 350 mm/year. However, their data show a lack of a significant relationship between density and MAP for 22 sites receiving less than approximately 175 mm MAP. The positive relationship appears to be driven by the discontinuous jump in heuweltjie density within only 6 sites, all in the upper half of the range of precipitation or NDVI (Normalized Difference Vegetation Index, a proxy measure of vegetation density and primary productivity derived from satellite imagery). Subsequently, Cramer & Midgley (2015) investigated heuweltjie spacing and density using a considerably larger number of aerial imagery sampling sites than used by Picker et al. (2007) (7117 vs. 34 sites) and concluded that there is no relationship between mound density and vegetation productivity.

Figure 10.1.18 A–D: Contrast between heuweltjie densities at two sites located between Steinkopf and Port Nolloth, Northern Cape. **A:** 27 km W of Steinkopf showing an area 500 x 500 m (25 ha) containing 161 heuweltjies (center of view -29.25647°, 17.46429°). **B:** 14.5 km W of Steinkopf showing same sized area (25 ha) containing 99 heuweltjies (center of view -29.25703°, 17.58615°). **C:** View of a typical heuweltjie with only slightly raised relief and little vegetation cover at the western site, located on thin soils of Pleistocene age, containing impenetrable pedroduric horizons within 10 cm of the surface. Lower precipitation at this site, combined with limited rooting depth (in off-mound locations) limit overall productivity. 23 October 2016. **D:** View of considerably more productive, denser vegetation of eastern site. View towards east taken along roadway shown in B. Dense vegetation in foreground is that of a heuweltjie cut by the roadway (left of center in B). Deeper soils combined with greater precipitation enhance productivity. 22 October 2016.

Differences in spacing and density of heuweltjies certainly exist among different areas, but given the equivocal evidence and contrasting conclusions stated above, factors responsible for these differences have yet to be convincingly demonstrated. Considerable variation in soil characteristics exists throughout the Namaqualand region of western South Africa (Francis et al., 2007) and some of this variation is related directly to landform age and associated pedogenic development. A possible contributor to the spacing and density of heuweltjies that has not been investigated is the influence of landform age. Figure 10.1.18 shows two sites separated by 12.5 km along the route from Steinkopf to Port Nolloth. The sites are positioned along a sharp gradient of decreasing precipitation over the 83 km distance from Steinkopf (MAP = 140 mm), west to Port Nolloth on the Atlantic coast (MAP = 72 mm). Although the sites are separated by only 12.5 km, the western site is 130 m lower in elevation than the eastern site and is more distantly separated from an abrupt topographic rise of mountains to the east that contributes to orographic uplift and greater precipitation. The considerably lower plant productivity at the western site reflects greater aridity (Fig. 10.1.18C, D). Despite the di-

minished productivity of the western site, density of heuweltjies (6.99/ha) is 63% greater than that of the less arid, more productive site (3.96/ha). This decline in density of heuweltjies with increasing productivity is opposite to the model predictions of Laurie (2002) and the empirical results of Picker et al., (2007).

The contrasts in densities of heuweltjies may be related in some way to differences in age of surface deposits of the two sites. The western site (Fig. 10.1.18A) is located on a broad, gently sloping plain consisting of mixed aeolian sand and sandy alluvial deposits. Soils consist of very thin (~ 10 cm depth), clay-enriched B horizons over thick and very strongly reddened, massive and strongly cemented silica-cemented layers (petroduric horizons or *duripans,* abbreviated as Bqm horizons in soil profile descriptions, and commonly called *dorbank* in South Africa). This degree of development and cementation requires considerable time to develop, indicating those deposits are at least late Pleistocene in age. In contrast, the less arid site to the east (Fig. 10.1.18B) consists of more recently deposited, sandy-fine gravelly alluvium delivered from the steeper, surrounding hillslopes, and deposited *on top* of
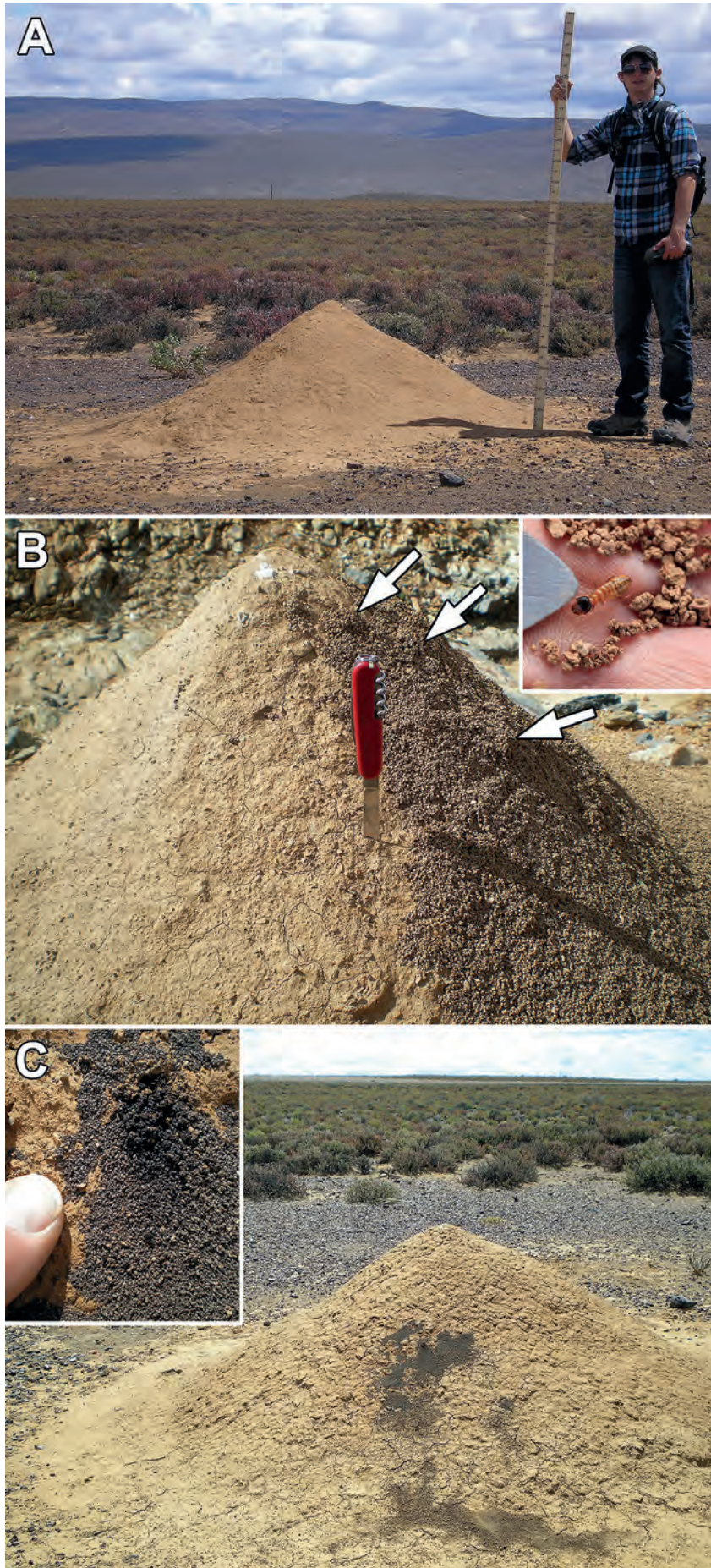
a more ancient surface that contains a massive petroduric horizon. Those more recent deposits exhibit only slight pedogenic change, and lack of cementation, consisting of B horizons with only slight structural and color development (Bw horizons), indicating geologically recent deposition during the Holocene. Beneath those relatively young deposits at depths of 70 cm or more is an older surface consisting of the same kind of thick petroduric horizons found at the western site, which represents an older (Pleistocene) surface buried by deposition of the younger material.

The actual cause of the considerable difference in densities of heuweltjies on the two contrasting geomorphic surfaces is unknown, but here are some possibilities. If indeed formation of a heuweltjie requires the presence of a colony of *M. viator*, the substantial contrasts between the sites in physical soil conditions may directly affect the termites in some way, leading to closer colony spacing on the older surface. Another possibility is that since some heuweltjies can be extremely old (>30,000 years; see later discussion in the section *Age of heuweltjies*), the higher density of heuweltjies on the older surface may represent a gradual increase over a much longer span of time that has been available on the younger geomorphic surface of the eastern site. The greater span of time may have led to the occasional "overprinting" of older, potentially unoccupied mounds with more recently developed ones, eventually generating the visibly higher density of mounds. The geologically older surface (Fig. 10.1.18A) possesses more pairs of mounds that are extremely close together, and in some cases overlapping, which may reflect such a process. Further investigation is clearly required to better understand factors responsible for variation

Figure 10.1.19 A–C:
A: Conical cemented mound housing colony of *M. viator* in arid upper Doring River Basin (Tankwa Karoo). Site with very thin soils (< 25 cm) over impenetrable, metamorphosed shale.
B: Soil dumps expelled by termites through openings in surface of conical mound. Expelled materials simply tumble down the surface, forming the regularly inclined sides. Removal of freshly expelled materials revealed workers of *M. viator*. Inset shows a member of the worker caste.
C: Frass expelled by *M. viator* on surface of conical mound. Inset shows dark appearance of moist, freshly expelled material.
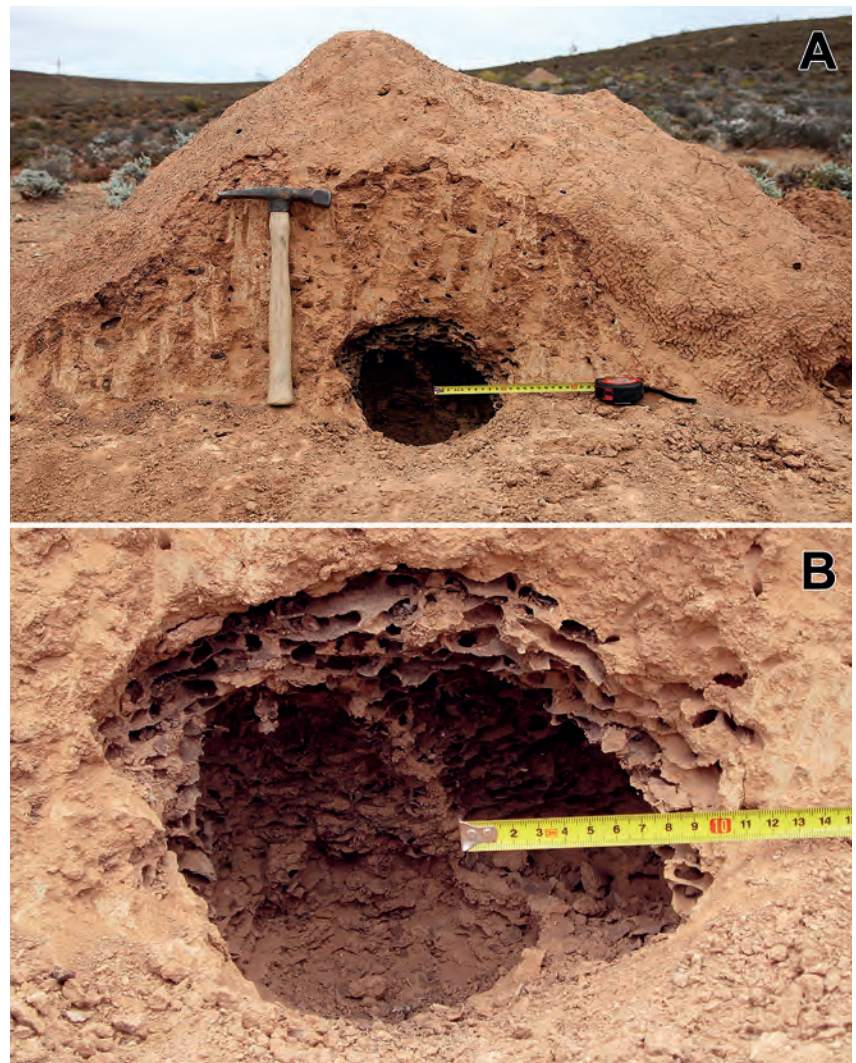
in the spacing and density of heuweltjies at this location and across the entire geographic range of heuweltjies.

