MULTI-TROPHIC INTERACTIONS AND BIOLOGICAL CONTROL

ECOLOGICAL CASCADES AND DUNG BEETLE POPULATIONS IN AUSTRALIAN GRASSLANDS

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Background

Before the First People arrived in Australia 40 to 60 thousand years ago (Flannery, 2002), the continent was populated by an array of large (> approx. 45 kilograms) herbivorous marsupials, some as large as the rhinoceros (Dodson, 1989), and it is likely that there existed a corresponding suite of large dung beetles that specialised in disposing of their dung, much as is found in regions of Africa, where the megafauna have persisted to the present day (e.g. in West Africa, Table 1). In southern African habitats where large mammals (e.g. rhinoceros, elephant) have persisted, there is a corresponding array of very large dung beetles (e.g. the *Heliocopris* tunnellers and the *Pachylomera*, *Kheper* and *Scarabaeus* ball rollers) that are scarce or absent from adjacent pastoral lands (B.M. Doube, unpublished data), supporting the view that the large dung beetle species depend on the dung of these large mammals and that their disappearance leads to the disappearance of the associated dung beetle fauna.

Table 1.
Species richness in relation to biome and habitat

Biome and habitat	Species number (±SD)
Tropical savanna with elephants	50.4 ± 3.4
Tropical savanna with cattle	47.3 ± 3.2
Tropical savannah without large mammals	29.7 ± 2.6

Source: Hanski and Cambefort, 1991

Similarly, in Australia, megafauna extinctions that followed human colonisation (Dodson, 1989) are presumed to have resulted in the disappearance of the dung beetle fauna that specialised in their dung (Doube and Marshall, 2014). The majority of Australia's 474 dung beetle species (Monteith, 2015) do not have any serious impact upon the dung of introduced stock, being primarily adapted to the dung of native marsupials, which is often small, hard, dry and pelletised (Waterhouse, 1974). However, there is a small group of native species that, at times and in some places, bury substantial amounts of cattle and horse dung (Doube et al., 1991; Doube and Marshall, 2014): these may be a relic of the megafauna dung fauna that has again prospered since large mammals were re-introduced to Australia.

So, when Governor Arthur Phillip and the first fleet arrived in Botany Bay in 1788, with seven cows, two bulls, four horses and 44 sheep (Waterhouse, 1974), a new era began in the dung production history of Australia. Since that time the Australian national herd has grown to about 27 million cattle and 71 million sheep (ABS, 2015) (and about 1.2 million horses). In parallel, woodlands were cleared, new grasses and legumes replaced native grasses, and domestic stock largely replaced the native dung producers. Furthermore, irrigation and improved plant varieties increased primary production, with corresponding increases in stock numbers and the dung they produced.

Ecological cascades

As a consequence of the low levels of activity of the native dung beetles in the dung of introduced stock, huge amounts of dung accumulated on Australian grazing lands, where it smothered pasture, retained nutrients on the soil surface, polluted waterways and became an important resource for the infective stages of gut parasites of livestock. Further, this increasing domestic dung supply provided a massive new resource for numerous species of dung-breeding fly, and their parasites and predators. In particular, the native bush fly, *Musca vetustissima*, and the introduced buffalo fly, *Haematobia irritans exigua*, became serious pest species in southern and northern Australia respectively (Doube and Marshall, 2014).

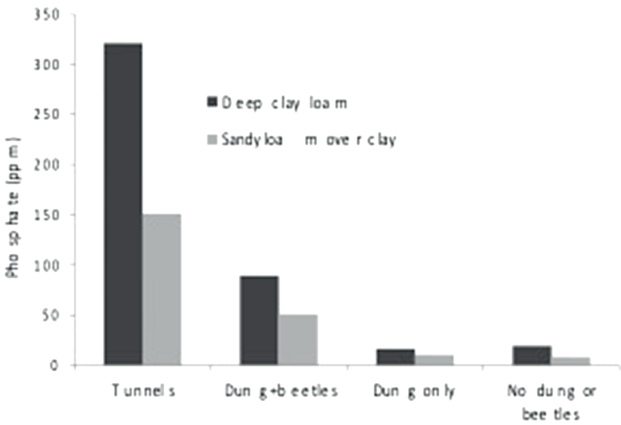
Dung beetles that bury and recycle the dung of domestic stock became the primary missing component of the emerging grazing systems in Australia. In the 1960s, CSIRO initiated a dung beetle importation program which has continued, intermittently, until today. Overall, 53 species were introduced to the CSIRO laboratories, 43 were released to the field and 23 have established. Another two species are now breeding well in field nurseries in South Australia. The original CSIRO dung beetle project (1965–1985) has only partially resolved the dung pollution issue and more species are needed.

