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# Three birds with one stone: moas, heteroblasty and the New Zealand flora

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**Key words:** biological nomenclature, endophytes, mycorrhizas, systematic, taxonomy.

## Three birds with one stone: moas, heteroblasty and the New Zealand flora

An intriguing article in this issue of *New Phytologist* (pp. 495–501 by Fadzly and colleagues) is relevant to at least three interesting issues in plant evolutionary biology. Although understandably somewhat short on data, it raises a new hypothesis on the co-evolution of plants and their now-extinct moa herbivores in New Zealand. As such it adds to the small body of research on assessing plant traits in a palaeoecological context; it is also an example of the use of accessory pigments to alter leaf appearance, thereby reducing herbivory; and it adds fuel to the controversy of the function of heteroblasty in New Zealand plants.

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First, some brief background on moas and the New Zealand flora. Moas evolved on the North and South Islands from ratite ancestors, most closely related to Australian emus and cassowaries (Worthy & Holdaway, 2002). Ten species in six genera are recognized from the Pleistocene; some species were restricted to higher-altitude habitats; and most species were restricted to the South Island. The giant moas, of the genus *Dinornis*, which stretched to heights of >3 m, lived in forest on both islands. They fed on the foliage of shrubs and trees within their reach and were capable of ingesting fairly tough tissue by grinding it in very large gizzards. The last of the moas became extinct in the 15th century, presumably primarily as a result of hunting pressure by the Maori.

The New Zealand flora is distinctive for its diversity and endemism, for the high incidence of divarication in shrubs and juvenile trees (10% of all native woody species; Greenwood & Atkinson, 1977) and for the high frequency of

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heteroblasty (some 200 tree species; Cockayne, 1912). Many species produce leaves of remarkably different morphology and appearance at different life history stages. Lancewood (*Pseudopanax crassifolius*), examined by Fadzly *et al.*, is one of many such heteroblastic species in the New Zealand flora. Divarication and heteroblasty occur in the floras of islands in general (Carlquist, 1965), although their incidence is greatest in New Zealand.

The functions of divarication and heteroblasty in New Zealand plants, and the selection pressures that have led to their evolution, have long been controversial matters, going back to the 19th century (Hill, 1913). Some have argued for physiological functions, as reductions in stress from wind or radiation (the literature is well-reviewed in the article). More recently, divarication has been viewed as an adaptation to reduce herbivory by moas (Greenwood & Atkinson, 1977). Fadzly and colleagues extend this argument to the appearance of leaves in lancewood. Seedling leaves are narrow and mottled with dull brown splotches (as a result of the production of anthocyanins along with the chlorophylls), and look similar to leaf litter to our perception. Juvenile leaves are linear, with sharply toothed margins, and each is highlighted by a light-coloured patch. Adult leaves produce oblong leaves of normal appearance. Fadzly *et al.* argue that the seedling leaves are camouflaged, thereby avoiding herbivory by moas, and that the juvenile leaves are aposematic, with teeth 'advertised' by the coloured patches, and also would have been avoided by moas. The normal adult leaves are produced above heights that could be reached by the giant moas.

This is a novel hypothesis, explaining the evolution of heteroblasty in lancewood, and is perhaps relevant to other species. The authors provide two lines of evidence to support it. The first is that a closely related lancewood, on a nearby island group that did not have moas, produces leaves with little heteroblasty and a normal green appearance at all stages. A second line of evidence is based on the results of a detailed optical analysis of the lancewood leaves, showing clear differences in appearance that would have been perceived by moas, if we can accept that their visual physiology was similar to that of the related ostrich (a reasonable assumption). These birds would easily have detected the colour/contrast differences in the leaves of juveniles (and avoided them) and seedlings (not recognized them). They also show that the optical properties of leaves of the Chatham Islands plants are identical to those of normal green leaves of plants in the New Zealand flora.