Occurrence of *Microhodotermes viator* in areas lacking heuweltjies

Colonies of *Microhodotermes viator* exist in some environments where heuweltjies are absent. Paradoxically, a comprehensive understanding of these situations is necessary in order to fully understand how and under what circumstances heuweltjies form.

a) Small conical mounds

In some environments, colonies of *M. viator* construct small, conical mounds with maximum heights typically less than a meter and basal diameters less than 2 m (Fig. 10.1.19A). The mounds are created through the accumulation of soil materials and frass expelled by the termites at tunnel openings on the mound surface. The termites close the external openings after the materials are expelled. Construction of the mounds is apparently a passive process on the part of actions by the termites because they neither actively position the dumped materials nor cement those materials together. Rather, the regular conical shape apparently takes shape through the gravitational sliding of piles of dumped materials down the inclined sides (Coaton, 1958; Coaton & Sheasby, 1974; Fig. 10.1.19B, C). Wetting by precipitation and subsequent drying hardens the accumulated materials into an indurate mass that is extremely difficult to excavate or penetrate, particularly on older, larger mounds. The internal nest, which has the same spheroidal shape and internal structure as those found in heuweltjies, is positioned centrally at the base of the mound, or slightly below the level of the surrounding land surface, protected by the thick, overlying mass of indurated soil materials. Systematic excavation and internal measurements taken from set of 9 conical mounds at one site (Van Ark, 1969) indicated that the internal nests were circular in horizontal section and slightly compressed along the vertical axis. Nest diameter was positively correlated with mound height, and nests were positioned closer to the exterior surface of the northern sides of mounds than the southern sides. The nest contains sub-horizontal, comb-like sheeting of carton constructed of dark organic material (Fig. 10.1.20), which is highly enriched with nitrogen and organic carbon (Van

Ark, 1969). Tunnels with diameters slightly less than 5mm extend from openings in the domed roof of the nest through the indurated mass of the mound, connecting with the mound surface (Coaton, 1962). Unlike the large, chimney-shaped, and intricately structured mounds of some fungus-cultivating termites (*Macrotermes* spp.), other than the spheroidal nest, the conical mounds of *M. viator* lack large, internal cavities or prominent external openings that facilitate atmospheric circulation and exchange and temperature regulation. Although it is possible that the structure of conical mounds and nests of *M. viator* may significantly influence internal atmospheric conditions and somehow facilitate circulation, investigations on this possibility have not been conducted. However, the indurated, conical mounds probably serve an essential function by protecting, to a degree, the colony from excavating predators, particularly aardvarks (*Orycteropus afer*). Another species of termite, the snouted harvester

Figure 10.1.20 A, B:
A: Cross-section of conical mound of *M. viator* showing internal, basal positioning of nest. The conical mound had been previously breached by an aardvark excavation; the damaged side was cut away further to reveal the internal structure.
B: Close-up view showing internal structure of the centrally located nest with sub-horizontal sheeting composed of dark carton composed of organic material. 25 km NE of Vanrhynsdorp, Western Cape. October, 2016.

Figure 10.1.21 A, B:
A: Dome-shaped epigial mound of colony of the snouted harvester termite, *Trinervitermes trinervoides*, approximately 50 cm diameter and 35 cm tall; 6.5 km S of Laingsburg, Western Cape.
B: Nasute soldiers of *T. trinervoides*, photo by M. Timm Hoffman.

Figure 10.1.22:
Small shrub engulfed by a young conical mound of *M. viator*. The common occurrence of this association suggests that areas beneath plant canopies provide protected environments for the founding of a new colony by a nuptial pair of alates (reproductive, flying adults). This mound was breached by an aardvark and the extremely weathered external appearance suggests the colony was eliminated in the process. Mounds like this can be observed in areas between heuweltjies on substrates where underlying bedrock or other impenetrable materials prevent location of the nest at a sufficient depth below the surface. In these settings, construction of the conical mound provides a measure of protection from predators like aardvarks. Photograph from the Inverdoorn study area where heuweltjies are present (see Fig. 10.1.29).

termite (*Trinervitermes trinervoides*) occurs in the some of the same environments occupied by *Microhodotermes viator*, and also constructs small epigeal mounds that can reach similar heights and diameters. However, in contrast to the conical mounds of *M. viator,* the mounds of *T. trinervoides* are dome shaped (Fig. 10.1.21A). Additionally, unlike the thick, solidly indurated earthen walls of mounds of *M. viator,* the relatively thin, outer walls of mounds of *T. trinervoides* are very easily penetrated. Breeching of the mound's exterior generates an immediate response by nasute soldiers, which contain a frontal projection (nasus) on the head that discharges substances that repel predators (Fig. 10.1.21B).

In some settings, colonies of *M. viator* exclusively occupy the smaller, conical mounds, and heuweltjies are entirely absent. These settings are often characterized by extremely shallow soils over impervious bedrock, preventing deeper positioning of the nest. In such settings, like heuweltjies, the conical mounds exhibit highly regular spacing and distance between neighboring mounds within the range observed for heuweltjies (McAuliffe et al., 2019a). Conical mounds with colonies of *M. viator* can occur together with heuweltjies, but are typically located between existing heuweltjies, often at the base of a shrub or other structure providing support or protection (Fig. 10.1.22). Such mounds appear to be transient phenomena, with very limited chances of long-term persistence due to competition from considerably larger, long-established colonies as well as high rates of destruction by aardvarks. The small conical mounds also occur within the footprints of eroded heuweltjies where erosion by water has removed nearly all of the fine-textured soil materials of the heuweltjie, creating an environment where impenetrable bedrock is exposed or only covered with a thin layer of soil, preventing deeper positioning of the nest (Fig. 10.1.23). Consequently, cemented, conical mounds are apparently constructed in those settings to provide a measure of protection from predators, especially aardvarks. Relatively deep positioning of the spheroidal hive within the thicker soils of an intact heuweltjie affords the colony sufficient protection, and a cemented conical mound is usually not constructed on the surface.[1]

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[1] Fig. 10 of Cramer et al. (2012) contains a photograph of a termite mound identified as a "*M. viator* nest" on the surface of a heuweltjie. However, the rounded, dome-like appearance of the pictured mound suggests that it was constructed by *Trinervitermes trinervoides*, rather than *M. viator*.

Figure 10.1.23: Cemented conical mound within footprint of a heuweltjie that has been nearly completely removed through erosion by water. The footprint of the original heuweltjie is revealed by the presence of the silt-rich soils emplaced on top of the shale bedrock. Exposed bedrock strata are visible in the foreground. Areas between mounds have extremely thin soils (~ 10 cm) over bedrock. With the loss of a deep soil environment offered by intact heuweltjies, new colonies that occupy eroded remnants like this construct the indurated, conical mounds apparently as the only possible means of defense against burrowing termite predators. The conical mound pictured had been breached by an aardvark (photograph on 2 November 2012), but repeat photography of the mound in October 2016 showed that the mound was reoccupied by *M. viator* and completely repaired. 25 km NE of Vanrhynsdorp, Western Cape.

b) Absence of above-ground mounds

In relatively deep soils and substrates that permit deep excavation by *M. viator,* the spheroidal nests of colonies can be positioned deeply under the soil surface, and lack any kind of overtopping mound structure (Fig. 10.1.24). Although such colonies lack a clearly identifiable, above-ground mound structure, direct evidence of such underground colonies and associated nests is the accumulation of frass on the soil surface and tunneling just below the surface, as well as locally altered soil conditions (higher salinity and higher $CaCO_3$ content, readily detected by effervescence in dilute HCl; Fig. 10.1.11C). Foraging excavations by aardvarks are often focused on those areas (Fig. 10.1.25).

Figure 10.1.24: Remains of spheroidal, subterranean nest of *M. viator* exposed in collapsed bank of alluvial terrace along an ephemeral stream west of Prince Albert (in shadowed area). Inset photo shows close-up view of nest. Nest is 38 cm wide, 32 cm tall; upper edge 80 cm below top of terrace. Nearly all of the internal, organic shelving has disintegrated and disappeared with exceptions of small remnants. Note abundant small holes above nest—passageways and tunnels excavated by the termites. M. Timm Hoffman is pictured, 8 October 2016.
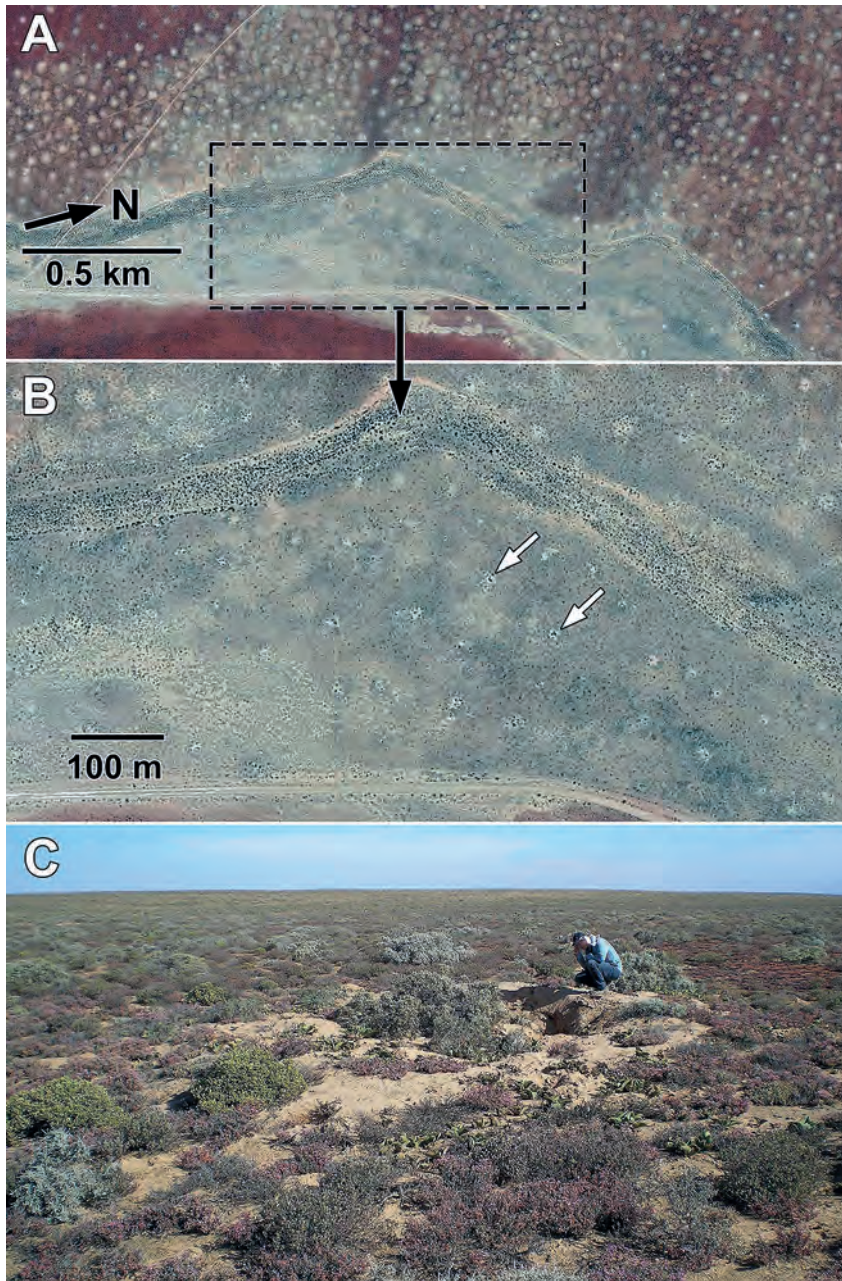
Figure 10.1.25 A–C:
A: Google Earth™ view within Namaqua National Park, Northern Cape. Upper half of view are uplands covered with ancient aeolian sand deposits, the light-colored spots are heuweltjies. The light gray-colored zone through the lower half is a geologically recent (Holocene) alluvial terrace associated with the ephemeral stream that cuts through the center of view. The area enclosed in the rectangle is enlarged in B.
B: Enlarged Google Earth™ view showing multiple, light-colored patches (white arrows) distributed across the Holocene alluvial terrace. Like heuweltjies, these patches tend towards regular spacing, but do not consist of raised mounds. Coordinates at center of view are -30.02100, 17.46340.
C: Ground view of one of the light colored patches with an excavated aardvark burrow. Termite tunnels were present along the excavated, vertical surfaces of the burrow, indicating the action of *M. viator*. Soil alteration by *M. viator* (accumulation of $CaCO_3$), was also evident in the immediate vicinity of this feature, as indicated by effervescence in the presence of 10% HCl. Soils further away from the structure were non-effervescent. In settings like this where deep, permeable substrates are present, nests of colonies of *M. viator* are positioned deep below the surface, and above-ground, cemented, conical mounds are not constructed.

