

Are mima-like mounds the consequence of long-term stability of vegetation spatial patterning?



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ABSTRACT

The origins of large (>5 m diameter, >1 m height) and regularly spaced (i.e. over-dispersed) non-anthropogenic earth mounds (e.g. mima mounds, heuweltjies, nabkhas) that occur across all biomes remain unresolved. An extensive literature documenting diverse explanations for mound genesis has accumulated that primarily ascribes mound formation to faunal agents. Recent modeling efforts suggest that both abiotic and biotic processes commonly interact to produce striking vegetation patterning (e.g. spots, labyrinths). The hypothesis that many earth mounds, apart from those with a clear faunal genesis (e.g. termitaria), may result from vegetation trapping of sediment or aeolian dust and/or protection of soil from erosion is reviewed here. The literature on the occurrence and properties of some of these mima-like mounds is reviewed, and the evidence for their origins evaluated. Some mounds, such as coppice dunes (otherwise known as nabkhas), clearly form as a consequence of aeolian deposition of sediment around vegetation patches. However, the clay, stone and rock content of some mima-like mounds is not consistent with purely aeolian origins. Instead it is suggested that non-aeolian mound over-dispersion, elongation, volumes, soil properties and stratigraphy are consistent with vegetation patches protecting soil from erosion, resulting in preferential erosional deflation of the inter-mound area leaving regularly spaced mounds. Although mima-like mounds around the world are formed in diverse vegetation types, climates and edaphic conditions, many may be long-term products of vegetation spatial patterning in which plant canopies and root systems increase sediment capture and reduce erosional losses.

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1. Introduction

Regularly spaced non-anthropogenic mounds and hollows in landscapes have piqued the curiosity of the public and scientists for at least the last two centuries (e.g. de Lafora 1776, cited in Kinnaird, 1958) and the debate continues unabated. Examples of such features include mounds in Brazil (campos de murundus, meaning mound fields; e.g. Silva et al., 2010), North America (pimple mounds, hogwallow mounds, prairie mounds or mima-mounds; e.g. Cox, 1984; Horwath Burnham and Johnson, 2012a, 2012b), southern Africa (heuweltjies, meaning small hills; Moore and Picker, 1991; Midgley et al., 2002; Picker et al., 2007; Potts et al., 2009) and possibly also in Australia (Noble, 1993). These generally circular or slightly elongated mounds range in average size from 2 to 15 m in diameter and are commonly significantly over-dispersed (i.e. non-random) with R-values >1.4 (Table 1). The origins of these mounds are controversial, partly because diverse abiotic and biotic processes may produce similar mounding patterns in different environments. The fact that the mounds may persist in landscapes for thousands of years further complicates explaining their genesis. Explanations for mound genesis include (amongst others listed by Horwath Burnham and Johnson, 2012a, 2012b) 1) abiotic mechanisms (e.g. freeze/thaw, expanding/shrinking clays, aeolian, seismic), 2) faunal agents (e.g. fossorial rodents and termites) and 3) spatial vegetation patterning coupled to aeolian and hydraulic deposition and differential erosion.

Non-random spatial patterning is common in natural systems, requiring only the existence of positive feedbacks to destabilize uniform states and lead to large-scale patterns (e.g. sand ripples, dunes, ocean swells, cloud streets and cracking clays; Meron, 2012). Self-organising spatial vegetation pattern is also common worldwide (e.g. Rietkerk and van de Koppel, 2008) and has been implicated in diverse cases of mound formation. For example, spatial patterning of vegetation combined with aeolian deposition of sediment is thought to explain the formation of some sandy hillocks in arid areas (i.e. nabkhas or coppice dunes, Section 3). A diversity of tree islands that occur in wetlands (e.g. Florida Everglades) are also thought to form as a result of vegetation trapping sediment (e.g. Ross and Sah, 2011; Section 4). Spatial patterning of vegetation combined with erosion has also been suggested to account for non-aeolian dryland mound formation in Patagonia (Rostagno and del Valle, 1988), Brazil (de Araujo Neto et al., 1986; Furley, 1986; Silva et al., 2010), South Africa (Cramer et al.,

2012) and in the USA (e.g. Gibbs, 1854; Le Conte, 1874; Holland et al., 1952; Cain, 1974). Despite the historic roots of this hypothesis, an extensive literature has accumulated primarily ascribing mound formation to faunal agents (Fig. 1).

Here the diversity of repeating mound landscape features is reviewed, and it is hypothesized that vegetation spatial patterning combined with differential erosion and sedimentation successfully explains many mound phenomena. In this synthesis both biotic agents (faunal and vegetation spatial patterning) and abiotic factors potentially responsible for pattern formation are considered and it is concluded that the many large (>5 m diameter) and regularly spaced mounds may primarily be the consequence of vegetation effects on sediment accretion and erosion processes, and that faunal agents are likely a secondary agent that contribute to sediment bioturbation, but not primary mound construction.

2. Terminology

The terminology for dryland mounds has not been standardised, and is complicated by the fact that not all non-anthropogenic mounds have a common origin (Johnson and Horwath Burnham, 2012). Here clearly aeolian mounds are differentiated as nabkha-like, which is derived from the Arabic word nabkha (sometimes spelt nebkha) referring to mound-like accumulation of wind-blown sandy sediment collected within and behind, and stabilised by, vegetation (Khalaf et al., 1995; West and Johnson, 2005). This includes coppice dunes and probably pimple mounds (Seifert et al., 2009). Following Washburn (1988) non-aeolian mounds are referred to as mima-like. The term mima, derived from the name of the site (Mima prairie) where striking mounds occur in Washington State (USA), has been used to refer to mounds in the USA and elsewhere in the world and is commonly understood. The regional terms murundus and heuweltjies are retained for the South American and South African mounds, respectively, to distinguish these from mima-like mounds in the USA, despite arguing in what follows that these are essentially mima-like in their genesis.

3. Nabkha-like mounds

Wind and sand produce a diversity of regularly spaced abiotic structures ranging from sand ripples to spectacular dunes. These are all formed by windward saltation and leeward grain-flow (Werner,

Table 1

Comparison of mound/clump characteristics and site slopes for sites with mima-like mounds (USA), murundus (Brazil), heuweltjies (South Africa), nabkha-like mounds and bush clumps. Values are the 5–95 percentiles for measures obtained from Google earth (see Appendix S1 and S2 in Supporting Information for methods and sites). These include site slope, mound density, distance between peripheries of mounds, mound diameters, mound landscape occupancy (LO, % land surface area), mound elongation (ratio long axis to short axis) and mound over-dispersion (R = 1 for random distributions and 2.15 for maximum dispersion in a hexagonal lattice; Clark and Evans, 1954). The number of sites included in the analyses is indicated (n). Elongation was subject to a Z-test, which showed that the averages for all mound types exhibited significant ($P < 0.05$) departures from a circular plan (i.e. elongation = 1).

