

Ontogenetic colour changes in an insular tree species: signalling to extinct browsing birds?

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Summary

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- Animals often use colours to hide from predators (crypsis) or advertise defences (aposematism), but there is little evidence for colour-based defence in plants.
- Here, we test whether ontogenetic changes in leaf colour of lancewood (*Pseudopanax crassifolius*) may have been part of a defensive strategy against flightless browsing birds called moa, which were once the only large herbivores in New Zealand. We tested this hypothesis by conducting spectrographic measurements on different-sized plants grown in a common garden. We also compared these results with observations on a closely related, derived species that evolved in the absence of moa on the Chatham Islands.
- Spectrographic analyses showed that birds would have difficulty distinguishing seedling leaves against a background of leaf litter. Conversely, brightly coloured tissues flanking spines on sapling leaves are highly conspicuous to birds. Once above the reach of the tallest known moa, adults produce leaves that are typical in appearance to adult leaves. The Chatham Island species lacks ontogenetic colour changes entirely.
- Overall, the results indicate that *P. crassifolius* goes through a remarkable series of colour changes during development, from cryptically coloured seedlings to aposematically coloured saplings, which may have formed a defensive strategy to protect against giant browsing birds.

Introduction

Plants are attacked by a bewildering array of herbivores. In response, plants have evolved a variety of defences to deter herbivores. In addition to defences such as thorns and noxious chemicals, there is growing speculation that plants might also use colours to defend themselves (Stone, 1979; Lev-Yadun & Inbar, 2002). For example, aposematic or warning colours could be used to signal defensive structures (Lev-Yadun, 2001, 2009a). Alternatively, plants could be cryptically coloured in ways that make them difficult for herbivores to locate (Barlow & Wiens, 1977; Wiens, 1978; Givnish *et al.*, 1994; Watson, 2004; Lee, 2007). Although aposematic and cryptic colour patterns are common in animals, there is little evidence for their existence in plants.

We investigated ontogenetic shifts in leaf colours of *Pseudopanax crassifolius* Araliaceae, a heteroblastic tree that is endemic to New Zealand. To the human eye, *P. crassifolius* goes through a strange series of morphological transitions from germination to maturity (Fig. 1). Seedlings (< 10 cm tall) produce small,

narrow leaves that are mottled in appearance to the human eye. Saplings (10–300 cm tall) produce larger, more elongate leaves that have thorn-like dentitions along their margins, each coinciding with a distinctive patch of different coloured tissue. Adult plants (> 300 cm tall) produce oblong leaves that are more ordinary in appearance.

These morphological changes could be adaptations to changing environmental conditions as plants grow vertically (Gould, 1993). Alternatively, they might also deter herbivory (Greenwood & Atkinson, 1977, see also Boege & Marquis, 2005). Before human arrival, New Zealand lacked native land mammals (except for two species of bat) and, instead, was home to massive, flightless birds called moa (Worthy & Holdaway, 2002; Wood *et al.*, 2008). If the mottled colours of seedling leaves make them difficult to distinguish against a background of leaf litter, their colours may have provided some defence against moa herbivory. Moa lacked teeth and swallowed leaves by placing them in their bill and snapping their head forward to orient them down the oesophagus (Bond *et al.*, 2004). Several distinctive features of plant species