Age of heuweltjies

a) Radiocarbon dating of calcium carbonate accumulations

Bioaccumulation of calcium by termites through the collection of calcium oxalate-rich plant materials is apparently the principle means by which the tremendous amounts of calcium become concentrated within mounds. The massive, thick petrocalcic horizons in mounds (up to a meter thick in some cases; Fig. 10.1.8), indicate a considerable amount of time required for formation. In appropriate geologic contexts (no inputs of groundwater or marine carbonates), those cemented materials provide a potential means by which the minimum age of the mounds can be discerned through radiocarbon dating. Over time, the carbonate-rich soil horizons form mainly through the dissolution of $CaCO_3$ within upper portions of the soil (e.g., $CaCO_3$ recently formed in the vicinity of termite colonies via the oxalate-carbonate pathway) and transported in solution (as ionic Ca^{2+}) downward through the soil. In arid and semiarid soil moisture regimes, as the soil dries, the soil solution becomes saturated with respect to Ca, precipitating $CaCO_3$. Carbon dioxide (CO_2) in the soil atmosphere is the source of carbon in the precipitated $CaCO_3$. That CO_2 is derived from either respiration by plant roots, decay of plant and animal material, or in the case of heuweltjies, respiration by members of the resident, underground termite colony. Given that the termites ingest recently collected plant materials, the ^{14}C signature of the CO_2 they respire will reflect those materials, and will be nearly identical to that of the CO_2 derived from either respiration by plant roots or the decay of plant or animal material that had recently died. However, to preserve the original ^{14}C signature contained within the precipitated $CaCO_3$, it is essential that dissolution of that material does not recur. With dissolution, the original ^{14}C signature will be lost, and with re-precipitation of $CaCO_3$, a new ^{14}C signature will be acquired, which will reflect CO_2 in the soil atmosphere at that more recent time, ultimately yielding a younger radiocarbon date. Although it is generally impossible to know the history of repeated dissolution and precipitation of soil carbonates, samples collected from the interiors of large, well-cemented layers or masses that are impermeable to movement of water can provide radiocarbon dates that reflect a minimum age of the initiation of carbonate horizon formation (Wang et al., 1996).

Three studies have reported radiocarbon ages of cemented calcium carbonate from heuweltjies (Moore & Picker, 1991; Midgley et al., 2002; Potts et al., 2012). Since the carbonate-enriched horizons form exclusively within heuweltjies, this information also indicates the minimum age of the mounds. Each of the studies reported results as radiocarbon age (^{14}C yr BP), but only the most recent of the three converted those data to calibrated ages (years before AD 1950 = Cal yr BP). In order to directly compare results from the three studies, Table 10.1.1 shows the originally reported radiocarbon ages and corresponding calibrated ages using the most recent radiocarbon calibration curve for the southern hemisphere, SHCal 20 (Hogg et al., 2020). Ages of material examined by Moore & Picker (1991) range from 8,500 to 6,640 Cal yr BP (early to middle Holocene), whereas all ages reported in Midgley et al. (2002) and Potts et al. (2012) are late Pleistocene in age, ranging from 37,500 to 22,330 Cal yr BP, during the latter half of MIS-3 (Marine Isotope Stage 3) and the early part of MIS-2, a period of concurrent glacial advances in North America, Europe, and South America (Late Wisconsin Glacial, Weichselian High Glacial, and Late Lianquihue Glacial, respectively).

These dating results clearly indicate that heuweltjies with well-developed petrocalcic horizons are very old and persistent landscape features. Given the antiquity of the mounds, Midgley et al. (2002) concluded that *M. viator*, despite its modern-day presence, is unlikely to be the species responsible for originally forming the mounds, suggesting instead that some other species of termite no longer present was responsible. In other words, heuweltjies represent relict landscape features that are no longer forming in the present-day climate regime, but simply offer suitable environments for present-day occupation by colonies of *M. viator*.

b) Younger age of some heuweltjies

Although much attention has been focused on the antiquity of heuweltjies, particularly those that contain large, massive accumulations of $CaCO_3$, little attention has been directed towards directly investigating *how young* some mounds might be. Consequently, the pervasive perception that the mounds are extremely old, dating to the late Pleistocene, has led many to conclude they are relict features of the landscape, no longer capa-

Table 10.1.1: Summary of radiocarbon dating results reported for calcrete samples collected from heuweltjies, all with newly calibrated ages

Source	Sample ID	Location	Sample notes	^{14}C yr BP [a]	Cal yr BP [b]
Moore & Picker (1991)[c]	5215	Kleinfontein	Basal calcrete	7,590 ± 80	8,520 – 8,180
	5277	Clanwilliam Dam	Basal calcrete	5,970 ± 70	6,930 – 6,640
Midgley et al. (2002)	7906	Clanwilliam Dam		24,600 ± 380	29,650 – 27,850
	7930	Elands Bay	Mound 1 nodule (top)	25,400 ± 270	30,100 – 29,120
	7932	Elands Bay	Mound 1 nodule (bottom)	25,500 ± 460	30,750 – 28,810
	7931	Elands Bay	Mound 2 basal plate	29,800 ± 640	35,450 – 32,260
Potts, et al. (2012)	I-01	Worcester	Surrounding matrix	26,230 ± 530	31,180 – 29,290
	I-06	Worcester	Upper nodule	31,290 ± 820	37,500 – 34,100
	I-07	Worcester	Lower nodule	30,860 ± 810	36,940 – 33,660
	III-01	Worcester	Topmost layer	18,770 ± 190	23,000 – 22,330
	III-07	Worcester	Bottommost layer	25,210 ± 420	30,260 – 28,590

[a] Radiocarbon years (^{14}C yr BP) are expressed in years before AD 1950.
[b] Conventional radiocarbon ages (^{14}C yr BP)were converted to calibrated years before AD 1950 (Cal yr BP) with the Calib8.20 online calculator (http://calib.org/calib/calib.html), using the SHCal 20 calibration curve for the southern hemisphere (Hogg, et al., 2020).
[c] In addition to reporting conventional radiocarbon ages (^{14}C yr BP), Moore & Picker (1991) listed *estimated ages* derived by subtracting 2000 yr from the conventional radiocarbon age. This adjustment was made because the authors assumed that the petrocalcic horizons were derived from $CaCO_3$ contained in groundwater containing a lower initial ^{14}C content than terrestrial plants or animals, thereby giving the deposited carbonate a radiocarbon age older than the actual age. The 2000 yr figure was determined by measuring the radiocarbon age of a sample of organic carton from a nest of *M. viator* and also of $CaCO_3$ contained in the same nest, assuming the latter was derived from groundwater. The age of for the organic carbon sample was subtracted from that of the $CaCO_3$ to obtain a value for the apparent initial age of carbonate in the groundwater. However, the older radiocarbon age of $CaCO_3$ contained in the nest is more likely due to the mixing and incorporation of older carbonate from other parts of the mound, rather than being derived from groundwater. Consequently, only the original ^{14}C yr BP data from that paper are listed here, along with calibration using the most recent radiocarbon calibration curve.