Mound type	Slope (m m ⁻¹)	Density (ha ⁻¹)	Distance (m)	Diameter (m)	LO (%)	Elongation (m m ⁻¹)	R	n
Mima-like	0–0.38	5–109	2–14	5–22	5–39	1.0–1.5	1.3–1.8	47
Murundus	0	21–247	1–3	4–15	25–39	1.0–1.1	1.6	4
Heuweltjies	0.03–0.24	3–8	7–24	19–32	14–31	1.1–1.4	1.4–1.9	6
Nabkha-like	0	2–50	3–29	8–26	7–30	1.0–1.3	1.2–1.6	4
Bush-clump	0–0.09	1–11	12–26	12–67	9–35	1.0–1.2	1.3–1.8	5

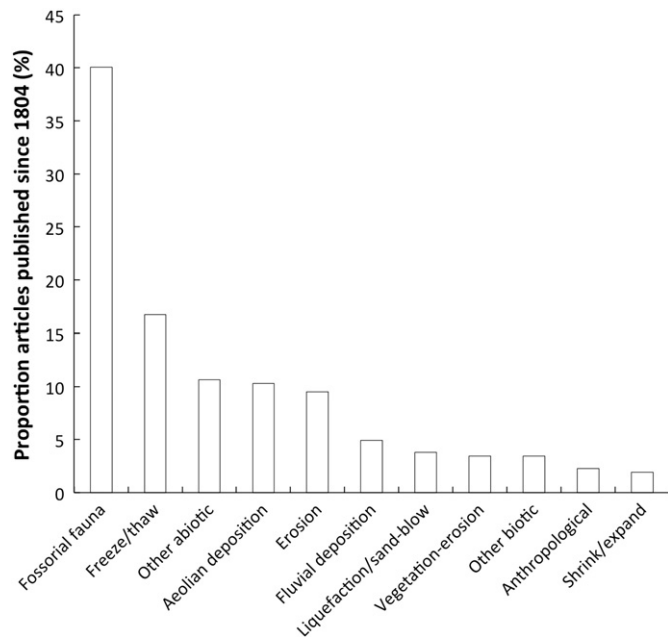


Fig. 1. The proportion of 263 publications supporting various hypotheses for the origins of mima mounds listed in the bibliography of [Horwath Burnham and Johnson \(2012a, 2012b\)](#) containing 274 articles published between 1804 and, 2011. Other biotic (commonly, but not exclusively, wind induced tree throw) and other abiotic are diverse abiotic hypotheses that were not categorised.

1995), resulting in a gentler windward slope where the sand is pushed up the dune and a shorter steeper leeward slip face. Nabkhas result from aeolian deposition around individual shrubs or clumps of vegetation ([Quets et al., 2013](#); [Fig. 2a, b](#)) and are common in semi-arid regions around the world, e.g. Mali ([Nickling and Wolfe, 1994](#)), Burkina Faso ([Tengberg, 1995](#)), USA ([King et al., 2006](#)), South Africa ([Dougill and Thomas, 2002](#)), Kuwait ([Khalaf et al., 1995](#)), and China ([Wang et al., 2006](#)). Nabkhas are mostly composed of sand or silt with very little gravel (e.g. <2% w/w, [Khalaf and Al-Awadhi, 2012](#)). The sizes, density and over-dispersion of nabkhas depend on factors governing sedimentation/erosion (e.g. wind properties and sediment loads; [King et al., 2006](#)) as well as on vegetation spatial properties ([Wolfe and Nickling, 1993](#)). Nabkhas generally depart from circular plans due to leeward deposition and windward erosion ([Nickling and Wolfe, 1994](#)), also resulting in coarser sand on the windward flank ([Khalaf and Al-Awadhi, 2012](#)).

While currently forming nabkhas are readily distinguishable, ancient nabkhas that may have formed during former arid periods may have more cryptic origins. Large mounds (0.5–1.5 m in height) across a range of ecosystems in the USA have been suggested to originate as nabkhas (e.g. [Barnes, 1879](#); [Ellis and Lee, 1919](#); [Seifert et al.,](#)

[2009](#)). Nabkhas are over-dispersed ($R = 1.2\text{--}1.6$), of variable size (8–26 m diameter) and significantly elongated ([Table 1](#)), with clear textural asymmetry between the windward and leeward flanks. While some nabkhas may be currently active (e.g. [Wang et al., 2006](#)), others are ancient. Optically stimulated luminescence (OSL, measures time since burial of geologic sediments) ages of nabkha-like mounds in Arkansas range from ca. 1000 to 6770 yr BP, with sediment age since burial increasing strongly with depth in the mounds ([Seifert et al., 2009](#)). The fact that surface sediment is consistently younger than deeper sediments rules out extensive bioturbation in the formation of these mounds, which would tend to homogenise the soil ages without precluding horizonisation ([Wilkinson et al., 2009](#)). These authors concluded that nabkha-like mounds of south-central USA originated during a multi-decadal drought in the mid-Holocene.

4. Vegetation islands in wetlands

Vegetated wetland islands occur throughout the world ([Wetzel, 2002](#)), and their origins are relatively uncontroversial. In the Florida Everglades (USA) these islands are commonly referred to as tree islands or hammocks ([Ross and Sah, 2011](#)). The islands are initiated by establishment of plants in a wetland, subject to positive and negative feedback interactions between the plants and the physical environment ([Ross and Sah, 2011](#)). Directional water flow results in aggradation through sediment deposition, with vegetation contributing through litter accumulation ([Wetzel, 2002](#)), raising the mound surface above the water level (e.g. 0.2–1 m in the Everglades; [Wetzel et al., 2005](#)). These islands occur in flat landscapes and their size and density are related to vegetation properties, the flow of water and the occurrences of disturbance (e.g. fire, flooding, drought). The islands are very variable in size (10 m² to >700 000 m² in the Everglades), but are generally elongated in the direction of water flow, with distinct sediment physical and chemical properties between the upstream and downstream portions of the islands ([Wetzel et al., 2005](#)). The long-term persistence of such islands results in the creation of resource heterogeneity, both between the islands and surroundings and within the islands itself (i.e. upstream portion has more nutrient than downstream portion). For example, hammocks in the Everglades accumulate 6–100-fold more P than surrounding marshes and also precipitate calcium carbonate ([Wetzel et al., 2005](#)). Accumulation of nutrients and precipitation of carbonate have also been reported for vegetation islands in the Okavango delta in Botswana ([McCarthy et al., 1993](#)).

