



# Unique parasite aDNA in moa coprolites from New Zealand suggests mass parasite extinctions followed human-induced megafauna extinctions

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Having split early from Gondwana, Zealandia (now modern New Zealand) escaped discovery until the late 13th century, and therefore remains an important glimpse into a human-free world. Without humans or other land mammals, diverse and peculiar birds evolved in isolation, including several flightless moa species, the giant pouakai eagle (*Harpagornis moorei*), the kiwi (*Apteryx mantelli*), and the kakapo parrot (*Strigops habroptila*). This unique community has fascinated paleoecologists, who have spent almost two centuries devising new ways to glean information from ancient bird remains. In PNAS, Boast et al. (1) apply one recent technological advance, ancient DNA (aDNA) metabarcoding, to confirm previous discoveries and report new details about moa and kakapo diets, parasites, and niches. Their efforts confirm Zealandia was a lot different before humans arrived.

Zealandia's most diverse avian oddities were the moa. Moa research goes back to the early 1800s, when the Māori told legends to colonizing Europeans about giant birds and showed them fossilized moa bones in caves. Those fossils belonged to at least nine moa species ranging from 1 to 4 m tall, some with notable sexual dimorphism (2). The moa species have different fossil distributions, morphology, and gizzard contents, suggesting they partitioned Zealandia's resources into distinct ecological niches. To better understand how moas coexisted and interacted with other species, paleontologists have turned to another abundant deposit that moas left behind: coprolites (fossilized dung). The 2,000 moa coprolites that have been collected thus far contain plants, fungi, microbes, and intestinal parasites (3), a priceless resource for creating ecological snapshots from Zealandia. Until the aDNA revolution, however, these snapshots were blurry (4).

Sequencing aDNA allows paleontologists to identify dung-encased organisms at finer resolution than they see with a microscope. Studying aDNA is nerve-racking, because it degrades over time and each

sample can become contaminated where it lies or during sample handling, transport, and storage. However, dedicated aDNA facilities and rigorous protocols help reduce contamination (5). Even then, authentic aDNA fragments can be hard to decipher, because short diagnostic DNA barcodes are still unavailable for most plants and animal species (1). Thus, scientists who work with aDNA need to be careful, both in their techniques and their interpretation. When it works, the effort pays off with insights not imaginable when paleontologists cracked open that first moa coprolite.

Boast's research group has been around the aDNA block before, having used first-generation sequencing techniques on plant, microbe, and parasite aDNA from moa coprolites to yield family- and even genus-level taxonomic resolution for several taxa that the moa interacted with (6, 7). However, first-generation techniques are too time-consuming and expensive for compiling a comprehensive ancient food web. To make the most from their samples, Boast et al. (1) switched to high-throughput sequencing, which confirmed previous first-generation results and unearthed several hitherto unknown ecological interactions between the moa and plants, fungi, and parasites. In addition to describing these new results, Boast et al. (1) synthesize past findings to add resolution to the Zealandia food web.

In this enhanced snapshot from Zealandia (Fig. 1), an upland moa (*Megalapteryx didiformis*) stops to eat moss under a southern-beech tree (Nothofagaceae) and then defecates feces laced with parasite eggs on the forest floor. As with many other upland moa, it acquired parasitic trematodes when feeding at a small alpine pond and heterakoid nematodes when eating contaminated ferns and other vegetation. However, the moa's real concern is the pouakai, the world's largest eagle and the only moa predator. A nearby South Island giant moa (*Dinornis robustis*) has no interest in the upland moa's moss. Instead, it lunges

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southern-beech tree hosts decline unless they adapt to use new spore dispersers or moa deextinction ideas become reality (13).

Other species were not robust. Without moa, the pouakai starved. Pouakai is the most obvious secondary extinction to follow the moa, but Boast et al. (1) suggest that other species fell like a teetering Jenga tower after a critical piece is pulled. In particular, several heterakoid nematode species had coevolved to specialize on moa, and have not been seen since the moa disappeared. Other moa and pouakai parasites (most likely several never-seen, host-specific lice) were probably lost. These secondary extinctions result because coevolved complex systems cannot evolve robustness to swift, unpredictable events like the Māori's arrival and rapid domination (14). How many secondary extirpations or extinctions occurred is not yet clear, and will remain unknown until there are larger sequence libraries from extant species that can be used to confirm their absences. To understand the past with aDNA, one must also sequence the present.

Between the ancient moa extinctions and the present, Europeans and their introductions further altered New Zealand's biodiversity. Winners included weeds, pests, and people. Their parasites were winners too. On the other hand, specialist parasites, particularly those with complex life cycles, should be least robust to secondary extinction (15) and should go down with the ship. To that end, parasite extinctions have continued in New Zealand. In 1904, scientists discovered the kakapo tapeworm *Stringopotaenia psittacea* (16), which has not been seen since the kakapo's dramatic decline toward near extinction. Soon after,

a chewing louse (*Huiacola extinctus*) went extinct (17), along with its host, the huia (a wattlebird hunted for its feathers). More recently, the louse *Rallicola (Aptericola) pilgrimi* was lost after its host, the smallest kiwi (*Apteryx owenii*), was translocated to predator-free islands (18). Therefore, most New Zealand extinctions have probably been parasite extinctions.

Society will decide whether we preserve, ignore, or extirpate species we find insignificant, threatening, or disgusting. Some point out that parasites deserve protection because they can play important roles as consumer species (19). Others consider that ignoring these associated species is taxonomic chauvinism (20); it is like counting sunken ships in a naval battle, without mourning the sailors that go down with those ships. The extent to which we value host vessels or their parasite passengers is most often answered by veterinarians. When veterinarians treated the last remaining California condors in 1987, they found the condor louse, *Colpocephalum californici*, a symbiont whose ancestors had flown with condors over plains populated by mammoths and saber-toothed tigers; they then exiled the condor louse to extinction with an insecticide treatment (20). Had moa survived to face Europeans, New Zealand veterinarians would have likely done the same to moa parasites.

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