ble of being formed under current environmental conditions. However, comparative investigations of soil characteristics of heuweltjies, including the degree of $CaCO_3$ accumulation, provide evidence that some heuweltjies are quite young and have actively formed under present-day climatic conditions during the Holocene, and in some places, occur in the same environments occupied by extremely old mounds. At a site south of Soebatsfontein in the Northern Cape, McAuliffe et al. (2014) examined a pair of heuweltjies separated by only 400 m that contrasted greatly in soil $CaCO_3$ accumulation and the degree of calcic horizon formation. Both mounds were cut through their centers by road construction activities, allowing examination of the soil characteristics across the breadth of entire cross-sections
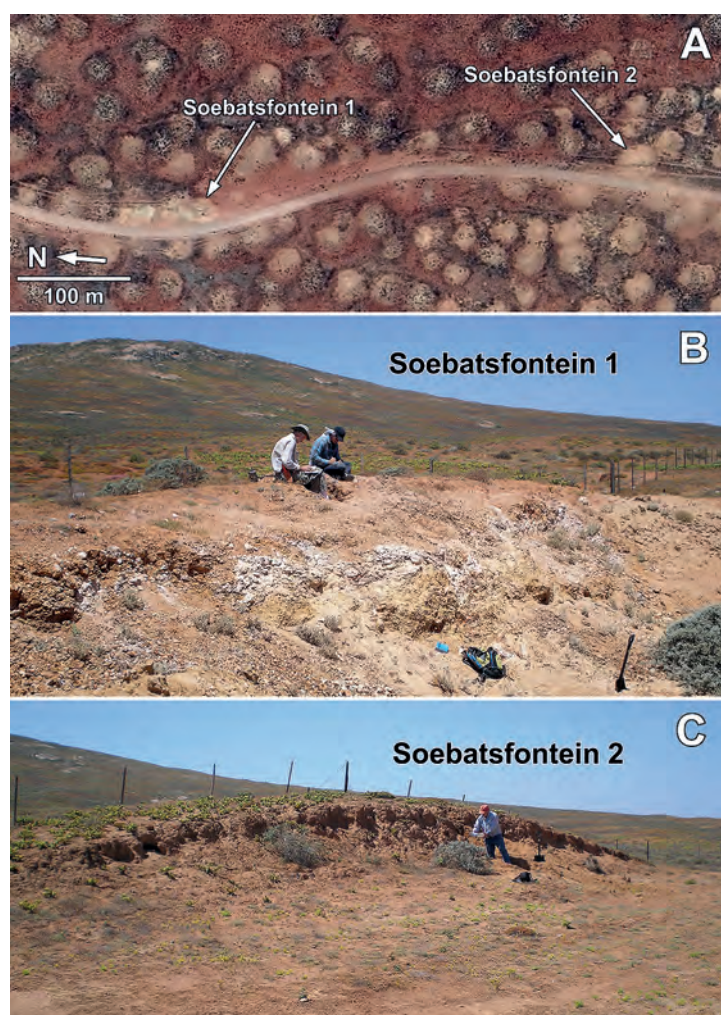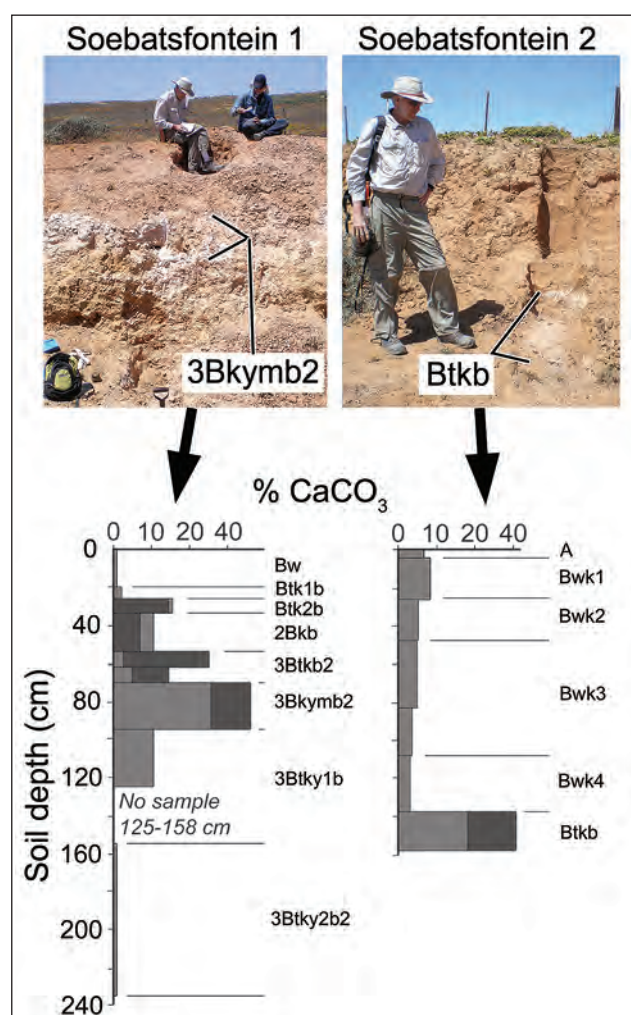
Figure 10.1.26 A–C:
A: Google Earth™ view showing the locations of two heuweltjies investigated at a site 7 km S-SW of Soebatsfontein, Northern Cape. The mounds (1 and 2) have diameters of 30 and 33 m and heights of 1.4 and 2.0 m, respectively (Soebatsfontein 1: -30.17371°, 17.55374; Soebatsfontein 2: -30.17718°, 17.55423°)
B: The white layer in the Soebatsfontein 1 heuweltjie is a petrocalcic horizon, which indicates considerable antiquity of the mound.
C: The lack of cemented calcic horizon and minimal pedogenic alteration in the Soebatsfontein 2 heuweltjie indicates the mound is considerably younger than the other one, located only 400 m away.

Figure 10.1.27:
Horizon names in the soil profiles of the Soebatsfontein 1 & 2 heuweltjies, and calcium carbonate contents of soil horizons of each (the "y" subordinate designation in some B horizon names indicates gypsum accumulation; see caption to Fig. 10.1.9 for definitions of other horizon names). The dark segments of histogram bars indicate the contribution of calcium carbonate contained in large petrocalcic fragments to total carbonate content. The gray shaded portion represents the fine (<2 mm) sieved soil fraction. Details on laboratory methods used are described in McAuliffe et al. (2014).

(Fig. 10.1.26). The Soebatsfontein 1 mound possessed strongly cemented petrocalcic horizons similar to those that have yielded late Pleistocene radiocarbon ages, as well as other features of advanced pedogenic development that require substantial time. These included development of strongly reddened, clay- and carbonate-enriched argillic (Btk) horizons, including those with gypsum accumulations (Fig. 10.1.27).

In contrast, accumulation of $CaCO_3$ in the Soebastfontein 2 heuweltjie was considerably less and a petrocalcic horizon was entirely absent

(Fig. 10.1.27). Accumulation of $CaCO_3$ and development of calcic horizons in soils of arid and semi-arid regions are strongly time-dependent. The lesser degree of reddening, low $CaCO_3$ content, and the relatively non-cohesive nature of the upper 138 cm of the mound soil indicates the extent of pedogenic change that can be expected in Holocene deposits of arid and semi-arid regions (McFadden & Tinsley, 1985; McFadden, 1988; Harden et al., 1991; McFadden et al., 1991). At 138 cm depth, an abrupt transition to a layer with substantially higher $CaCO_3$ content is interpreted as the original surface of an older heuweltjie,

buried by more recently accumulated material. Recognition of buried, former soil surfaces such as this is essential for deciphering depositional history in any setting.

The occurrence of heuweltjies that exhibit very little soil development, which indicates more recent formation, together in the same vicinity with considerably older mounds containing pet-rocalcic horizons has also been observed in other locations (McAuliffe et al., 2014). Cramer et al. (2012) trenched heuweltjies at the Clanwilliam Dam site where Midgley et al. (2002) had report-ed Pleistocene ages of samples of petrocalcic ma-terial contained in mounds. At that site, Cramer et al. (2012) reported that some of the mounds altogether lacked cemented calcic horizons, con-sisting instead of earthen, silt-rich material that varied little in appearance and texture through the entire excavation depth. The minimal pedo-genic change exhibited within mounds like this likewise indicates an age much younger than Pleistocene. Clearly, in some places, heuweltjies have formed under "modern" climate conditions of the Holocene. However, what is the source of the younger, mounded earthen materials and how does that material accumulate to form the mounds?

Formation of heuweltjies

Debate regarding origins

As has been the case for fairy circles, processes responsible for the formation of heuweltjies have been the subject of considerable debate. Over more than 80 years, many different hypotheses have been proposed. Lovegrove (1991) sum-marized the different hypotheses for the origin of heuweltjies, dividing them into two separate categories—those involving abiotic physical processes vs. those involving soil movement by burrowing animals. Since then, additional ex-planations have appeared, generating continued debate. Table 10.1.2 summarizes the principal hypotheses proposed to date. Although it is pos-sible that elements of several hypotheses may be simultaneously involved, clearly not all can be true—some are mutually exclusive. At least one of the hypotheses listed in Table 10.1.2 (lime-stone faulting hypothesis) is no longer consid-ered because heuweltjies occur widely on other kinds of bedrock and substrates, including gran-ite and deep aeolian sand deposits. Advances in

Table 10.1.2: Hypotheses for the formation of heuweltjies. The table lists informa-tion originally presented in Lovegrove (1991), together with hypotheses that have been more recently proposed.

Abiotic physical processes	
1. Limestone faulting – faulting within horizontal beds of limestone and shale produced irregular projects and lumps of limestone at the surface.	Van der Merwe, 1940
2. Dorbank erosion – irregular erosion of an ancient soil layer cemented by calcium carbonate generated patches of the cemented material protected from subsequent erosion by vegetation	Slabber, 1945
3. Aeolian sediment accumulation beneath trees – African olive trees trapped windblown sediment, leading to further accumulation of organic material (tree leaves) and faeces of birds and animals using the trees	Van der Merwe, 1940
4. Sediment deposition (aeolian and alluvial) not associated with any particular pattern of vegetation cover	Ten Cate, 1966
5. Initiation of mound development through erosion of the land surface by water, followed by aeolian sediment accumulation	Von Holdt, et al., 2022
Biological processes	
1. Relict termite mounds - heuweltjies are the partially eroded, collapsed remains of large termitaria constructed long ago by a species other than *M. viator*	Burgers, 1975; Midgley et al., 2002
2. Action of termites and burrowing mole rats – *M. viator* initiates process by constructing small, cemented conical nests; mole rats occupy those mounds as a flood-free refuge, and create the heuweltjie over time by burrowing outward, moving soil towards the center of the mound in the process	Lovegrove & Siegfried, 1986; Cox et al., 1987
Combined physical and biological processes	
1. Vegetation self-organization. Interplay between competitive and facilitative interactions among plants produce localized patches of vegetation. Those patches protect the underlying soils from erosion, thereby forming the mounds.	Cramer, et al., 2012
2. Movement of soil materials by termites towards center of the mound combined with vertical displacement of soil volume through the accumulation of $CaCO_3$ and formation of thick, cemented petrocalcic horizons.	Francis et al., 2012
3. Nutrient enrichment of areas around termite colonies promoting denser vegetation growth, in turn serving to intercept and accumulate aeolian sediments.	McAuliffe, et al., 2014, 2018, 2019b

understanding in any scientific discipline depend on the proposal of testable (i.e., potentially fal-sifiable) hypotheses, and rejection of those that fail critical testing. The considerable unresolved debate and confusion that persist regarding ex-planations for the formation of heuweltjies re-flects a need for a conceptual "housecleaning" through more rigorous examination and testing. Any explanation of the processes involved in the formation of heuweltjies must be able to account for multiple features and patterns:

- Distinct soil chemistry, including higher lev-els of macro- and micro plant nutrients and substantial accumulations of $CaCO_3$ and solu-ble salts
- Finer soil textures of heuweltjies in compari-son to the surroundings
- Highly regular spacing
- Variation in mound sizes (diameter, height & volume) among different regions
- The occurrence *M. viator* in environments where heuweltjies are absent

Although this variety of features may appear to point to many different explanations, the opposite is also possible. Unless a particular hypothesis is

capable of accounting for all of the above observed features and characteristics, that hypothesis is potentially deficient in terms of a comprehensive, general explanation of how heuweltjies form.

The various hypotheses listed in Table 10.1.2 can be re-classified into four general categories of contrasting explanations for the origin of the raised relief of the mounds, irrespective of whether those explanations involve either physical or biological processes:

Category 1: upward, direct vertical displacement of existing soil materials
• Includes soil displacement by animals (termites, burrowing mammals) as well as by physical processes, including upward displacement due to the accumulation of $CaCO_3$ and formation of petrocalcic horizons.

Category 2: localized movement of soil materials from the immediate surroundings centrally to the mound location
• Includes soil displacement due to the directional movement of soil by fossorial mammals inward towards a central location, resulting in accumulation of soil volume at the central location.