5. Characteristics of non-aeolian dryland mounds: case studies

Non-aeolian dryland mounds are common around the world and form for a variety of reasons. Because of this and uncertainties in the literature regarding whether many mounds in the USA and elsewhere are aeolian, gilgai, mima-like or in some cases anthropogenic, further review of non-aeolian mounds is restricted to three extensively

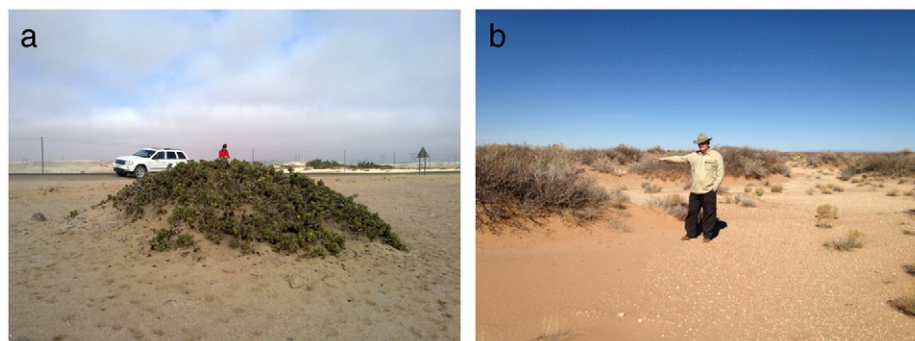


Fig. 2. Nabkha mounds in a) the Namib Desert (ca. 4 m diameter; $-22.676^\circ, 14.583^\circ$) and b) Chihuahuan Desert (USA, ca. 6.5 m diameter; $32.281^\circ, -106.205^\circ$).

documented areas including the mima mounds in the vicinity of the Puget Lowland area of Washington State, heuweltjies in the western Cape (South Africa) and the murundus of central Brazil.

5.1. Mima mounds

The maritime climate of the Puget Lowland area is cool with dry summers and mild wet winters (Washburn, 1988). The underlying geology of the area is ascribed to post-glacial outwash that occurred ca. 14 890 yr BP (Porter and Swanson, 1998). The bulk soil organic carbon of mima mounds of Mima prairie (Fig. 3a, b) has been radiocarbon dated (Fig. 4) to between 1692 and 4242 yr BP (Washburn, 1988), which, due to overprinting (i.e. potential inclusion of recently fixed carbon), represents minimum ages for the mounds. Consistent with this, thermoluminescence dating of mounds at sites outside Puget Lowland (Manatash Creek and Thorp prairie in Washington, <150 km from Mima prairie), which measures the time since burial of geological sediments, yielded (limiting) sediment ages (0.45 m deep)

of 7800 ± 700 and 5600 ± 500 yr BP, respectively (Bandow, 2001). In Puget Lowland, the period from ca. 5000 yr BP represented a change from an earlier warmer and drier climate to a modern cooler and wetter climate regime (Sea and Whitlock, 1995) with less frequent fires (Cwynar, 1987) favouring more mesophytic vegetation. Mound material consists of dark coloured (often black) unstratified gravels and pebbles within a sandy-loam matrix overlying a lighter coloured bedded glacial outwash, which is close to or on the surface between mounds. Gravel forms 58% and 49% of mound and inter-mound soil, respectively. The mound soil matrix is composed of 80% sand, 16% silt and 4% clay, which is similar to the inter-mound soil matrix with 72% sand, 23% silt and 5% clay (depth-averaged from Washburn, 1988). Clay concentration generally decreases with depth through the mounds and there are no strong discontinuities in soil clay with depth (Washburn, 1988). Pebbles are predominantly less than 6.4 cm in length, but small boulders (<0.5 m length, Ritchie, 1953; 13×15 cm, Ross et al., 1968; 2.2 to >7.5 kg, Washburn, 1988) to large boulders (Freeman, 1932) have been found embedded in the mounds.



Fig. 3. Mima mounds in a) Washington state (ca. 11 m diameter; Mima Mounds Natural Area Preserve; 46.905° , -123.050°) and b) viewed in Google Earth; c) a heuweltjie (ca. 22 m diameter; South Africa; -31.994° , 19.011°); d) heuweltjies (South Africa; -31.672° , 18.725°) viewed in Google Earth; e) rocks (ca. 0.3 m diameter) on the surface of a heuweltjie (South Africa; -31.994° , 19.011°) and f) a road-cutting through a heuweltjie (-31.917° , 18.713°) exposing the calcrete horizon and a root cast (inset).

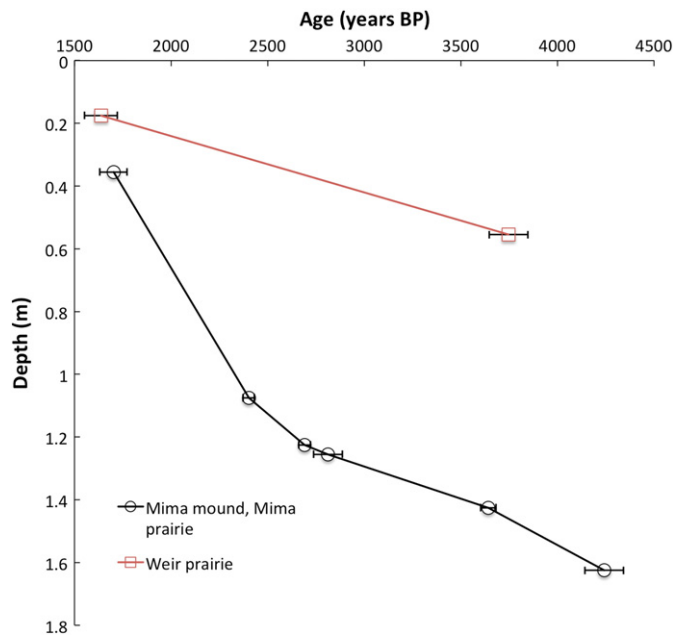


Fig. 4. Synthesis of radiometric ^{14}C dates for bulk soil organic carbon from mima mound sediments (Mima prairie, Washington, USA) and Spanaway soils (data from Washburn, 1988). Weir Prairie lacks mounds and is ca. 20 km NE from Mima Prairie. Note that these dates are likely subject to overprinting (i.e. potential inclusion of recently fixed carbon) and therefore represent minimum ages for the associated soil carbon.