Ideas of colour changes leading to camouflage or warning have generally been limited to animals. However, leaf mottling was recognized by Stone (1979) as a mechanism for camouflage, and this idea was reviewed extensively by Givnish (1990). Mottling is a form of variegation in leaves, and silvery variegation reduces herbivory (Soltau *et al.*, 2009). As for warning coloration, Lev-Yadun (2001) was the first to

advocate its role in advertising thorns, part of a larger argument for aposematism in plants, and Fadzly and colleagues applied these concepts to the moa 'problem'.

Colour variations in seedling and juvenile leaves are partly a result of the production of anthocyanins in sectors of the leaf. Although the majority of research on anthocyanin function in leaves has investigated senescence (Archetti *et al.*, 2009), there is growing evidence for a multitude of anti-herbivory functions of anthocyanins in leaves, at all developmental stages (Lev-Yadun & Gould, 2008). The moa-lancewood interaction is a contribution to this new, but rapidly expanding, research area. However, anthocyanins have known photoprotective and antioxidative activities, and a co-evolutionary role in defense does not exclude the possibility of a physiological role (Lev-Yadun & Gould, 2008).

Lastly, the hypothesis of camouflage/aposematism and moa herbivory is another example of the need to look at the palaeoecological conditions under which traits were selected, because extinction of a major guild of interactors, such as herbivores, may obscure our understanding of their selective advantage. The now classical example of the Pleistocene extinction of large herbivores (or 'gomphotheres') was argued by Janzen & Martin (1982), as the loss of the major selection agents in the evolution of large fruited and seeded trees in Central and North America. In a case similar to moas and New Zealand plants, Givnish *et al.* (1994) argued that thorn-like prickles in *Cyanea* evolved several times in the Hawaiian Archipelago in response to flightless avian browsers. Although they built a robust phylogeny showing the multiple appearances of spines, particularly on the older islands, they had no direct evidence of defense against herbivory. The fundamental problem of such palaeoecological hypotheses is how to critically test them. Janzen & Martin (1982) used evidence from a thorough examination of the literature, and they employed a modern substitute of the extinct gomphotheres: the horse.

Fadzly *et al.* used the evidence of actual leaf optical properties along with the comparison of a sibling species from a non-moa island group, but presented no direct evidence of defense against herbivory. There is actually quite a substantial amount of information available on moas from the recent fossil record, including sexual dimorphism, nesting behavior, vocalizations, feeding and diet. In addition, there is an impressive amount of data available on plants and plant organs consumed by moas, based on gizzard function and content and, particularly, coprolites. Wood *et al.* (2008) showed (based on coprolite analysis) plant consumption by at least two moa species at a site on the South Island. Another list of plants in the moa diet was compiled from analysis of gizzard contents from another South Island site (Horrocks *et al.*, 2004). Coprolites and gizzard contents allow identification of both the moa species and what they ate. DNA extracted from tissues provides identity of the moa species involved (Baker *et al.*, 2005). Perhaps the greatest challenge

in using such evidence to test hypotheses of herbivory is that a successful defense will exclude the plant from the diet, and accompanying evidence that the species in question was present in the palaeoflora consumed by the moa may be lacking. Thus, data from a single species of moa from a locality with evidence of plant communities present at that time will be necessary to test more critically this antiherbivory hypothesis. The large exotic invasive herbivores now in New Zealand are not a substitute for the moa and do not contribute to our understanding of these ecological interactions.

Despite the limitations of the evidence presented by Fadzly *et al.*, and the difficulty of obtaining more direct evidence on the browsing habits of emus, the hypothesis raised by them, explaining the evolution of heteroblasty in the New Zealand flora, will stimulate more research on the subject and will illuminate other work in palaeoecology, the roles of leaf display in evolution and the functions of anthocyanins in leaves. In that way the authors have clearly struck three birds with a single stone.

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**Key words:** aposematic coloration, camouflage, coevolution, divarication, heteroblasty, moas.