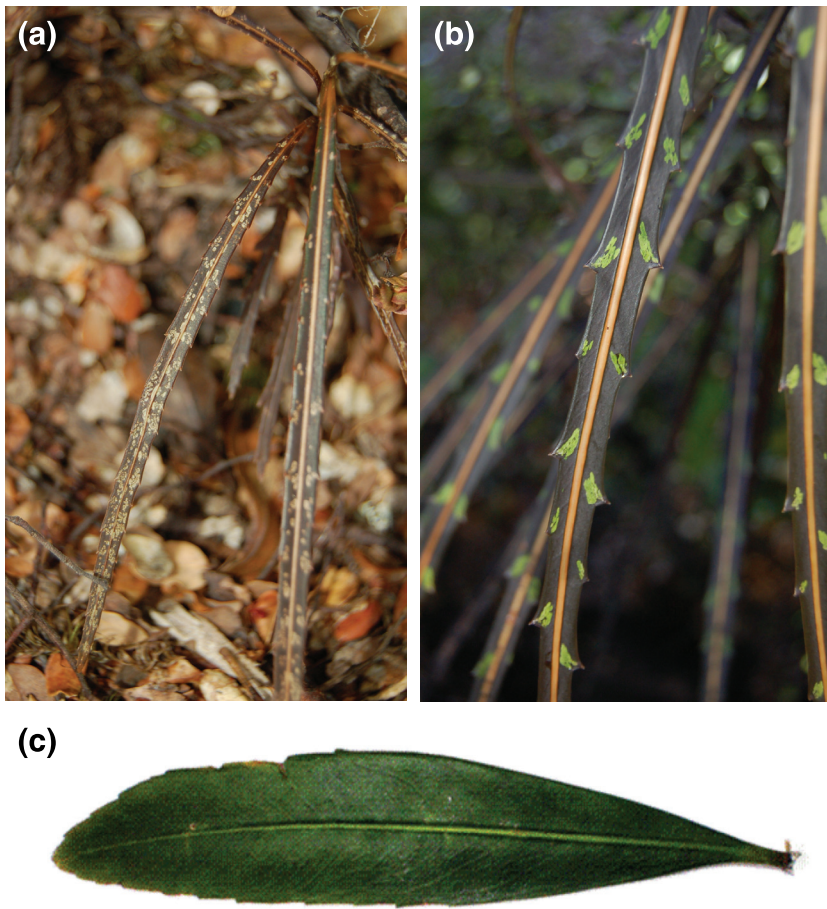


Fig. 1 A healthy *Pseudopanax crassifolius* seedling (a), sapling (b) and adult leaf (c) from Nelson Lakes National Park, South Island, New Zealand.

inhabiting other isolated islands, such as divaricate branching and heteroblastic leaf morphology, may have complicated their ingestion by toothless browsers (Greenwood & Atkinson, 1977; Diamond, 1990; Givnish *et al.*, 1994; Bond *et al.*, 2004; Eskildsen *et al.*, 2004; Burns & Dawson, 2006; Bond & Silander, 2007). Unusual attributes of plants inhabiting other locales, such as excessively large fruits, have previously been linked to extinct 'megafauna' (Janzen & Martin, 1982; Janzen, 1986; White, 1988; Barlow, 2000; Hansen & Galetti, 2009). Similarly, the unusually long, rigid leaves produced by *P. crassifolius* saplings, coupled with the spine-like projections on their margins, may have made them difficult for moa to swallow, and the distinctive colour patches associated with spines could have served as a reliable warning signal of structural defence. The maximum browsing height of the largest moa was approximately 300 cm (Worthy & Holdaway, 2002). Therefore, colour-based defence would not have been advantageous as plants grew above the reach of moa, perhaps leading to more typical leaf characteristics.

The Chatham Islands are a small group of islands of recent geological origin located 800 km east of New Zealand. The Chatham Island flora appears to be derived from overseas dispersal from New Zealand (see Trewick, 2000; Tre-

wick *et al.*, 2007). A notable example is *Pseudopanax chathamicus* Araliaceae.

Recent molecular analyses indicate that *P. chathamicus* is derived from a *P. crassifolius* ancestor in New Zealand (Mitchell & Wagstaff, 1997; L. Pierre, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand, pers. comm.). Unlike New Zealand, the Chatham Islands lacked large browsers, including moa. Dawson (1991) and Greenwood (1992) commented that plant taxa that are heteroblastic in New Zealand appear to have reduced morphological differentiation between adult and juvenile plants in the Chatham Islands (see also Burns & Dawson, 2009). If ontogenetic changes in the colour of *P. crassifolius* evolved in response to moa herbivory in New Zealand, ontogenetic colour changes may be reduced in *P. chathamicus*, which evolved in the absence of moa.

We conducted spectrometric analyses to quantify ontogenetic colour changes in *P. crassifolius* from the perspective of birds to test four predictions arising from the moa browsing hypothesis: *P. crassifolius* seedlings resemble the reflectance properties of leaf litter, making them difficult to distinguish against their natural background (i.e. crypsis); as plants grow taller, saplings advertise sharp spines along their leaf margins with conspicuous colour patches (i.e. aposematism); once plants grow above the

reach of the tallest known moa, they produce leaves that are ordinary in size, shape and colour; *P. chathamicus*, a closely related species that evolved in the absence of moa, has lost the ontogenetic changes in leaf colour displayed by *P. crassifolius*.