The mounds at Mima prairie range from 2.5 to 12 m diameter and 0.3–2 m in height and occur at densities of 20–25 mounds ha^{-1} (Dalquest and Scheffer, 1942) with volumes of $<40 \text{ m}^3$ (Scheffer, 1984). Mounds across the USA occur in a wider variety of sizes, densities and spacings (Table 1). Mounds are generally elliptical and arranged in curving patterns following drainage (Ritchie, 1953). The mounds occur on both level ground and on hill slopes where the upslope flank of the mound is steeper than the downslope flank (relative to the landscape slope; Washburn, 1988). The mostly tree-less mounds are covered with prairie vegetation comprising grasses, mosses and lichens (del Moral and Dearthoff, 1976), although in at least the case of Mima Mounds Natural Area Preserve the prairie is maintained by fire (according to management information) and felling of encroaching trees (pers. obs.).

5.2. Heuweltjies

Heuweltjies (Fig. 3c–f) occur in the western and southern Cape of South Africa in a Mediterranean climate zone characterised by low-stature shrubby vegetation. The geological substrates are variable, but commonly Table Mountain sandstones (Moore and Picker, 1991), Dwyka tillites (Milton and Dean, 1990) and Malmesbury shales (Rahloa et al., 2008). Heuweltjies commonly have significant calcrete layers, often within 0.3–0.5 m of the soil surface (Fig. 3f). The carbonate of the calcrete of heuweltjies has been dated to 3970–5590 yr BP (Moore and Picker, 1991), but Midgley et al. (2002) reported ages of 20 000–30 000 BP at the same location. These dates represent minimum ages for heuweltjies because calcretes are likely subject to overprinting and are only associated with the mounds, and must consequently have developed after the formation of the mounds. The mound soil at the site reported on by Cramer et al. (2012) is composed of 72% sand, 11% silt and 17% clay, which is similar to the inter-mound soil with 77% sand, 5% silt and 18% clay. Soil particle size analysis indicated little change in sand, silt and clay concentrations with depth or across the profile of the heuweltjies. Rocks may occur on or buried within these mounds, many weighing in excess of 10 kg (Fig. 3e).

Heuweltjies average 17 m in diameter and 1.45 m in height (Moore and Picker, 1991) and may occupy 14–31% of the land surface (Table 1). The mound volumes are extremely variable, but can exceed 363 m^3 (Cramer et al., 2012). Mound density ranges from 3–8 ha^{-1} (Table 1) and increases with rainfall (Moore and Picker, 1991). The mounds are non-randomly dispersed with an R, averaged across a wide variety of sites, of 1.7 (Lovegrove and Siegfried, 1989). The mounds also show evidence of downslope slumping with a steeper upslope flank than the downslope flank (relative to the landscape slope), possibly caused by erosion (Cramer et al., 2012). The vegetation on the mounds varies regionally, but is commonly distinct from the inter-mound vegetation (e.g. Kunz et al., 2012).

5.3. Murundus

The murundus are rounded earth mounds that occur in the *cerrado* (savanna) of central and western Brazil (Silva et al., 2010). The mounds occur both in areas with semi-permanent surficial ground water and in areas with little contact with ground water (Furley, 1986). The soils of the murundus differ from those of surrounding inter-mounds by being well drained. In some areas there is evidence of water channelling between the mounds. The mound soils comprise 54% sand, 25% silt, and 21% clay, which is slightly less sandy than that of the inter-mound areas (58% sand, 28% silt and 14% clay; de Oliveira-Filho, 1992). There are also no strong discontinuities with depth through the mounds (Silva et al., 2010). These mounds are generally elliptical, 0.05 to $>2 \text{ m}$ in height (de Araujo Neto et al., 1986), occur at a density of 21–247 ha^{-1} occupying 25–39% of the land surface area (Table 1) with volumes ranging from 0.01 to 142 m^3 (de Araujo Neto et al., 1986). The distribution of the mounds is over-dispersed ($R = 1.6$), but more so for larger than for smaller mounds (de Oliveira-Filho, 1992). The mounds have steeper slope on the upslope flank than on the downslope flank (relative to the landscape slope; de Araujo Neto et al., 1986). The mounds are commonly vegetated by woody savanna species with grasses, sedges and other herbaceous plants in the inter-mound areas (Silva et al., 2010).

6. Non-aeolian landscape mounding mechanisms

The major hypotheses listed by Johnson and Horwath Burnham (2012) are categorized (Fig. 1) and the main mechanisms that have been proposed to be responsible for mound formation reviewed here, deferring evaluation of their potential role in mound genesis (see later).

6.1. Abiotic processes

Circular patterned ground (Fig. 5) results from freeze–thaw cycles in which ice lenses sort stones and soil, displacing soil towards soil-rich domains and stones towards stone-rich domains resulting in lateral transport of stones and their marginal accumulation (Kessler and Werner, 2003). A wide variety of patterned ground formations have been described, although resultant circular features and earth mounds are generally $<3 \text{ m}$ in diameter and $<0.5 \text{ m}$ high (Washburn, 1956). A similar mechanism involving freeze–thaw of water or perchlorate brines is thought to explain spectacular polygonal patterned grounds at high latitudes on Mars (Gallagher et al., 2011; <http://goo.gl/a1wSCP>).

The Australian term gilgai refers to a vertisol soil (i.e. clay $>30\%$) micro-relief formation in which the land surface develops a pattern of mounds and depressions (amplitude $<1 \text{ m}$) and a wavelength of 0.26–5.1 m (Edelman and Brinkman, 1962; Wilson, 1964; Knight, 1980). Gilgai are also known from Eurasia (Florinsky and Arlashina, 1998), Africa (Stephen et al., 1956) and Texas (USA, Kishné et al., 2009). The Texan gilgai are also relatively small and closely spaced (amplitude 0.1–0.25 m, wavelength 6–7 m; Kishné et al., 2009). Gilgai formation results from alternate wetting and drying of clay (Costin, 1955). When clay soil dries and cracks, these cracks may be infilled



Fig. 5. Abiotically patterned ground in the Arctic as a consequence of freeze/thaw processes (Svalbard, Norway; photo H Grobe).

with surficial and sidewall soil material, resulting in characteristic distributions of clay (Miller et al., 2010). Following re-wetting, swelling of the infilled and adjacent soil mass leads to oblique and upward movement of the soil material resulting in gilgai formation (Wilding and Tessier, 1988). In the USA these gilgai landforms produce hollows that have been referred to as vernal pools (Hobson and Dahlgren, 1998a, 1998b) and hogwallows (Schulze, 2010), but the term hogwallow has previously been taken to be synonymous with mima mounds (e.g. Arkley and Brown, 1954). Gilgai, which are micro-relief formations, should be differentiated from larger mima-like mound formations.