Category 3: Differential erosion of the land surface
• Includes formation of mounds through protection of ancient land surfaces from erosion by dense vegetation patches

Category 4: external additions of soil materials from more distant sources
• Includes deposition and accumulation of materials such as aeolian or alluvial sediments

Table 10.1.3: Geochemistry and texture data for heuweltjie soils, off-mound soils, and bedrock at the Clanwilliam site

A. Bulk chemistry (% by weight)[1]			
	Heuweltjie soils	Off-mound soils	Quartz arenite bedrock
SiO_2	71.27	91.9	93.57
Al_2O_3	6.08	3.1	2.51

B. Terrigenous trace elements (ppm) (off-mound soils not measured)[1]			
	Heuweltjie soils		Quartz arenite bedrock
Zirconium	65.3		16.4
Rubidium	41.9		16.2
Hafnium	1.96		0.54

C. Mean particle size distributions (%); underlined values significantly different at P level listed			
	Heuweltjie soils	Off-mound soils	
Sand	72	__77__ (P = 0.003)	
Silt	__11__ (P < 0.001)	5	
Clay	17	18	

[1]From Midgley et al. (2012), Tables 1 & 2
[2]From Cramer et al. (2012), Table 2

Critical data for resolving debate

One investigation involving comparisons of soil and bedrock geochemistry provides an important, but little-recognized, critical test of the four categories of alternate hypotheses listed above. At one of the sites where ages of heuweltjies were investigated through radiocarbon dating (Clanwilliam Dam, Table 10.1.1), Midgley et al. (2012) compared bulk chemistry and trace element contents of soil from heuweltjies, surrounding off-mound soils, and the underlying bedrock. The only kind of bedrock at the site, as well as the entire surrounding area within a minimum of 25 km radius, is silica-cemented quartzitic sandstone (Nardouw Formation quartz arenite), which contains 93.6% SiO_2. Where not covered by heuweltjies, the bedrock is widely exposed on the surface or covered with thin soils (direct observations by the author). Those soils are similarly dominated by SiO_2 (91.9%), reflecting the major contribution of sandy residuum derived from weathering of the quartz arenite to the soil mass. In contrast, SiO_2 content of soil from heuweltjies averaged only 71.3%, but contained approximately double the Al_2O_3 content of both the bedrock and off-mound soils (Table 10.1.3A). The substantially higher content of Al_2O_3 of soils from heuweltjies indicates those materials are derived from aluminosilicate and phyllosilicate minerals (feldspars, micas, and clays), which are major components in many kinds of rocks, but not the silica-dominated quartz arenite of the site. Furthermore, concentrations of terrigenous, chemically conservative trace elements, including rubidium, zirconium, and hafnium, ranged from 2.5–4X greater in soils of heuweltjies than in quartz arenite (Table 10.1.3B). These geochemistry data unequivocally demonstrate that the soils of heuweltjies are not principally derived from the in-situ weathering products of the local bedrock or the off-mound soils next to heuweltjies. Neither the redistribution of soil materials derived directly from the local bedrock, nor differential erosion of such soils (i.e. Categories 1–3 listed above) can account for the distinct geochemistry of mound soils. An additional paper published in the same year (Cramer et al., 2012), provided further key information about the nature of heuweltjie soils and their source. Sand contents were significantly lower and silt contents were more than double in heuweltjie soils than in off-mound soils (Table 10.1.3C). The delivery of silt-rich sediments from distant sources with geochemical signatures
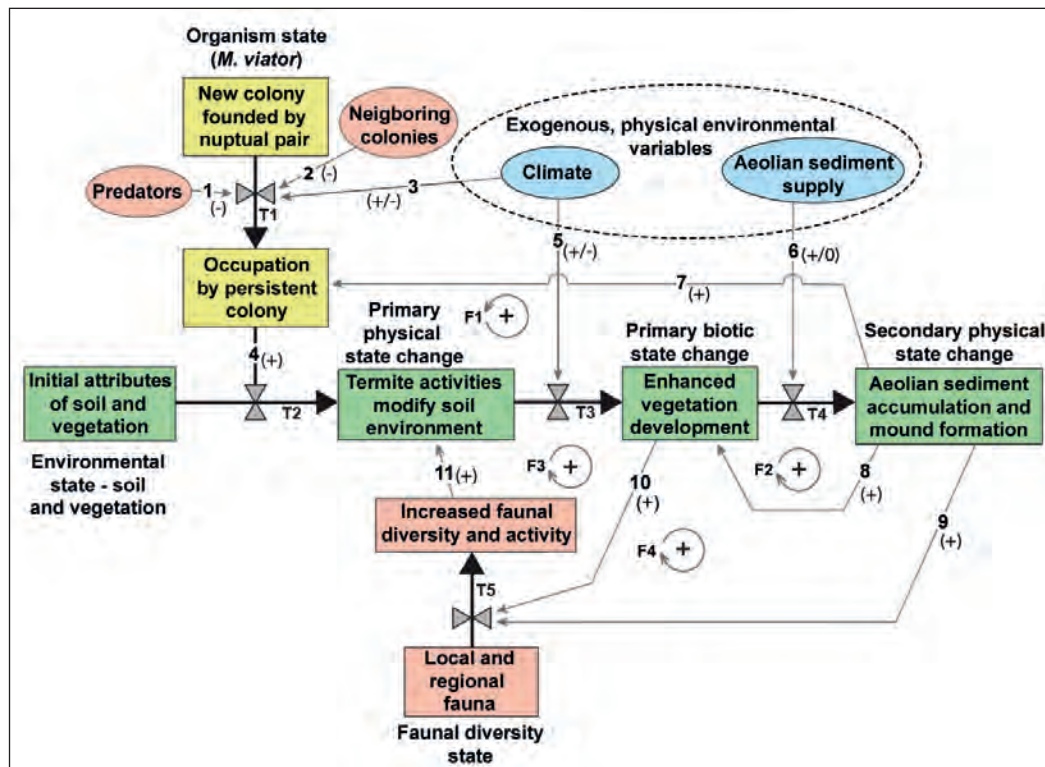
Figure 10.1.28: System dynamics model of processes involved in formation of heuweltjies, modified from McAuliffe et al. (2019b). Items enclosed in rectangles are states of various system components (yellow = a focal colony of *M. viator*, green – the combination of soil and vegetation characteristics of the occupied patch, pink = fauna other than the focal colony. Additional variables affecting the system are enclosed in ellipses. Variables enclosed within the large, dashed line ellipse are physical conditions that are relatively unaltered by localized changes within the system (for example, precipitation inputs and the delivery of aeolian sediments from more distant sources). Transitions between states (enclosed in rectangles) are indicated by bold black arrows (T1 through T5). Paired, hourglass-like triangles indicate where various variables modulate transitions between states. Influences of various variables on these points of modulation or on various states are indicated by light gray arrows (labeled 1 through 11), and the potential positive or negative influences of each (+/-) are indicated within parentheses. For example, arrow 5 directed at the point of modulation of transition T3 indicates how climate (particularly precipitation) influences the capacity of vegetation to respond to soil nutrient additions. In the more arid environments, precipitation inputs are insufficient to generate enhanced vegetation development despite nutrient enrichment, therefore transition T3 does not occur. Positive feedback loops (F1 through F4) are indicated by the circular arrows that enclose "+" signs. The positive feedback loops occur when influences of a variable and all transitions along the patch of the feedback loop are positive.

that are markedly different from the local quartz arenite bedrock or off-mound soils explains the contrasting nature of heuweltjie soils. The site is located on a gentle hillslope, positioned ~20 m in elevation above the floodplain of the Olifants River and its tributaries, and there are no fluvial terrace remnants or other fluvial deposits present at the site that would indicate an alluvial delivery of those sediments from a distant source. In this particular setting, aeolian sediment transport is the only possible means by which the silt-rich materials with distinct geochemical signatures could have been delivered to generate the large soil volumes contained in heuweltjies at the site.

In light of these results, the first three general categories of hypotheses listed above cannot account for the kind of patterns documented at this site, and therefore must be rejected as principal processes by which heuweltjies form. Instead, the results convincingly demonstrate the accumulation of materials derived through aeolian sediment deposition, justifying further inquiry about how this process occurs. In addition, can aeolian sediment deposition and accumulation adequately account for the many features and patterns exhibited by heuweltjies that are listed at the introduction of this section?
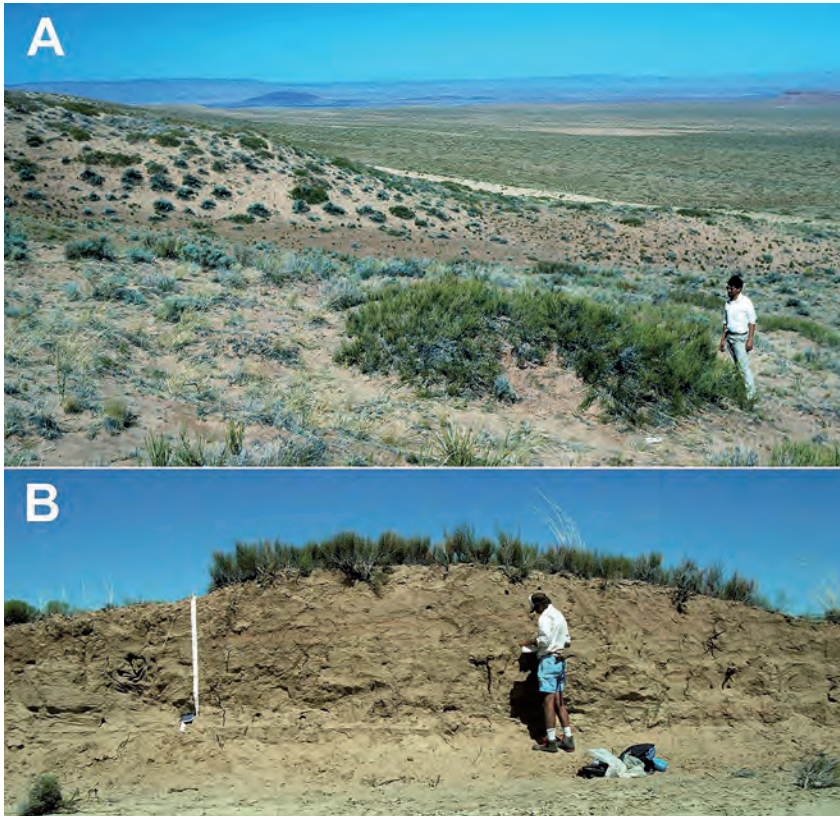
Figure 10.1.29 A, B: Large coppice dunes (nabkhas) associated with dense canopies of the shrub *Ephedra cutleri* in northeastern Arizona, U.S.A, south of Tuba City.
A: Author standing next to coppice dune formed beneath the canopy of *E. cutleri*, which is significantly taller and denser than the surrounding vegetation. Individuals of this shrub are long-lived and grow outward by vegetative (clonal) spread. The hillslope to the left and landscape in distance also contains these phytogenic aeolian landforms. 29 June 1991.
B: Soil scientist Leslie D. McFadden examining a cross-sectioned coppice dune beneath canopy of *E. cutleri*, naturally exposed on a terrace scarp above channel of an ephemeral stream. 1 July 1992.