Materials and Methods

All *P. crassifolius* (A. Cunn) C. Koch and *P. chathamicus* Kirk. plants used in the analyses were grown in a common garden located in Otari-Wilton's Bush, Wellington, New Zealand (41°15'S, 174°45'E). One randomly selected leaf was collected from 10 plants within three height classes. Seedlings were small enough to be consistently associated with a background of leaf litter. Saplings were too large to be associated consistently with leaf litter, but were within reach of browsing moa. Adults stood above the reach of the largest known moa. Sample sizes of adult plants of *P. chathamicus* were smaller ($n = 2$) because of their limited availability in the garden. Spectral readings were replicated five times for all leaves, which were then averaged before analyses. Leaf litter (i.e. dead leaves, earth and fallen branches) reflectance measurements were collected in 10 random locations within old-growth forest following Albert *et al.* (2004), which were averaged before analyses.

Spectral analyses were made using a USB Ocean Optics 2000 spectroradiometer and Xenon Pulse X2 lamp Ocean Optics light source. An object's reflectance properties were measured as the proportion of a diffuse, Teflon-based, white reflectance standard. The fibre optics probe was mounted inside a matte black plastic tube to exclude ambient light. The distance between each object and the probe was fixed at 1 cm. The angle of illumination and reflection was fixed at 45° to minimize glare. Spectra were calculated at 5 nm intervals from 300 to 700 nm with SpectraSuite software. We chose to restrict our analyses to wavelengths below 700 nm because the far-red spectrum cannot be discriminated by birds. Irradiance was measured with a cosine-corrected sensor and a D65 (normal daylight) light bulb as a reference.

We quantified the appearance of leaves using the contrast comparison method, which follows simple colour pattern measures related to photon capture (Vorobyev *et al.*, 1998; Schaefer *et al.*, 2004; Endler & Mielke, 2005; Schaefer *et al.*, 2007). A detailed explanation of the mathematical model is given elsewhere (Osorio & Vorobyev, 1996; Vorobyev & Osorio, 1998; Vorobyev *et al.*, 1998). This method quantifies the discriminability of any two spectra, provided only that receptor spectral sensitivities and noise can be estimated.

The receptor spectral sensitivity values were obtained from Endler & Mielke (2005) for both the U and V avian cones. As exact spectral discrimination data are not available for moa, we used the V model based on its closest living relative, *Struthio camelus* (ostrich) (Turvey *et al.*, 2005). We chose to use the ostrich receptor because of the close phylogenetic relatedness to moa and the widespread evolutionary conservatism in avian colour vision (see Ödeen & Håstad, 2003).

Colour is defined as a point in a perceptual space whose co-ordinate axes represent quantum catches of receptors (Poirson & Wandell, 1990). The discriminability of any two colours is described by the 'distance' ΔS between them in JND ('just noticeable differences') units. A colour patch with a JND value of more than unity is at the threshold of discrimination from the background. Increasing JND values indicate increasing ease of distinction (e.g. from a larger distance), whereas values of less than 1 JND are not discriminated. We calculated separate JND values for both chromatic (colour-based) and achromatic (brightness-based) spectral contrasts.

The exact working nature of achromatic or brightness signals in birds is still poorly understood (Campenhausen & Kirschfeld, 1998; Osorio *et al.*, 1999; Hart, 2001). Double cones have a broad spectral sensitivity, which overlaps with both long- and medium-wavelength-sensitive cones, and are used in achromatic signal processing (noncolour-based tasks) (Hart *et al.*, 2000; Jones & Osorio, 2004; Cuthill, 2006). The only available double cone receptor data sensitivity is based on *Leiothrix lutea* (red-billed *Leiothrix*). A detailed description of the methods used to quantify leaf reflectance properties is given in Supporting Information Notes S1.

To test whether *P. crassifolius* seedlings are cryptically coloured, we visually compared the reflectance curves of seedlings and leaf litter. We also tested whether *P. crassifolius* seedlings were less conspicuous against a background of leaf litter than were *P. chathamicus*, by comparing the JND values derived from seedling versus leaf litter spectral contrasts between species using *t*-tests. Two *t*-tests were conducted, both chromatic and achromatic contrasts.

To test whether *P. crassifolius* advertises the spines located on its leaf margins with conspicuously coloured tissues, we visually compared the reflectance curve associated with spines with the curve characterizing the region between spines (i.e. nonspines). We also tested whether the spines on *P. crassifolius* were more conspicuous than the vestigial spines on *P. chathamicus* by comparing the JND values derived from spine versus nonspine spectral contrasts between species using *t*-tests. Separate *t*-tests were again conducted for chromatic and achromatic contrasts.