6.2. Faunal processes

Species of pocket gophers of the family Geomyidae (order Rodentia) have been proposed to be the causal agent for mima-like mounds in many parts of the USA (e.g. Cox and Hunt, 1990; Horwath Burnham and Johnson, 2012a, 2012b). Pocket gopher species have a broad (Hall and Kelson, 1959), but generally allopatric distribution, across North America (Reichman and Baker, 1972). Gophers are heavily built with most species being 0.12 to 0.3 m long and weighing a few hundred grammes (<0.9 kg; Huntly and Inouye, 1988). All pocket gopher species are burrowers constructing heaps of ca. 0.2 m in diameter with a volume of ca. 0.0034 m³ (Spencer et al., 1985). Mounds may be a prominent component of the landscape; e.g. *Geomys bursarius* mounds can occupy 8% of land surface. Pocket gophers can move substantial amounts of soil with estimates varying between <20 (Buechner, 1942; Cox, 1990) and 85 tons ha⁻¹ annum⁻¹ (Richens, 1966). Pocket gophers use their burrows for foraging by intercepting plant roots, particularly of grasses, and pulling vegetation into burrows from below, or forage close to burrow openings (Howard and Childs, 1959). Pocket gophers are solitary and highly territorial (Zinnel and Tester, 1994) with no overlap in the subterranean burrows between different individuals or species (Reichman et al., 1982). As a consequence individual burrows are regularly spaced; e.g. *Thomomys bottae* burrows are ca. 4 m apart (Reichman et al., 1982).

In southern and eastern Africa and South America, mima-like mounds have commonly been attributed to termites (e.g. Ratter et al., 1973; Cox and Gakahu, 1984; Moore and Picker, 1991; Picker et al., 2007; Potts et al., 2009; Francis et al., 2013), although bathyergid mole rats have been suggested to play a secondary role (Cox et al., 1987). Termite mounds are an iconic feature of African savannas where termite biomass can be high (70–110 kg ha⁻¹; Dangerfield et al., 1998). Termitaria can be flattened or shaped as an inverted cone up to 6 m high with a basal area of 50 m² and occur at densities of up to 6 mounds ha⁻¹, although smaller (1–1.25 m high) less dense mounds (0.3–1.4 mounds ha⁻¹) are more common (Levick et al., 2010). Termite mounds are formed by the displacement of soil from below the mound and the import of material from around the mound. Termite mounds are

commonly over-dispersed (Collins, 1981; Lepage, 1984) due to territorial and competitive interactions between colonies (e.g. Levings and Adams, 1984; Korb and Linsenmair, 2001). While large termite mounds are common in highly productive African savanna systems, they are absent in the winter rainfall region in which heuweltjie earth mounds are found (Lovegrove and Siegfried, 1986). The proposed faunal agent for the creation of heuweltjies are many generations of the termite *Microhodotermes viator* that is endemic to the Western, Eastern and Northern Cape provinces of South Africa and southern parts of Namibia. *M. viator* mounds consist of a single, normally subterranean, nest up to 1.2 m deep with an above-ground spherical to sub-spherical shape up to 1.1 m in diameter and 1.2 m in height (Coaton and Sheasby, 1974).

The campos de murundus have been referred to as termite-savanna formations (Ratter et al., 1973) because these murundus have long been attributed to the action of generations of termites (Cole, 1960; Mathews, 1977; Prance and Schaller, 1982). *Cornitermes snyderi* and *C. bequaerti* nests of between 0.01 and 1.9 m³ are commonly (ca. 2 termites nests per earth mound) associated with murundus in central Brazil (de Oliveira-Filho, 1992).

6.3. Vegetation spatial patterning

Although plants cannot directly form large mima-like mounds, they may influence both hydraulic and aeolian soil erosion and sedimentation, resulting in mound formation. Aeolian and hydraulic erosion and sedimentation are likely to co-occur, but for mounds with significant clay and stone content it is possible that hydraulic processes are more important. Mounds may be produced through a combination of 1) competition/facilitation resulting in vegetation spatial patterning, 2) increased vulnerability of canopy interspaces to erosion, and 3) soil fines eroded from interspaces and water from interspaces flowing towards plant vegetation patches serving as a facilitative positive feedback to further plant growth. Erosion from canopy interspaces, sometimes accompanied by deposition to the nearest obstructions (i.e. vegetation patches), may contribute to mound formation. Across diverse biomes and climatic regimes, vegetation spatial patterning is the norm, rather than the exception (Hillerislambers et al., 2001). At one extreme, spacing of individual plants is a form of patterning, operating through limits on the proximity of similar life forms with intersecting niche occupancies to each other.

In savannas competitive interactions for resources account for the spacing of savanna trees with the size of neighbouring congeners inversely correlated with inter-neighbour distances (Meyer et al., 2008). Savanna tree species also often cluster together forming bush-clumps (Scanlon et al., 2007), commonly referred to as islands of fertility (e.g. Schlesinger et al., 1990; Schlesinger and Pilmanis, 1998; Schade and Hobbie, 2005), alluding to the fact that trees and shrubs locally increase plant resources (i.e. soil moisture and nutrients) creating a favourable environment for plants, but also providing cover and habitat for vertebrate species (Wenxuan et al., 2012). Higher vegetation density within vegetation islands facilitates soil water infiltration, reduces evaporation and results in a positive feedback that effectively harvests water from less vegetated surroundings (Rietkerk and van de Koppel, 2008). Other contributing mechanisms include N₂ fixation by some tree species, hydraulic lift and vertical nutrient redistribution in the soil (Ludwig et al., 2004). In some cases faunally mediated concentration of nutrients (e.g. urine and faeces) also occurs under larger trees (Callaway, 2010; Wenxuan et al., 2012). These facilitative interactions result in initial tree spacing setup by long range competitive interactions between neighbouring tree roots determining a wider species patterning through shorter range (mostly under canopy) facilitative interactions with other species.

Similar processes operate in other contexts. For example, formation of tree islands in wetlands (e.g. Florida Everglades) depends on litter deposition, faunal concentration of nutrients and transpiration-driven

mass flow of nutrients contributing to nutrient accumulation on the island (Wetzel et al., 2005). The concentration of nutrients on the islands results in depletion of nutrients from the surrounding areas resulting in competitive interactions between islands and positive feedbacks on the islands. An additional example is the expansion (<100 m) of *Araucaria* forests into grasslands in southern Brazil over a period of 4000 yr, which has been associated with the establishment of isolated trees in the grassland, resulting in positive edaphic feedbacks and the establishment of forest patches (Silva and Anand, 2011). If facilitation outweighs competition, such patches may close up over long periods to form continuous forests.