A model of heuweltjie formation through aeolian sediment accretion

Based on investigations of heuweltjie soils, McAuliffe et al. (2014, 2018) proposed that heuweltjies form through a linked set of biological and physical processes that are initiated by colonies of *M. viator*. Regularly spaced colonies generate fertile islands of nutrient-enriched soil. That enrichment enhances plant growth, generating a patch of vegetation that is denser and taller than that of the surrounding area. The denser vegetation functions as an aeolian sediment trap, leading to the accumulation of substantially greater amounts of wind-deposited sediment in that patch compared to the more sparsely vegetated surroundings, thereby producing the heuweltjie.

McAuliffe et al., (2019b) subsequently presented a more detailed system dynamics model of this process that included evidence for the action of several positive feedback loops within system, and also, the role of principal exogenous environmental variables (climate and aeolian sediment supply) in determining whether or not heuweltjies can form in a particular environmental setting (Fig. 10.1.28). An important point about this model is that *the termites do not actively construct the mounds*, as has been either commonly stated or implicitly assumed in many published papers about various aspects of heuweltjies. Rather, the termite colony is directly responsible for only the initial environmental state change, the localized nutrient enrichment of soils. Under the right combination of external environmental conditions (climate, aeolian sediment supply), the rest of the system is set in motion through responses of plants and the physical environment.

This model differs from earlier work that suggested aeolian sediment deposition was the principle cause of the mounds (Van der Merwe, 1941; Ten Cate, 1966; Table 2) because those proposals did not include a mechanism (fertile islands around termite colonies) to account for the regular spacing of heuweltjies. The localized accumulation of aeolian sediments beneath patches of denser vegetation is a widespread phenomenon in arid- and semiarid regions, producing phytogenic landforms called "coppice dunes" or "nabkhas" (Hodgkinson, 1983; Langford, 2000, McAuliffe et al., 2007; Fig. 10.1.29). The process of wind-borne sediment accumulation beneath denser vegetation associated with heuweltjies, although similar, differs in an important way – the remarkably regular spacing of heuweltjies as compared to the aforementioned phytogenic landforms. This can be attributed to territorial interactions between members of neighboring termite colonies, which consequently creates regularly spaced fertile islands (McAuliffe et al., 2019a).

The deposition and accumulation of aeolian sediments can account for the particular soil geochemical and textural attributes of heuweltjies at the site studied by Midgley et al. (2012) and Cramer et al. (2012). However, how does the model of McAuliffe et al. (2019b) described above compare with other hypotheses in explaining the many distinct features of heuweltjies listed above? Those various features are considered next.

Evaluation of model and other hypotheses

a) Distinct soil chemistry

Francis & Poch (2019) and McAuliffe et al. (2019a) demonstrated the direct role of *M. viator* in accumulating $CaCO_3$, soluble salts, nitrogen and phosphorus in the soils where colonies of the termites are located. These kinds of soil alterations are similar to those generated by many other termite species worldwide (Lobry de Bruyn & Conacher, 1990; Sarcinelli et al., 2007; Semhi et al., 2008; Mujinya et al., 2011; Tilajun et al., 2012; Seymour et al., 2014; Erens et al., 2015). Since ages of some heuweltjies can be thousands to a few tens of thousands of years, the hypothesis that such a long duration of occupancy of a patch by the termites does not contribute to substantial accumulations of these materials is untenable. Hypotheses that invoke mechanisms that do not include the action of termites, e.g., mound formation due to soil displacements by burrowing mammals alone, cannot account for the accumulation of such large concentrations of $CaCO_3$. Similarly, the suggestion that these concentrations of $CaCO_3$ could develop in the absence of termites through direct interception of calcium-bearing aeolian materials by vegetation, coupled with processes of soil water extraction by plants (Cramer et al., 2012), lacks the evidence required to support such a claim (see further detailed, critical assessment in Francis & Poch (2019, p. 8). Furthermore, the processes suggested by Cramer et al. (2012) cannot be responsible for the substantial accumulations of soluble salts in soils of heuweltjies.

b) Finer soil textures of heuweltjies in comparison to the surroundings

Silt-sized particles predominate in aeolian dust in mid-latitudinal arid and semi-arid regions (Tsoar & Pye, 1987; Reheis & Kihl, 1995; Lancaster, 2020), accounting for the higher silt contents of heuweltjie soils compared to surrounding soils. Globally, aeolian dust deposition plays an extremely important, but often overlooked role in shaping soils and landscapes (Simonson, 1995; McFadden, 2013, McAuliffe et al., 2018). The western half of South Africa has ample sources for the generation of aeolian sediment, and the denser vegetation of heuweltjies provides an effective sediment trap for accumulation of those materials.

The finer texture of mounds constructed by some termite species (e.g., *Macrotermes* spp.; Van Thuyne et al., 2021) is attributed partly to particle size sorting by the termites, and use of materials from clay-enriched subsoils in mound construction. However, this sort of size-selective redistribution of earthen materials by *M. viator* cannot account for the extremely large volumes of heuweltjies or the distinct geochemical signatures of the materials in mounds, as previously described. Similarly, the movement of soil materials by burrowing mammals cannot account for the distinct, silt-rich soils that characterize heuweltjies.

c) Highly regular spacing

As previously discussed, spatial overdispersion of mounds is a common phenomenon of many termite species, attributed to strong, agonistic interactions between members of different colonies. The limited evidence available indicates that *M. viator* exhibits the same kind of behavior and interactions (Coaton, 1958; Muna, 2013), thereby providing a mechanism capable of generating the highly regular spacing of heuweltjies. Cramer et al. (2012) speculated that the regular spacing of heuweltjies is due not to presence of the termites, but rather arises through spatial self-organization of the vegetation (Reitkerk et al., 2002); i.e., formation of discrete vegetation patches ("bush clumps") entirely through an interplay of competitive and facilitative interactions among plants. Cramer et al., (2012) concluded that differential erosion of the land surface (less in areas occupied by widely separated bush clumps, more in areas between them) then gave rise to heuweltjies. That process cannot account for the relative uniformity of spacing and density that occurs across the entire geographic range of the mounds where MAP (mean annual precipitation) varies from < 100 mm to > 400 mm, and over an extremely wide array of bedrock, soil conditions, and topographies. For example, the average spacing of 40-50 m between heuweltjies occurs on extensive aeolian sand deposits of the Sandveld of the Atlantic coastal region, as well as areas with extremely thin soil mantles (< 10 cm) over many kinds of bedrock (granitic, metamorphic, and sedimentary). The notion that such an invariant spatial scale of vegetated pattern over such a wide range of physical environmental conditions (precipitation, substrate-limited rooting depth, etc.) is generated exclusively by interactions between plants, particularly competition,

is entirely implausible. Subsequently, Cramer & Midgley (2015) retracted the earlier conclusion of Cramer et al. (2012), stating that "Since the vegetation of all sites where mounds are found in this region is generally < 1 m tall, it is unlikely that vegetation patches could experience direct root competition over long distances".

More recently, von Holdt et al. (2022) concluded that although mounds apparently contain aeolian sediments, erosion of landscape surfaces by water is responsible for initiating the process of mound development and their regular spacing. However, actual observations of stratigraphic relationship of materials contained within heuweltjies show that conclusion is mistaken. A single heuweltjie was excavated in Cramer et al. (2012), consisting of a trench that "was initiated outside the perimeter of the heuweltjie on bedrock and followed the bedrock through to the centre of the mound" (p. 191, Cramer et al. (2012). That description indicates the stratigraphic positioning of the fine-grained soil materials of the mound (which bear a geochemical signature that differs from the underlying bedrock, Table 10.1.3) on top of the bedrock, the same bedrock surface that is widely exposed in the surrounding, off-mound area.[2] Similarly, Cramer et al. (2016) examined the stratigraphy of seven heuweltjies at a different site with core samples and excavations. At the site, soil surfaces surrounding the mounds contained an abundance of coarse quartz gravel. The cores and excavations of heuweltjies revealed that those gravel-rich layers extended "as a relatively intact layer of uniform concentration from the inter-mound area into the mound at the same plane as the surrounding soil surface" (p. 1, Cramer et al. (2016). That observation likewise indicates the superposition of the fine-textured materials contained within heuweltjies on top of a former surface. Stratigraphic relationships of entire, cross-sectioned heuweltjies reveal the same pattern—the fine-grained material within

mounds is superimposed on top of the surrounding landscape (e.g., Fig. 10.1.9), without evidence of erosion of that landscape as the process that initiated mound development. The conclusion of von Holdt et al. (2022) that erosion by water initiates heuweltjie development and ultimately the regular spacing of the mounds is also rejected on the basis of actual, observable surface hydrological behavior of landscapes. Heuweltjies occur in settings that differ greatly in terms of surface hydrological behavior—e.g., nearly level landscapes of deep, permeable aeolian sand deposits that generate little or no runoff and completely lack surface drainage networks (e.g., the Sandveld, Fig. 10.1.14), as well as hillslopes underlain with thin soils over bedrock, which do generate substantial runoff required to cause erosion by flowing water (Figs. 10.1.15). Yet despite those considerable contrasts in surface hydrology, heuweltjies exhibit similar spacing and density. To date, the influence of termites, specifically interactions between colonies of *M. viator*, provides the best, evidence-supported explanation for the observed consistency in spatial patterning of heuweltjies across the entire range of substrate types and topography.

d) Variation in mound sizes (diameter, height & volume) among different regions

A convincing model for the formation of heuweltjies must account for the wide range of linear dimensions (diameter, height) of heuweltjies of different regions, and the corresponding, great contrasts in volume of mounds (more than twenty-fold; Fig. 10.1.11). As presented previously, heuweltjies are larger and the proportion of the land surface they cover is considerably greater in the Atlantic coastal region, as well as floodplains and valleys of the larger river systems, than most inland locations (Figs. 10.1.10, 10.1.11). This geographic pattern is directly related to substantial differences in aeolian sediment supply among

[2] For the Clanwilliam site, Cramer et al. (2012) reported the occurrence of isolated rocks within the fine-grained soil matrix of a heuweltjie (some individual rocks exceeding 10 kg) as well as on the surfaces of many heuweltjies. The paper stated that the presence of these stony materials on and within the mounds could not be attributed to their movement by smaller animals, and was "not the consequence of anthropogenic portage, because they are distributed throughout the soil profile of the mounds," Cramer et al. (2012) concluded that these observations supported the hypothesis that the mounds represent relics of an ancient land surface, protected from erosion by patches of denser vegetation. However, archaeological investigations have revealed an abundance of prehistoric, human-made stone artifacts throughout this area near the Olifants River, now impounded by Clanwilliam Dam (Hallinan, 2013; Hallinan & Parkington, 2017). The site of Cramer et al. (2012) is within 500 m of the shoreline of the Clanwilliam Dam Lake. For those heuweltjies located within the zone of the widely fluctuating lake level, fine soil material of the mounds is exposed to erosion by wave action, "and [stone] artifacts cemented into them are now eroding out as the heuweltjies degrade" (Hallinan, 2013). Consequently, a plausible explanation for some of the stone objects within the fine soil matrix of heuweltjies, including flat, tabular slabs such as pictured in Fig. 8D of Cramer et al. (2012), is actually the transport and placement of those materials long ago by humans, rather than representing an intact stratigraphic remnant of a former geological surface. Furthermore, the observation by Hallinan (2013) and Hallinan & Parkington (2017) of human-made stone artifacts eroding out of cemented (deeper) layers of heuweltjies in itself provides evidence of burial of these objects over time as the mounds formed.