To test whether the reflectance properties of adult leaves of *P. crassifolius* were similar to those of adult leaves of both *P. chathamicus* and other New Zealand tree species, we conducted spectrometric measurements on 29 common tree species using the same protocol as described previously (i.e. one randomly selected leaf from 10 plants). Spectral readings were replicated five times for each leaf, which were averaged before analyses. We then compared the resulting reflectance curves for *P. crassifolius*, *P. chathamicus* and the other tree species. In this comparison, JND values were not compared statistically because of a lack of a consistent spectral background for comparative purposes. All data were logarithmically transformed when necessary to improve normality, and all analyses were conducted in R (R Development Team, 2008).

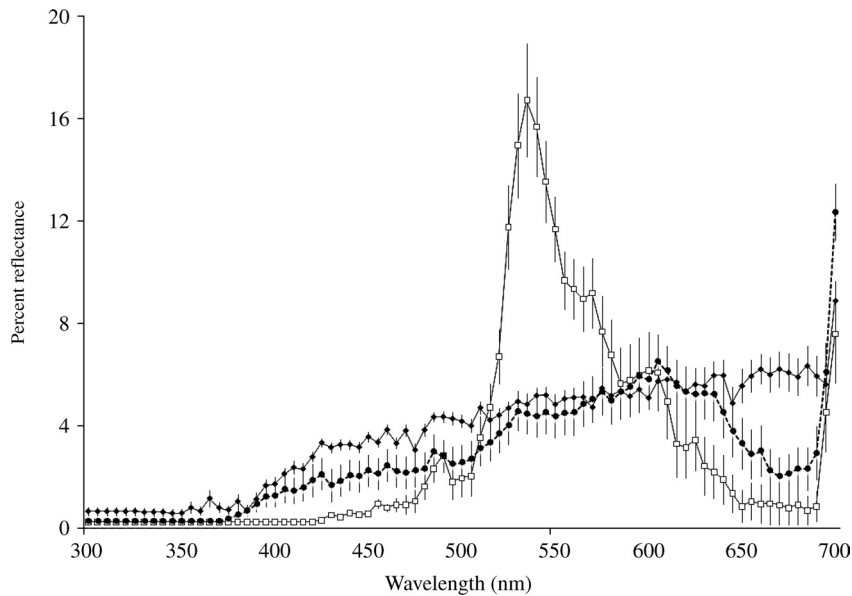


Fig. 2 Reflectance curves for *Pseudopanax chathamicus* seedlings (squares), *P. crassifolius* seedlings (circles) and leaf litter (diamonds).

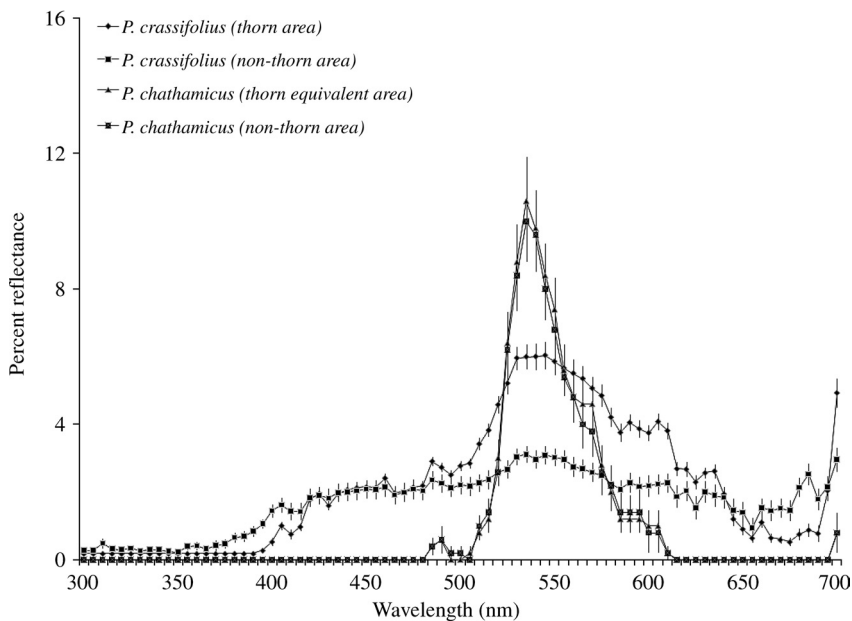


Fig. 3 Reflectance curves for *Pseudopanax chathamicus* and *P. crassifolius* saplings. For each species, separate curves are drawn for tissues adjacent to spines and tissues between spines. Vertical black lines are \pm standard error.