In many ecosystems environmental heterogeneity (e.g. edaphic or hydraulic heterogeneity) disrupts self-organising vegetation pattern. Striking examples of patterning (including stripes, labyrinths, spots and gaps), however, occur in environments with little underlying environmental heterogeneity (Rietkerk and van de Koppel, 2008). The factors that regulate the occurrence of these diverse patterns are landscape slope that dictates downslope water flows (Tongway and Ludwig, 1990) and resource availability (Meron, 2012). In Turing (1952) inspired models of vegetation pattern, decreases in precipitation are sufficient to simulate a change from gap vegetation, through labyrinths to spot vegetation (Gilad et al., 2007). In vegetation spatial patterning competitive interactions are thought to operate over longer distances than facilitative interactions, resulting in scale-dependent feedbacks (Fig. 6; Hillerislambers et al., 2001). The example of savanna tree spacing, which is dependent on long distance competitive interactions, indicates that this mechanism alone is sufficient to generate spatial pattern. In contrast, short distance feedback is responsible for determining the sharpness of vegetation patch borders, but not the regular spacing (Rietkerk and van de Koppel, 2008).

7. Evaluation of mechanisms proposed for non-aeolian mound genesis

7.1. Abiotic processes

Mima-like mounds have been suggested to form similarly to the formation of patterned ground (Eakin, 1932; Kaatz, 1959; Herriman and Parsons, 1979; Spackman and Munn, 1984). This hypothesis fails to explain mima-like mounds because there is a lack of evidence that the extreme climate needed to induce permafrost cracking of Puget Lowland soils was present over the time period in which the mounds were formed (Washburn, 1988). This hypothesis has not been suggested for heuweltjies or the murundus since there is no evidence

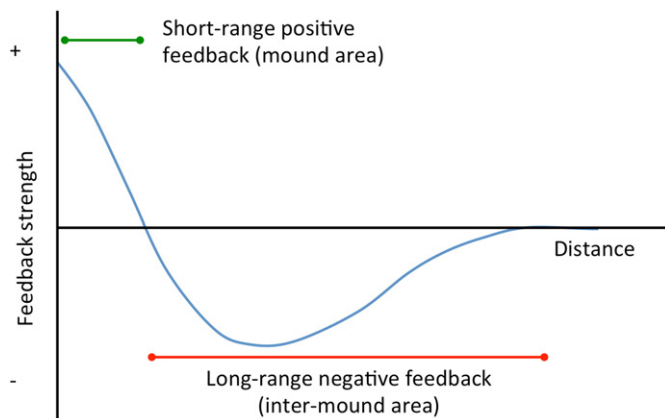


Fig. 6. Postulated role of feedbacks in mound development. Scale-dependent feedback in ecosystems with short-range positive feedbacks facilitating vegetation persistence and associated with mound development through increased aeolian deposition and/or reduced erosion and longer-range negative feedback associated with inter-mound areas. The scale over which feedbacks operate may differ depending on the mechanisms involved (modified from Rietkerk and van de Koppel, 2008).

that the climate is, or has been, appropriate. Furthermore, circular freeze/thaw patterning results in a distinctive displacement of rocks, and the sizes of the circular structures and associated mounds are smaller than mima-like mounds.

Clay cracking and swelling has been invoked to explain small mounds in Australia as well as the so-called hogwallows in the USA (Malde, 1964). The soils on which many mima-like mounds occur, however, have lower clay concentrations than those of the vertisols associated with these gilgai formations, with limited expansion on wetting, and do not crack readily (Washburn, 1988). Gilgai mounds (often referred to as micro-relief) are also much smaller than mima-like mounds. The possibility exists that some hogwallow mounds have been mistakenly identified as gilgai-like mounds, rather than mima-like mounds (Arkley and Brown, 1954).

7.2. Fossorial fauna

7.2.1. Mima-like mounds

The hypothesis that pocket gophers form mima-like mounds in the USA was proclaimed undoubtedly correct (Arkley and Brown, 1954) and continues to enjoy widespread support in the literature (e.g. Johnson and Horwath Burnham, 2012). A large number of pocket gopher genera have been attributed roles in mound construction, assuming that all have a similar propensity for constructing relatively large mima-like mounds. Pocket gophers are, however, currently absent from Mima prairie (Scheffer, 1947), the type-site for mima-like mounds, and also from some other sites where they have been attributed a causal role (Horwath and Johnson, 2006). The absence of gophers is consequently assumed to be a more recent development than the origin of the mounds and other fossorial mammalian fauna have been proposed to play a role in mound construction (Horwath Burnham et al., 2012).

Pocket gophers are capable of long-term (1000's of years) landscape transformation of the scale required for mima-like mound construction (Reed and Amundson, 2012). Despite the capacity of individual pocket gophers to move large volumes of soil over time (e.g. Buechner, 1942; Richens, 1966) there is no direct evidence for any North American fauna individually producing mounds averaging 7 m in diameter (Table 1), but up to 25 m in diameter (Cox and Allen, 1987). Gophers are solitary and fiercely territorial and thus large mounds cannot be attributed to communal action. In contrast, prairie dogs (genus *Cynomys*) do construct large communal mounds (Whicker and Detling, 1988), although these are not usually invoked as causal agents for mima-like mound formation. As a consequence, several generations of faunal agents are argued to continue the centripetal accumulation of soil. Despite the centripetal movement of soil being stated as a law of fossorial soil movement (e.g. Johnson and Horwath Burnham, 2012), there is only limited evidence (i.e. Cox, 1984) that gophers do in fact follow a centripetal pattern of soil accumulation. Gophers generally leave spoil dumps at regular intervals along their anastomosing burrowing tracks (Grant, 1948; Reichman et al., 1982) that provide access to grass roots for foraging. Pocket gopher heaps themselves are not only much smaller (<0.024 m³; reviewed by Zaitlin and Hayashi, 2012) than mima mounds, but pocket gopher territories are also more closely spaced (<10 m; Howard and Childs, 1959; Hansen and Remmenga, 1961) than most mima mounds (>10 m). Although the mounds have been suggested to function as nest chambers in thin and poorly drained soils to protect from predation, winter cold or high water tables (Cox and Scheffer, 1991), the mounds do occur on sites where slope results in good drainage and pocket gophers also occur in many areas without mima-like mounds. Thus the extra effort required on top of energetically demanding burrowing for pocket gophers to constantly move material upslope onto a relatively enormous mound (e.g. Reed and Amundson, 2012), with little direct potential survival benefit is worth considering.

While gophers are known to move small pebbles (generally less than 0.025 m in largest dimension; Hansen and Morris, 1968) the limit on the size of pebble a rodent can move is generally accepted to be 0.05 m in diameter (Cox and Gakahu, 1984; Cox et al., 1987; Horwath and Johnson, 2006). A number of mima mounds have large quantities of pebble (e.g. 58% w/w; Washburn, 1988) and in many cases the pebbles are larger than 0.05 m (Washburn, 1988) or on average 0.05 m in diameter (Horwath and Johnson, 2006; Horwath Burnham et al., 2012). Rocks have also been reported on a number of mounds (e.g. Ritchie, 1953; Washburn, 1988). As a consequence secondary activities of larger fossorial fauna (e.g. badgers) have been invoked to explain this (e.g. Johnson and Horwath Burnham, 2012).