different regions (McAuliffe et al., 2014, 2018, 2019b). The Atlantic coastal region of South Africa is a low-relief plain largely covered by aeolian sand deposits that extend inland more than 50 km in some places. Even at somewhat greater distances inland, low-relief hills and plateaus possess discontinuous mantles of aeolian sediment (Chase & Thomas, 2007; personal observations). The abundance of fine-grained sediments that are readily mobilized by the wind in this region fosters the development of larger heuweltjies and therefore the fraction of the land surface covered by the mounds. Cramer & Midgley (2015) corroborated this conclusion through quantitative analysis of aerial imagery throughout the entire geographic range of heuweltjies, measuring diameters of the mounds and the fraction of the land they covered. They demonstrated that heuweltjies occupy the largest portion of the landscape in sparsely vegetated areas with sandy soils, relatively strong winds, and summer droughts—physical conditions that characterize the Atlantic coastal region. Cramer & Midgley (2015) concluded that relationship supported the proposal that heuweltjies form through vegetation-induced deposition of aeolian sediments, another reversal of the earlier conclusion of Cramer et al. (2012) that differential erosion of the land surface forms the mounds. Alluvial sediments of river floodplains are another source of fine-grained materials that can be mobilized and transported by the wind (Bullard et al., 2008; Ellwein et al., 2018). The analysis of Cramer et al. (2017) showing a greater coverage of the land surface by heuweltjies in areas near large river systems also reflects the role of increased sediment supply in influencing heuweltjie size. Of all the hypotheses proposed for the formation of heuweltjies (Table 10.1.2), the model presented by McAuliffe et al. (2014, 2018; 2019b) is the only one supported by evidence that provides a plausible explanation for the great variation in size and coverage of heuweltjies over wide geographic areas.
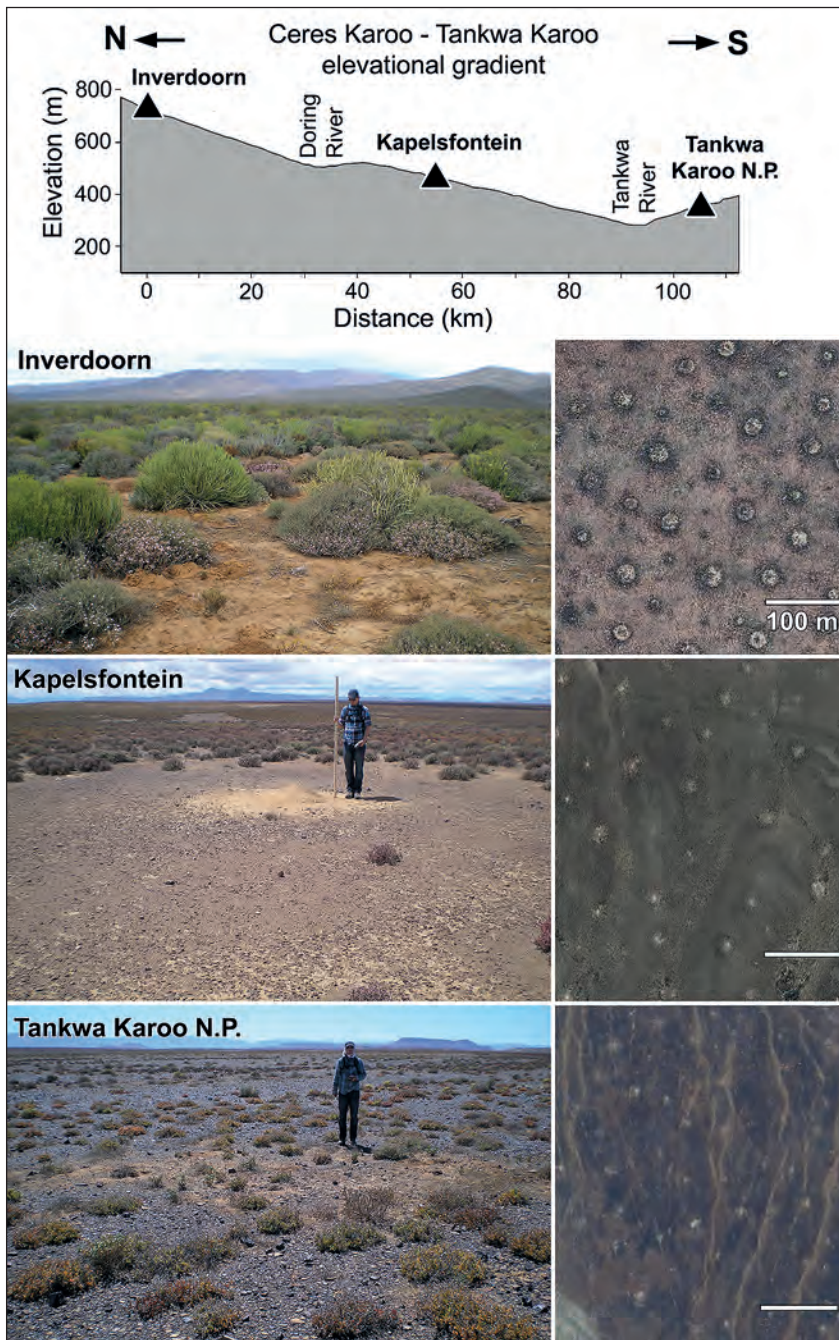
e) The occurrence of *Microhodotermes viator* in environments where heuweltjies are absent

Heuweltjies occur in only part of the entire distribution range of the termite *M. viator*. (Fig. 10.1.4). This incongruity has understandably led some researchers to conclude that this termite species is not involved in the formation of heuweltjies (Midgley et al., 2002; Cramer et al., 2017). That conclusion would indeed be reasonable if mound formation depended entirely on soil-displacement activities by the termites. However, that is apparently not the process by which the heuweltjies form. Instead, as described above, McAuliffe et al. (2014, 2018, 2019b) provides an evidence-supported model that describes how heuweltjies form through the action of a series of linked biological and physical processes. Once again, an essential point of the model is that *the termites do not construct heuweltjies*. Instead, termites directly create the initial environmental change (localized soil nutrient enrichment) that puts the entire system of subsequent processes in motion, consisting of (1) vegetation responses to soil enrichment and (2) the physical environmental response of aeolian sediment accretion due to the windbreak effect of denser vegetation of the patch. Although the "ultimate cause" of heuweltjie formation is the change in soil nutrient content generated directly by the termites, the *proximate process* by which mounds form is a physical response to the denser vegetation patch (localized reduction of wind velocity and the resultant deposition of windborne sediment). Conditions required for all of these processes, culminating in the formation of a heuweltjie, do not occur everywhere. Identifying the particular environmental characteristics necessary for the complete unfolding of the entire sequence of processes is central to understanding why heuweltjies form in some places, but not others, despite the presence *M. viator*.

The arid extreme

Even though long-term occupancy of a patch by colonies of *M. viator* inexorably generates a fertile island in terms of plant nutrients, responses of vegetation to that enrichment depend on the climate. At the arid end of the continuum, water rather than nutrients imposes the greatest limitation to overall plant productivity (Noy-Meir, 1973). With the exception of years of above-normal precipitation, nutrient addition has little effect on vegetation productivity in arid environments (Hooper & Johnson, 1999). Across the range of biomes from desert to topical forest, experimental addition of soil nitrogen increased above-ground net primary production everywhere except in deserts (LeBauer & Treseder, 2008). Consequently, in the most arid portions of the Succulent Karoo, increases in soil nutrients

around colonies of *M. viator* do not promote development of discrete patches of denser vegetation required as a sediment trap. This precipitation-dependent response of vegetation, and ultimately, the generation of conditions required for localized patches of aeolian sediment accumulation and heuweltjie formation, are displayed along a pronounced precipitation gradient from the semi-arid Ceres Karoo north to the most arid portions of the Tankwa River basin in Tankwa Karoo National Park (Fig. 10.1.30). The upper elevation at the southern end of this gradient (Inverdoorn) receives an estimated mean annual precipitation (MAP) of 258 mm (Schulze et al., 2001). The lower, most arid portions of the Central Tanqua bottomland plains (Tankwa Karoo NP) receives < 100 mm MAP (van der Merwe, 2015). Vegetation production along the gradient reflects the precipitation contrasts. Heuweltjies are prominent in the southernmost, semi-arid portion (Inverdoorn), but disappear entirely from the landscape in the arid, lower elevations to the north.

The analyses of Cramer & Midgley (2015) and Cramer et al. (2017) also showed that heuweltjies are absent in the most arid portions of western South Africa, despite the presence of *M. viator*. In those more arid regions, colonies construct and reside (1) within the small, conical cemented mounds where extremely shallow soils over impenetrable metamorphosed shale bedrock prevent deep positioning of the nests, or (2) in subterranean nests without any above ground mounding in areas where thicker soils allow deeper tunneling and establishment of the central nest below the surrounding surface (Fig. 10.1.30, Kapelsfontein (1) and Tankwa Karoo (2) sites). The two types of colonies exhibit the same spacing and density as

Figure 10.1.30:
Contrasts in the physical manifestations of the presence of colonies of *M. viator* along a pronounced precipitation gradient. At the mesic end of the gradient (Inverdoorn), heuweltjies are present throughout the landscape, on old alluvial fan surfaces as shown, as well as areas of shallow soils on bedrock. With increasing aridity at lower elevations, heuweltjies are completely absent. In those more arid areas where extremely thin soils occur over bedrock (Kapelsfontein), colonies of *M. viator* construct cemented, conical mounds. Ground view of mounds at this site are shown in Fig. 19A & C. However, in areas where deeper soils are found (Tankwa Karoo N.P.), nests of colonies are positioned far enough below the soil surface, and conical mounds are not constructed. The three small panels to the right show Google Earth™ vertical aerial views of each site, each at the same scale (white 100 m scale bar in each). The raised heuweltjies are clearly seen at the Inverdoorn site. The dimensions of 15 heuweltjies measured at this site had diameters ranging from 9–26 m (mean = 16.2 m), and heights of 20–105 cm (mean = 44.3 cm). At the more arid Kapelsfontein site, the conical mounds and the vegetation-free zones surrounding them show up as regularly spaced light spots in the aerial view. Likewise, although somewhat less conspicuous, locations of colonies of *M. viator* at the Tankwa Karoo N.P. site are visible as light-colored spots against the darker background of surface gravels and cobbles coated with rock varnish. Site locations, soil characteristics of the termite-related features of each site, and quantitative analyses of nearest-neighbor distances are presented in McAuliffe, et al., 2019a.

do heuweltjies (McAuliffe et al., 2019a). Conical mounds of *M. viator* and the immediately surrounding soils have elevated contents of N and P, (McAuliffe et al., 2019a), but despite this enrichment, there is no enhancement of vegetation growth due to the overriding limitation of water for plant growth. Instead, the cover and height of vegetation immediately surrounding the conical mounds are typically substantially reduced or altogether absent in these more arid settings. As a consequence, localized deposition and accumulation of aeolian sediments cannot occur.