Results

The average reflectance curve obtained for *P. crassifolius* seedlings was strikingly similar to that of leaf litter (Figs 1, 2). However, the reflectance curve for *P. chathamicus* was markedly different. Chromatically, *P. crassifolius* seedlings had lower JND values against a leaf litter background (16.6 ± 3.1) than did *P. chathamicus* (47.8 ± 1.9) ($t = -8.62$, d.f. = 18, $P < 0.01$). Achromatically, *P. crassifolius* seedlings also had lower JND values (-5.74 ± 3.8) than did *P. chathamicus* (4.0 ± 2.9) ($t = -2.05$, d.f. = 18, $P = 0.05$). Therefore, birds would have greater difficulty in distinguishing seedlings of *P. crassifolius* against a background of leaf litter relative to *P. chathamicus*.

Saplings of *P. crassifolius* produce long, narrow, rigid leaves that have spine-like structures along their margins, which are flanked by patches of lighter green coloration (Figs 1, 3). Conversely, *P. chathamicus* saplings produce leaves that appear to be phenotypically similar to adult leaves. The colour patches adjacent to spines in *P. crassifolius* had higher chromatic JND values (16.4 ± 1.7) against the background of the remainder of the leaf compared with *P. chathamicus* (6.7 ± 2.2) ($t = -3.34$, d.f. = 13, $P = 0.05$). Similar differences between *P. crassifolius* (10.5 ± 2.5) and *P. chathamicus* (0.7 ± 1.8) were found in achromatic comparisons ($t = 2.55$, d.f. = 13, $P = 0.02$). Therefore, the spines along the margins of sapling leaves of *P. crassifolius* are made more conspicuous by

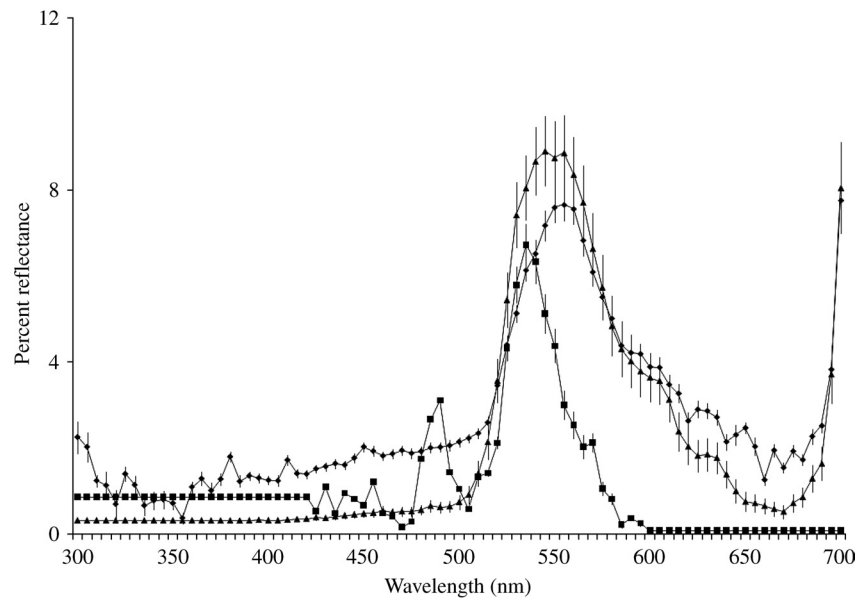


Fig. 4 Reflectance curves for adult leaves of *Pseudopanax chathamicus* (squares), *P. crassifolius* (diamonds) and the average of 29 common New Zealand plant species (triangles). Vertical black lines are \pm standard error.

the colour of adjacent tissue, and this signal has been lost in *P. chathamicus*.

Adult leaves of *P. crassifolius* and *P. chathamicus* showed similar reflectance curves (Fig. 4). Both were also broadly similar to the adult leaves of the 29 co-occurring adult plant species. Therefore, we failed to find marked differences in adult leaf colours between *P. crassifolius*, *P. chathamicus* and other common tree species.

Discussion

Pseudopanax crassifolius goes through a remarkable series of colour changes during ontogeny. Seedlings are mottled in appearance and are similar in colour to leaf litter. Saplings produce long, rigid leaves with spine-like projections on their margins, each of which is typically associated with a patch of brightly coloured tissue. Once plants grow above 3 m in height, they abruptly begin to produce leaves that are typical in size, shape and colour to co-occurring tree species. Similar colour changes were not observed in *P. chathamicus*, which produces similarly coloured leaves throughout ontogeny. Therefore, changes in the colour of leaves produced by *P. crassifolius* through ontogeny are similar to the ontogenetic colour changes in many insects, which shift from being cryptically coloured to aposematically coloured during development (see Grant, 2007).