7.2.2. Heuweltjies

The assumption that termites are responsible for the formation of large mima-like mounds in South Africa has been criticized (Cramer et al., 2012) on the basis of the following observations: 1) the volume of heuweltjies is a least an order of magnitude greater than the largest verifiable termitaria of the southern African sub-continent, which includes the highly productive savanna areas; 2) large epigeal termitaria generally occur over extensive subterranean nests, whereas some heuweltjies excavated in the Clanwilliam area are on bedrock; 3) the common termite species in the semi-arid area where heuweltjies occur (*M. viator*) makes small nests (ca. 2.1 m³) whereas heuweltjies may exceed 363 m³, requiring that several generations of nest building contributes to heuweltjie formation (e.g. van der Merwe, 1940; Cox et al., 1987); 4) the gravels in the soil of the heuweltjies are larger than the particles that termites generally utilise to construct termitaria, although Cox et al. (1987) argued that fossorial rodents (i.e. bathyergid mole rats) secondarily participate in the movement of gravels onto termite mounds; 5) there is little differentiation between mound and inter-mound particle sizes, which is atypical of termitaria; 6) many heuweltjies contained large (>10 kg) rocks either buried in the heuweltjies or on the heuweltjies surfaces. It may be argued, however, that the distribution of rocks in and on the mounds is due to bioturbation exerted by large mammalian fauna (e.g. humans, porcupines, aardvark; McAuliffe et al., 2014).

7.2.3. Murundus

Mounds in South America have been commonly ascribed to termite activity, although there has been the suggestion of the agency of fossorial rodents (Cox and Roig, 1986) in Argentina and humans in Brazil (Renard et al., 2012). The *cerrado* of Brazil is a C₄ grassland area in which woody species occur on the murundus (Silva et al., 2010). The relative lack of woody species in the grassland area may be due to seasonal flooding. Termite nests have been postulated to raise the micro-topography above the grassland vegetation enabling flood-intolerant woody species to survive there (de Oliveira-Filho, 1992; Ponce and Cunha, 1993). If the mounds emerged by termite activity in established grassland, the mound soil organic matter should have the $\delta^{13}\text{C}$ signature of C₄ grassland, which contrasts with that of the savanna C₃/C₄ $\delta^{13}\text{C}$ signature. The soil $\delta^{13}\text{C}$ values, texture and chemical traits all resembled those of savanna soils, leading Silva et al. (2010) to conclude that the murundus are not the consequence of termite activity.

7.3. Vegetation–erosion–deposition

One of the earliest explanations for the origin of mima mounds of the Puget Lowlands was that they are the consequence of the protection afforded by scattered bushes, roots, or grass to the particular spots constituting their summits, while the adjacent ground has gradually been washed away (Gibbs, 1854) with a similar explanation given independently by Le Conte (1874) and others (e.g. Holland et al., 1952; Cain, 1974). Both individual plants and clumps of plants (e.g. bush clumps and islands of fertility) take on an approximately circular plan, possibly explaining why most mima-like mounds are

approximately circular. Many mounds, however, show evidence of modification by drainage erosion (Washburn, 1988; Cramer et al., 2012). For example, the shape of mima-like mounds with steep upslope flanks (relative to landscape slope) and downslope slumping and elongation following drainage lines provides evidence of an association with erosion, consistent with the anchoring effect of vegetation and development of the mounds by erosion during floods. Greater mound (mima-like, heuweltjies and murundus) downslope elongation with increased slope (Waters and Flagler, 1929; de Araujo Neto et al., 1986; Cox, 1990; Cramer et al., 2012; Reed and Amundson, 2012) may also be a consequence of greater erosion on steeper slopes.

While it is argued here that erosion is often important in the formation of mounds, there is no doubt that, similar to nabkha formation, sediment deposition is likely to contribute to mound formation. The extent of the contribution of erosion and/or deposition to the creation of mounds is likely to be context specific, depending on the interactions between fluvial/aeolian erosion and the availability of wind-blown sediment and the ability of vegetation to trap such sediment. Woody plants with greater leaf areas contribute to surface roughness and act as dust traps (e.g. White, 1971; Leprun, 1999) thus facilitating aggradation of mounds.

If mima-like mounds are the product of vegetation spatial patterning, then the sizes and dispersal of mima-like mounds are determined by the sizes and dispersal of the vegetation patches, which may interact with the landscape slope, erosion, soil texture and climate. The sizes of vegetation clumps are determined by interplay between facilitation and competition. For mima-like mounds to develop from vegetation patterning, the spatial pattern must be stable over long periods of time, to allow deposition to the mound and erosion to effect removal of inter-mound soil (e.g. erosion rate 0.2–0.6 m kyr⁻¹; Reed and Amundson, 2012). Do such persistent vegetation patterns exist that could explain mima-like mound genesis?

In Puget Lowland, pollen analyses of Lake Washington core sediments (Leopold et al., 1982) and of mima mounds on Mima prairie (Washburn, 1988) indicate that the sites were occupied by forest species dominated by *Pseudotsuga menziesii* (Douglas fir), perhaps explaining the central depressions in some mounds and the root-like intrusion of black overburden into the glacial outwash (Bretz, 1913), although these could also be a consequence of faunal burrowing (i.e. krotovina). Tree density in large (DBH >1 m) old-growth Douglas fir in the Olympic National Forests in Oregon (USA) and Washington is 19 trees ha⁻¹ (Acker et al., 1998) and trees are over-dispersed (Ripple et al., 1991), possibly providing a model for the establishment of mima mounds (regionally 20–25 mounds ha⁻¹). In addition, soil mounds do occur around forest trees, which may result from stabilisation of soil by roots and/or displacement of soil by trunk and root growth, especially around old growth forest trees (e.g. Cain, 1974; Fig. 7a). Although wind-throw of trees creating so-called pit and mound microrelief would disturb the stratigraphy (Roering et al., 2010), mounding around tree-trunks followed by fire could produce rounded mounds, according to an eyewitness account of this process and outcome (Farnsworth, 1906). This is consistent with the organic rich soil of mounds in Puget Lowlands (ca. 20% organic matter; Walkley–Black method) and the presence of charcoal in mima mound sediments, Lake Washington sediments (Washburn, 1988) and Spanaway-type soils of the area (Ugolini and Schlichte, 1973). Changes wrought on soils by individual trees generate microsites for recruitment of future generations, resulting in self-reinforcement of the pedologic pattern (Phillips and Marion, 2004). This results in clumping of trees (Fig. 7b), as observed for Douglas fir (Lefsky et al., 1999; He and Duncan, 2003; Getzin et al., 2006). Thus it is possible that once microsites are established, these are preferentially re-colonised by future generations, resulting in stable vegetation patterns and sufficient time for erosional/depositional mounds to form.