The mesic extreme

The distribution of *M. viator* extends to areas receiving > 600 mm MAP in the Western Cape where the greater precipitation typically supports closed-canopy fynbos vegetation dominated by taller shrubs. Despite the presence of colonies of *M. viator* in those environments (Coaton & Sheasby, 1974; Picker et al., 2007), heuweltjies are rare or absent (Cramer et al., 2017). Colonies of *M. viator* are capable of altering soil conditions in areas surrounding their colonies in these settings, and those alterations often contribute to vegetation patches with plant species compositions that differ from the surroundings (personal observations, Tygerberg Nature Reserve, 16 km E-NE of Cape Town; MAP > 600 mm). However, despite the contrast of plant species identities, in the closed-canopy vegetation, nutrient additions in areas of higher precipitation apparently do not foster the development of pronounced changes in vegetation structure (canopy height & density) required to produce discrete, island-like sediment traps. Aeolian sediments are distributed and deposited in denser fynbos vegetation (Soderberg & Compton, 2007). However, without the necessary spatial contrasts in plant canopy architecture, those sediments are deposited more uniformly across the landscape, rather than selectively accumulating in distinct, widely separated patches.

In summary, there is apparently a particular climate range—a "Goldilocks zone" for heuweltjie formation—that is neither too dry nor too moist—within which the structurally distinct vegetation patches can develop, beneath which aeolian sediments accumulate and eventually form the mounds. To date, the existence of colonies of *M. viator* in very different settings—large heuweltjies, small cemented mounds, or subterranean with no above ground structure—has con-

founded attempts to understand how heuweltjies form; the linked set of processes proposed by McAuliffe et al. (2014, 2018, 2019b) explains this variation.

Past climate changes

Major climate changes associated with the Pleistocene-Holocene transition likely shifted the geographic distribution of environmental conditions required for active development of heuweltjies through aeolian sediment accumulation. Palaeoclimate reconstructions, based on marine core and terrestrial records for the Atlantic coastal region of South Africa and Namibia, indicate a shift to warmer and more arid conditions in the latter part of MIS-2, around 16–14 ka (Shi et al., 2000; Dewar & Stewart, 2016). That shift provides an explanation for the existence of the very sparsely vegetated or completely barren heuweltjies that occur throughout the more arid portions of the Succulent Karoo in areas that now receive < 100 mm MAP in coastal areas of northwestern South Africa and the Richtersveld region (Petersen, 2008). Since heuweltjies can be extremely old (> 30 ka) structures, the barren heuweltjies in those regions (Figs. 10.1.16, 10.1.18A, C) may represent mounds that formed during a time of greater effective moisture in the late Pleistocene. Under those less arid conditions, the termite-produced nutrient enrichment of soils would have been more likely to promote development of localized, denser vegetation patches capable of intercepting and accumulating aeolian sediments. The heuweltjies that exist in these areas today apparently represent persistent, relic landforms of mounds that formed in the past. However, *M. viator* continues to occupy mounds in these drier regions (Francis et al., 2021), probably because of the locally altered soil conditions that enable burrowing and deep positioning of the nests.

Secondary influences

In addition to the processes of aeolian sediment deposition and accumulation, other abiotic and biotic processes potentially influence heuweltjies. The system dynamics model of McAuliffe et al. (2019b; Fig. 10.1.28) does not exclude these processes, but rather includes them in a general representation of their integrated influences. In addition to the direct influence of aeolian sediment deposition on mound formation, indirect effects derived through positive feedback loops within

the system play a role in reinforcing the process of formation and maintenance of heuweltjies.

For example, excavations by mammals (aardvarks, Brant's whistling rats, and in some places, mole rats, and others) occur widely on surfaces of heuweltjies. The resulting bioturbation can significantly modify the soil environment by reducing soil bulk density, thereby increasing the volume occupied by a given soil mass. These kinds of soil displacements alone cannot account for the size and volume of large heuweltjies. However, they can markedly change soil conditions (infiltration, soil moisture status), thereby potentially contributing to continued enhancement of vegetation and maintenance of the capacity to intercept and accumulate aeolian sediments (Fig. 10.1.28; positive feedback loops F3 & F4). This sort of bioturbation in off-mound areas is typically rare or entirely lacking, most often at sites with shallow soils over impenetrable bedrock (e.g., Figs. 10.1.11B, 10.1.12C, 10.1.15C). Consequently, initial accumulation of a looser, fine-grained soil by aeolian accretion in such settings is necessary before significant mammalian bioturbation of the patch occurs.

Another secondary influence contributes to the higher nutrient content of heuweltjie soils. Initial, direct action of termites initiates the process of enhancing the fertility of a patch. The increased vegetation development on that patch subsequently attracts many other animals for a variety of reasons—food resources, burrowing or nesting sites, and concealment and protection. Deposition of faeces and dung on the mounds by these animals (Milton & Dean, 1990) further enriches the soil, and constitutes another positive feedback loop that maintains the system.

Accumulation of $CaCO_3$ in heuweltjies, a process initiated by the termites, eventually can form thick, cemented petrocalcic horizons. Over time that accumulation requires an upward, vertical expansion or inflation of the soil profile to accommodate the increased volume (Capo & Chadwick, 1999). Francis et al. (2013) attributed the raised relief of heuweltjies to this process, combined with the transport of material into the heuweltjie by termites. Although accumulation of $CaCO_3$ and formation of petrocalcic horizons can potentially contribute to the raised relief of heuweltjies, this process, combined with the incidental transport of soil materials ingested by the termites, cannot account for the widespread occurrence of large heuweltjies (e.g., > 2 m tall) within which petrocalcic horizons are entirely absent (Figs. 10.1.11A, 10.1.26C, 10.1.27). Again, this process is secondary to aeolian sediment accretion in mound formation, particularly in areas with large aeolian sediment fluxes, such as the Atlantic coastal region.

Biodiversity and conservation

The Succulent Karoo is a recognized biodiversity hotspot and possesses a richer flora than any other arid to semi-arid region of the world that receives winter precipitation (Cowling et al., 1998). Marked variability of soils throughout the region, including the unique soil environments of heuweltjies, contributes significantly to this diversity (Francis et al., 2007). Contrasts between soils of heuweltjies and their surroundings generate compositionally distinct vegetation patches, thereby significantly expanding local diversity. Furthermore, considerable differences in the vegetation composition of heuweltjies throughout the entire geographic range of the mounds enhances the entire region's floral diversity.

The distinct soil and vegetated environments of heuweltjies also foster faunal diversity. Environmental characteristics of heuweltjies, including unique soil conditions, plant species composition, and vegetation cover provide habitat and food resources to many kinds of animals that in the absence of the mounds, would be relatively unavailable or altogether absent. The substantially thicker, looser soils of heuweltjies are occupied by burrowing mammals such as Brandt's whistling rat (*Paratomys brantsii*) and the aardvark (*Oryctoperus afer*). Excavations by both create small-scale disturbances, thereby increasing environmental heterogeneity and providing opportunities for establishment of different plant species (Louw et al., 2017). Both mammals also depend significantly on the mound environment for their principal food supplies (plants for the herbivorous whistling rat, termites for the aardvark). Likewise, heuweltjies provide mammals such as the bat-eared fox (*Otocyon megalotis*), meerkat (*Suricata suricata*), steenbok (*Raphicerus campestris*), and others with suitable sites for denning, food resources, or other uses (Milton & Dean, 1990). Plant species dispersed by mammals and birds are more common on heuweltjies than on adjacent plains (Milton,

Figure 10.1.31: Fenceline contrast showing extreme reduction of vegetation cover to left side of fence on a heuweltjie. The worn path along the fence is a livestock trail. This area, 7 km S-SW of Soebatsfontein has a documented history of heavy use by livestock (Schmiedel et al., 2016). The dominant plant species on both sides of the fence is *Mesembryanthemum guerichianum*, a prostrate, annual succulent that commonly grows in disturbed areas and is unpalatable to livestock (Esler et al., 2006). Despite its unpalatability, its abundance and cover is much reduced on the heavily used (left) side of the fence. The predominance of this species on both sides of the fence indicates the recent construction of the fenceline, and the overall heavy use by livestock in this area. This is the Soebatsfontein 2 mound located 7 km S-SW of Soebatsfontein (see also Figs. 26C, 27). The right half of the mound was removed in construction of the roadway paralleling the fenceline. 25 October 2012.

1990). Bird-dispersed perennial plants that bear small fleshy red or black fruits (*Asparagus* spp., *Lycium* spp., *Rhus undulata*, and *Euclea undulata*) occur almost exclusively on heuweltjies in some areas (personal observations). Heuweltjies undoubtedly provide environmental conditions required by some invertebrates. For example, McAuliffe et al. (2019a) documented that the land snail *Trigonephrus namaquensis* at a site in the Succulent Karoo was almost entirely restricted to $CaCO_3$-enriched soils surrounding mounds constructed by *M. viator*, probably because those soils are the only significant source of calcium required for shell development. The physical environment of heuweltjies and the resources the mounds supply are essential for a wide range of animals, both invertebrates and vertebrates, but

these ecological relationships have not yet been explored in depth.

Given the role heuweltjies play in enhancing the biodiversity of the Succulent Karoo Biome, conservation of the environmental conditions that the mounds provide is essential. As discussed earlier, a long history of heavy use of the Succulent Karoo environment for livestock farming has greatly altered the vegetation in many areas, and with heavy grazing pressure, vegetation of heuweltjies often suffers the greatest impacts. Although the use of these lands for raising livestock, primarily sheep, peaked in the late 1950s and has been declining ever since (Hoffman & Rohde, 2007), many areas that were heavily impacted decades ago have exhibited relatively little

recovery, particularly in drier areas with MAP < 200 mm (Seymour et al., 2010; Schmiedel et al., 2016). Consequently, in some areas, heuweltjies possess less vegetation cover and lower plant species diversity than surrounding areas (Fig. 10.1.31; Kunz et al., 2012). Large portions of the area over which heuweltjies occur, especially Namaqualand, are economically impoverished, and people there rely on a healthy and productive natural environment in many ways. Owners of private sheep farms and those employed in such operations, as well as members of communal farms, benefit in the long term through the recognition and practice of sustainable land use. The region's unusual flora and landscapes are world-renowned and contribute to a substantial ecotourism industry that attracts large numbers of visitors from around the world, especially to witness the vibrant spring bloom. Further environmental degradation of the portions of the Succulent Karoo can only hurt this increasingly important source of revenue.

An understanding of the actual processes responsible for the formation of heuweltjies has important implications for conservation of the biodiversity and the unusual landscapes of the Succulent Karoo region. The evidence indicates that formation of heuweltjies depends on the creation of fertile islands by termites, coupled with the development of vegetation patches capable of trapping and accumulating aeolian sediments. Any use of landscapes that diminishes the sediment-trapping effect of vegetation on heuweltjies impairs or eliminates the very processes by which sediments are added and maintained on the surface. Depending on the environmental setting, long-lasting impacts like this are potentially compounded by increased soil erosion of the sparsely vegetated mounds. In the more arid regions where deeper soil layers of heuweltjies have accumulated high salt content, severe erosion of the surfaces of heuweltjies exposes those deeper highly saline layers, leaving the landscape in a relatively permanent state of degradation (McAuliffe et al., 2014). To conserve the productivity, biodiversity, and beauty of the region, any use that leads to damage or significant loss of vegetation cover on heuweltjies should be carefully avoided. Heuweltjies can serve as sensitive and important indicators of ecosystem health (Stokes et al., 2009), and in doing so, provide a region-wide "canary in the coal mine" indicating which kinds of landscape uses are sustainable, and which are not.

Acknowledgements

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