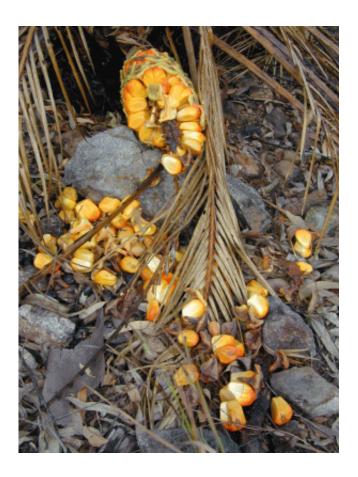


Ancient cycads found to be pre-adapted to grow in groves

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Disintegrating female cone of the Australian cycad macrozamia miquelii, showing the brightly coloured layer of fruit-like flesh that forms the outer layer of cycad seeds. Is this an adaptation for dispersal by megafauna? Credit: John Hall.

The ancient cycad lineage has been around since before the age of the



dinosaurs. More recently, cycads also co-existed with large herbivorous mammals, such as the ice age megafauna that only went extinct a few tens of thousands of years ago. Cycads that are living today have large, heavy seeds with a fleshy outer coating that suggests they rely on large bodied fruit-eating animals to disperse their seeds. Yet there is little evidence that they are eaten and dispersed by today's larger-bodied animals, such as emus or elephants. If these plants are adapted for dispersal by a set of animals that has been missing from Earth's fauna for tens of thousands of years, then how can they still be around today? A new study proposes that the clumped dispersal mechanism these ancient plants most likely relied upon still serves them well today.

Fossil cycads are recorded from 280 million years ago around the time coniferous forests first arose. The ecological distribution pattern of many living cycads today suggests they have limited and ineffectual <u>seed</u> dispersal. For example, *Macrozamia miquelii*, a cycad endemic to Australia, is found in highly clumped, dense, numbers, where it dominates the understory. Moreover, large areas of seemingly suitable habitat often separate populations from each other. These patterns suggest that few to none of the seeds are being dispersed large distances away from <u>parent plants</u>, one of the long-standing tenets of the advantages of seed dispersal.

John Hall and Gimme Walter (University of Queensland, Australia) were interested in determining whether the seed dispersal and seedling distribution pattern of *M. miquelii* might indicate that it is maladapted to its current dispersers. They proposed a new twist on the functional significance of the megafaunal dispersal syndrome and published their findings recently in the <u>American Journal of Botany</u>.

"Naturalists are very comfortable with the idea of animals gaining a biological advantage by choosing to live together in high density 'colonies'—such as ant nests or seabird rookeries—in certain parts of the



landscape," notes Hall. "But when it comes to plants, there is a bit of a subconscious assumption that the purpose of seed dispersal is to simply spread seeds as far and as evenly as possible across the broadest possible area."

Hall and Walter decided to investigate whether cycads might be a type of plant that forms such colonies. "The main idea behind our research," Hall clarifies, "is to ask the question: when it comes to the spatial ecology of plants, could it be useful to think of some plant species as also forming and maintaining 'colonies' or 'groves' in the wider landscape?"

"Australian cycads once co-existed with <u>megafauna</u> that could have dispersed their large, heavy seeds—such as giant ground birds, bigger then present day emus, and Diprotodon, a rhino sized marsupial quadruped," explains Hall. "The large, heavy and poisonous seeds, surrounded by a fleshy and non-toxic fruit-like layer, seem well adapted to being occasionally swallowed whole *en masse* by megafauna, which would then pass the many seeds simultaneously at a new location: the genesis of a new grove."

Female cycads produce one to two cones that contain multiple, large seeds, each covered with a thin outer fleshy sarcotesta. By tagging ten large seeds from the single cone of 12 plants with a small steel bolt, the authors were able to track how many of the seeds were removed from the parent cycad and how far the seeds were dispersed.

They found that within three months virtually all of the seeds had their sarcostesta eaten—primarily by brushtailed opposums, which scrape the flesh off and discard the large seeds. Camera traps at two fruiting females and hair traps baited with seeds confirmed the disperser identity. However, almost all (97%) of the tagged seeds that the authors recovered had been moved less than one meter away; only a few were



moved beyond the vicinity of the parent plant and in all cases they were found less than 5 meters away.

Moreover, although most of the seeds ended up under the parent cycad, almost no seedlings were found within a 1.5 m radius of adult cycads, suggesting that most seeds within the vicinity of the parent perish.

These patterns suggest that despite their large seed size, the primary dispersers of these cycads today are smaller bodied animals; these animals do not spread the seeds far and wide, nor take them to potentially new colonizable habitats. Yet, these plants seem to be doing well by sprouting up near the adults and forming mono-dominant stands.

"Since their potential Australian prehistoric megafaunal dispersers became extinct around 45,000 years ago, why haven't Australian cycads begun to evolve smaller seeds, that would be more readily dispersed by flying birds or possums for example, over the interim?" posits Hall.

"We argue that the answer to this question is that cycads are actually disadvantaged by dispersing as lone individuals that may travel long distances, but in so doing so, become isolated from others of their kind," Hall states.

Moreover, Hall points out that cycad plants are all born either male or female, and rely completely on host specific insect pollinators—so a lone cycad that dispersed a long way from others of its kind would probably be disadvantaged rather than advantaged in terms of reproduction.

Thus, if cycads evolved to be dispersed by large-bodied frugivores, these animals would most likely have deposited many cycads <u>seeds</u> in their dung at once, and thus these plants may be adapted to grow in groves—an aspect that plays to their favor today, despite the loss of these megafauna dispersers.



"There's no doubt that cycad ancestors were contemporary with herbivorous dinosaurs for many hundreds of millions of years, so it's plausible that cycad seed dispersal ecology and "colony forming" behavior may be extremely ancient, and echo the ecology of dinosaurplant interaction" he concludes, "but of course we now enter into the realm of speculation."

Hall's interest in the spatial ecology of 'colony' forming plants does not stop at cycads; he is currently planning to explore these ideas in other plants and landscapes, especially in forest understories.

More information: John A. Hall and Gimme H. Walter. 2013. Seed dispersal of the Australian cycad Macrozamia miquelii (Zamiaceae): Are cycads megafauna-dispersed "grove forming" plants? *American Journal of Botany* 100(6): 1127-1136. DOI: 10.3732/ajb.1200115

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