In the absence of floristic data for ancient (>30 000 yr) heuweltjies, Cramer et al. (2012) declined to speculate on the possible flora that



Fig. 7. a) Mounding around an individual tree stump in an old-growth forest (MacMillan Provincial Park, BC, Canada; 49.288°, – 124.668°); b) clumps of Douglas fir on mima mounds (ca. 15 m diameter; Mima Mounds Natural Area Preserve; 46.905°, – 123.050°).

might have initiated mound development. Drawing on regional vegetation patterns, however, it was speculated that the pattern might have been initiated by bush-clumps, which also exhibit an over-dispersed spatial distribution and are associated with a degree of mounding, often with similar dimensions (Table 1). For the murundus the vegetation that initiated pattern formation is hypothesized to be the savanna vegetation of the campos (including woody C_3 species), with erosion resulting in susceptibility of lower lying areas to flooding and a consequent replacement of the inter-mound vegetation by shallow rooted species (Silva et al., 2010).

Emphasis has been placed on mound stratigraphy (e.g. cobble layers beneath mounds) to support the fossorial rodent hypothesis (e.g. Horwath Burnham et al., 2012; Reed and Amundson, 2012). It is suggested here that the existence of cobble layers within mounds is simply the consequence normal sedimentary soil development of a particular region. Although bioturbation may play a role in the formation of such layers (e.g. Johnson, 1989, 1990), abiotic processes such as chemical leaching and differential movement between the matrix and the coarse (stone or cobble) fragments may also result in accumulation of such layers by downward migration (Lecomte, 1988; Brown et al., 2004). Furthermore, the accumulations of stone around the periphery of mounds, referred to as stone nets (Washburn, 1956) or stone pavements (Malde, 1964), are readily explained by erosional deflation of inter-mound soil that originally contained stone, without invoking fossorial fauna (e.g. Cox and Allen, 1987). A similar argument has been presented for the accumulation of rock in the inter-mound areas between heuweltjies (Cramer et al., 2012). Where mounds occur over gravel beds (e.g. glacial outwash at Mima prairie) or cobble layers (Laguna formation; Reed and Amundson, 2012) or bedrock (heuweltjies at Clanwilliam), this is possibly because further erosion is limited by the more resistant substrate, potentially limiting the size of

the mounds. Furthermore, the radiocarbon dating of mima mounds on Mima prairie (Washburn, 1988) shows a curvilinear increase in soil carbon age with depth (Fig. 6), which may not be consistent with bioturbation of the mounds, which should homogenise the soil.

Calcium carbonate rich horizons occur in heuweltjies (Potts et al., 2009; Midgley et al., 2013) and mima-mounds (e.g. Ross et al., 1968; Cox et al., 1987; Irvine and Dale, 2012), but are absent from inter-mound areas. Calcretes are also commonly associated with plant roots (e.g. Curtis, 1965; Alonso-Zarza, 1999; Candy et al., 2004; Kholodov, 2007) that also form Ca-concretions called rhizoliths and rhizocretions (Fig. 3f). For example, islands of fertility are associated with caliche, the formation of which is enhanced by water uptake by plant roots and release of CO_2 into the soil atmosphere (Shreve and Mallery, 1933; Schlesinger and Pilmanis, 1998). These persistent indurate structures are the consequence of plant roots utilising soil water and accumulating the soil minerals, particularly Ca, around the roots as a result of transpiration-driven mass-flow of nutrients (Cramer and Hawkins, 2009). This is analogous to the mass-flow accumulation of Ca in wetland mounds (McCarthy et al., 1993; Wetzel et al., 2005). Based on work with strontium isotopes, the Ca in heuweltjie calcrete at Clanwilliam is of marine origin (Midgley et al., 2013), raising the possibility that woody vegetation may have also facilitated trapping of marine-derived Ca, contributing to the formation of islands of fertility and the mounds.

8. Conclusions

Faunal hypotheses have almost become de facto explanations for mound genesis worldwide, despite a lack of direct evidence. Vegetation patterning is clearly implicated in the formation of nabkha-like mounds and vegetation islands in wetlands. Although non-aeolian dryland mounds are polygenetic in origin (Johnson and Horwath Burnham,

Table 2
Evaluation of evidence for various hypotheses for mima-like mound origins (including murundus and heuweltjies, but excluding nabkha-like mounds and gilgai). (+) Indicates evidence favouring the hypothesis, (–) contrary evidence, (0) neutral evidence and (+/–) indicates possibly favouring or contrary, depending on circumstances. Modified from Washburn (1988).

Mound characteristics	Hypotheses					
	Freeze/thaw	Liquefaction/sand blows	Shrink/expand clay	Aeolian	Fossorial fauna	Vegetation-erosion
Over-dispersed	+	–	+	+	+	+
Over-dispersion correlated with landscape occupancy	+	–	+	+	+	+
Elongated	0	0	0	+	0	+
Large volumes	–	0	–	+	–	+
Upslope flank steepest	0	0	–	0	0	+
Stone/rocks (>0.05 m diameter)	+	–	0	–	–	+
Sub-mound gravel layers	0	0	–	0	+	+
Continuous soil chronology with depth (i.e. not homogeneous)	–	–	–	+	–	+
Fossorial fauna present	0	0	0	0	+	0
Underlying bedrock	0	–	–	0	+/–	0
Calcrete/caliche (in mound)	–	–	–	+	+/–	+

2012), there is sufficient evidence to suggest that genesis of the mima mounds of Mima-prairie, heuweltjies and murundus may be largely a consequence of vegetation/erosion interactions, an explanation consistent with data collected over the past century and more (Table 2). The diversity of mound morphology is likely to be dictated by environmental factors (e.g. edaphic, geomorphology, climate and wind) and vegetation properties. For mound formation to occur, the vegetation patterning needs to be stable for sufficiently long periods for erosion to deflate the inter-patch vegetation, although the possibility of fluvial or aeolian deposition contributing to mound development is not excluded. Thus, although not rare, mound formation is a special phenomenon requiring stable vegetation patterning and erosion and/or deposition. Although we argue that vegetation spatial patterning is the initiating factor in mima-like mound formation, there is no doubt that fauna are at least secondary occupants and contributors to mound development. It is hoped that this synthesis serves as a stimulus for further directed tests of the vegetation–erosion–deposition hypothesis.

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Appendix A. Supplementary data

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