The unusual leaf colours in *P. crassifolius* could be a series of adaptations to enhance physiological performance in the changing environmental conditions experienced by plants as they grow from the forest floor into the canopy (Day, 1998; Howell *et al.*, 2002). *Pseudopanax crassifolius* seedlings are known to possess traits (for example, thin lamina and low specific weight) that promote photosynthetic capability under low-light conditions (Gould, 1993; but see Gamage & Jesson, 2007). Furthermore, phenotypic differences between *P. chathamicus* and

P. crassifolius could result from historical differences in climate between New Zealand and the Chatham Islands (McGlone & Webb, 1981). New Zealand was heavily glaciated during the last glacial maximum, but the Chatham Islands were substantially warmer as a result of the ameliorating climatic effects of the ocean. The unusual leaf colours in *P. crassifolius* could increase leaf temperatures, which may have enhanced photosynthetic efficiency in the colder conditions that occurred in New Zealand. However, for climate to provide a convincing explanation for the results, vertical gradients in environmental conditions (i.e. from the ground to the forest canopy) would need to be more pronounced in New Zealand than in the Chatham Islands. Although these data are unavailable, forest structure appears to be broadly similar in both locales (K. C. Burns, pers. obs.), which suggests that this explanation is unlikely.

Alternatively, ontogenetic changes in leaf colours may represent a series of adaptations to first avoid and later deter moa browsing. The mottled colours of seedling leaves are similar to the appearance of leaf litter, which would reduce the probability of their detection by avian herbivores. Their unusual coloration may also reduce the appearance of leaf outlines and help camouflage leaves against the sunlight-dappled forest floor (Givnish, 1990). Saplings produce long, rigid leaves with spine-like projections on their margins that are consistently associated with bright colour patches that produce high achromatic contrasts. Interestingly, achromatic contrasts are particularly important in the detection of object borders in birds, humans and insects (Osorio *et al.*, 1999), and may explain why plant spines are often coloured white or associated with white markings (Lev-Yadun, 2001, 2003, 2009b; Midgley, 2004). Furthermore, the avian eye consists of four types of single cone and one 'double cone' (Cuthill, 2006), which is unique to birds. The double cone has a broad spectral sensitivity and is associated with achromatic perception (i.e. intensity-based tasks). Therefore, birds would

be particularly sensitive to the colour of sapling leaf spines, which are characterized by high achromatic contrasts.

A precise quantitative description of the visual acuities of moa is unlikely to ever be obtained because they are now extinct. We chose to make our reflectance calculations using the ostrich (V-type eye), because this species is a close relative to moa in the ratite family. However, to assess how sensitive the results might be to this choice of avian cone type, we recalculated the spectral data using the receptor sensitivity of a passerine (U-type eye). The results from this analysis were statistically indistinguishable from the results based on the ostrich eye. Therefore, the results do not appear to be sensitive to avian cone type.

Once plants grow above 3 m, the maximum height of the largest known moa, leaves are typical in size and shape to the adult leaves of many other New Zealand tree species (Clearwater & Gould, 1994). Their average spectral properties are also ordinary, that is mostly within the standard error of the leaves of syntopic species. Their colours are also consistent with the reflectance properties of the primary pigments involved in photosynthesis (chlorophyll *a* and *b*), which have peak absorption values above and below the peak in reflectance of adult leaves at 545 nm.

Insects are prominent herbivores in New Zealand, as they are on the Chatham Islands and elsewhere in the world, and may have played a role in the development of unusual colours in *P. crassifolius*. However, the spine-like projections on saplings are too large to provide protection against insect herbivores. A more likely explanation seems to be browsing by moa, which went extinct following the arrival of humans in New Zealand approximately 750 yr ago. Because the putative selection agent is now extinct, the effectiveness of leaf colours in deterring moa herbivory cannot be tested directly. However, future work could still test the hypothesized link between leaf reflectance patterns and herbivore damage. For example, cafeteria-style experiments, similar to those of Bond *et al.* (2004), could be conducted to evaluate whether extant ratites (for example, emu) have trouble locating seeding leaves against a background of leaf litter, or whether they struggle to swallow sapling leaves and avoid those with brightly coloured spines.

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Supporting Information

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Notes S1 Materials and methods – equations

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