Many of the current introduced dung beetle species have reached the natural limits of their potential distribution in Australia but a small number of species occupy only part of their potential range and are currently being redistributed. This has commonly been achieved by commercial operations that harvest beetles from the field where they have become abundant (at times up to several thousand per dung pad) and release them into suitable regions from which they were previously absent. Many hundreds of thousands of beetles have been spread in this way.

The ecological consequences (cascades) that followed the widespread success of introduced dung beetles took a number of different forms:

→ **Transforming the soil profile:** Soil is essentially 'ploughed' by the dung burial process, whereby subsoil is brought to the surface and the dung deposits (with their plant nutrients and organic carbon residues) transferred from the soil surface into the soil profile, with different species burying at different depths, so that much of the soil profile is potentially fertilised by buried dung. Deep dung burial substantially increases levels of plant nutrients (phosphate, nitrate, sulphur, ammonia, soil organic carbon), and increases the pH, especially in the soil in and surrounding the dung beetle tunnels (Figure 1).

Figure 1.
Dung beetle activity increased the levels of phosphate in the subsoil (30–50 cm deep) 20 months after burial had begun



→ **Buffering water transfer through the landscape:** Rain and irrigation water flows down dung beetle tunnels and through the soil, rather than across the surface (Figure 2), thereby slowing the flow of water through the landscape, purifying it and extending the time during which it is available to plants.

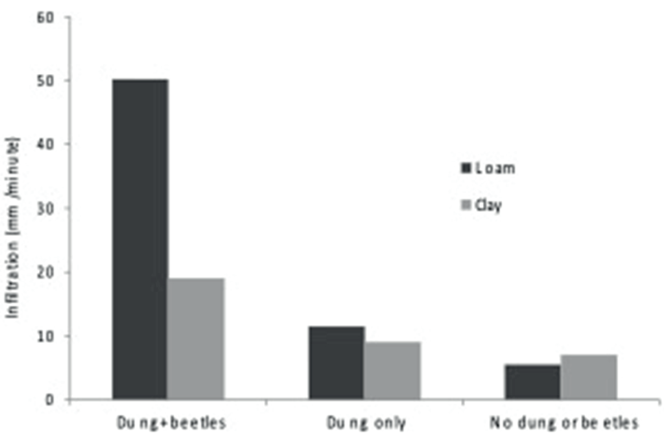
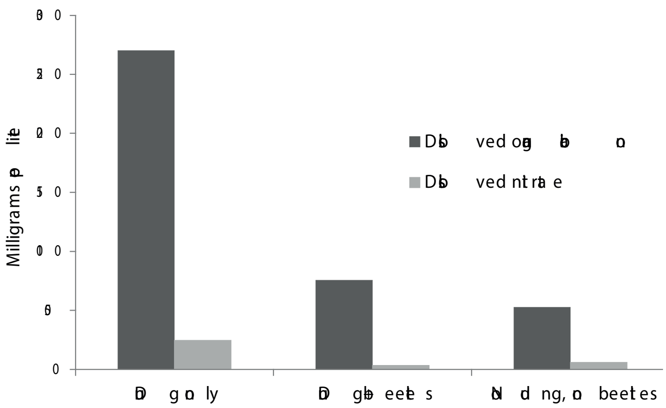


Figure 2.
Dung beetle activity markedly decreased the time taken for water to soak into clay soil and loam soil

- **Increasing pasture production:** Annual pasture production in temperate ecosystems commonly ranges from about 1 tonne to 20 tonnes of dry matter per hectare (Doube and Marshall, 2014). This can be increased by dung burial activity. Southern Australian studies in pastures producing 1–4 tonnes of dry matter per hectare suggest that deep burial of cattle dung during winter can increase annual pasture production by about 1 tonne per hectare (Doube and Marshall, 2014).

- **Removal of surface dung.** Rain on unburied dung can release unwanted nutrients into free surface water (Figure 3). These nutrients can pollute rivers and reservoirs, contributing to problems such as blue-green algal blooms that make water toxic to stock and humans. This problem can be resolved by allowing beetles to bury the dung.

Figure 3.
Dung burial decreased the amount of dissolved organic carbon and nitrate in run-off water from plots 3 months after dung burial began



- **Biological control of the bush fly in southern Australia:** A radical reduction in the numbers of summer bush flies in the moister regions of southern Australia occurred in the short space of a decade following the widespread establishment of summer-active dung beetles imported from Europe and South Africa.

Conclusion

Beetles that recycle the dung of domestic stock have been the primary missing component of modern agricultural systems in Australia. The CSIRO dung beetle introduction program has only partially resolved this issue. However, the introduction of dung beetles as high-level consumers of a major environmental resource has set off a trophic cascade that has restructured the composition of above- and below-ground food webs associated with dung pads in localities where beetles have become abundant.

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