Is crypsis a common defensive strategy in plants? Speculation on signal deception in the New Zealand flora

Kevin C. Burns
School of Biological Sciences; Victoria University of Wellington; Wellington, New Zealand

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Colour is a common feature of animal defence. Herbivorous insects are often coloured in shades of green similar to their preferred food plants, making them difficult for predators to locate. Other insects advertise their presence with bright colours after they sequester enough toxins from their food plants to make them unpalatable. Some insects even switch between cryptic and aposomatic coloration during development. Although common in animals, quantitative evidence for colour-based defence in plants is rare. After all, the primary function of plant leaves is to absorb light for photosynthesis, rather than reflect light in ways that alter their appearance to herbivores. However, recent research is beginning to challenge the notion that colour-based defence is restricted to animals.

Temperate deciduous forests provide what is arguably the most extraordinary display of colour in nature. Prior to leaf-fall in autumn, the leaves of many deciduous tree species in Asia, Europe, and North America turn red, leading to brilliantly coloured landscapes. Once thought to be a by-product of chlorophyll re-absorption prior to leaf abscission, autumn flushes in red leaf colours are now known to result from the active synthesis of red-coloured pigments. Although the exact reason for the production of red-coloured pigments prior to leaf-fall is unknown, it has recently been hypothesized to be a form of defence. Aphids are common phloem-feeding herbivores in deciduous forests, which disperse from the forest floor into tree crowns in autumn, and the synthesis of red pigments could signal the timing of leaf fall and the reduction in the supply of photosynthate. Although there are also physiological explanations, red leaf colours could be a reliable signal of unpalatability to herbivores.

Lev-Yadun and Holopainen recently showed that there are fewer red-coloured deciduous tree species in Europe than in North America, and they speculate that historical processes are the cause. During the advance and retreat of glaciers in the Pleistocene, the European Alps would have hindered the movement of plants and their herbivores in response to long-term climate change. Mountain ranges in North America run perpendicular to the equator, which would facilitate these migrations. Therefore, if red leaves are signals to herbivores, geographic differences in leaf pigmentation may be ‘anachronistic’. In other words, they may result from historical coevolutionary dynamics between plants and their herbivores, rather than present day selection pressures alone.

Despite these important insights, our understanding of colour-based defence in plants is in its infancy and progress hinges on quantitative tests in other parts of the globe. Previous work is also restricted largely to aposomatic, or warning colours. Given that cryptic colouration is widespread in animals, it might also be common in plants. Yet we are far from determining if this is true.

Here, I discuss several New Zealand plant species that seem to be coloured in ways that would make them difficult for herbivores to locate. I suggest that these plants are anachronisms; their unusual appearance is the result of selection from flightless browsing birds called moa, which went extinct following the arrival of humans in New Zealand 750 years ago. I also discuss the difficulties associated with testing for crypsis in plants and finish by outlining a methodological approach to test for colour-based defence in plants when the putative herbivores are either unknown or extinct.

New Zealand Lancewood

Pseudopanax crassifolius (A. Cunn) C. Koch Araliaceae, or New Zealand lancewood, is one of the strangest looking plants on Earth (Fig. 1). The primary reason for its peculiar appearance is that it is strongly heteroblastic, meaning its gross morphology undergoes sudden and dramatic changes during ontogeny. Although heteroblasty is unusually common in the New Zealand flora, it is exceptional in P. crassifolius. In fact, it changes in appearance so completely during ontogeny that Sir Joseph Banks, the famous botanist that accompanied James Cook on the voyage of the Endeavour, named the juvenile and adult forms of P. crassifolius as separate species.

After germinating, P. crassifolius seedlings (<10 cm tall) are immediately unusual. Instead of being green, seedling leaves are a strange mottled-brown colour. However, once plants reach approximately 10–20 cm in height, they begin to produce strikingly different-looking colour. These juvenile leaves are very long, stiff and narrow. They also produce strange thorn-like dentitions along their margins, each coinciding with a distinctive patch of differently coloured leaf tissue. A final morphological transformation occurs once plants grow to approximately three metres in height, when they begin to produce green, oblong leaves that are rather ordinary in appearance.
down the oesophagus. Thorns that arise from stems, such as those produced by many species of Acacia for protection against large mammals, are ineffective deterrents to bird browsers and are correspondingly rare in the New Zealand flora. In order to deter bird browsers, plants need other types of defence.

Fadzly et al. found that colour may have been a critical component of a defensive strategy that evolved in *P. crassifolius* to deter moa browsing. Spectrographic analyses of seedling leaves from the perspective of birds indicate that their mottled brown colour would have made them very difficult for moa to locate amongst a background of leaf litter on the forest floor. The juvenile leaves would have been difficult for moa to swallow, given that moa lacked teeth. Without the ability to chew, they had to swallow leaves whole or at least in large pieces, which would have been a difficult task, thanks in part to their long, rigid shape and sharp lateral spines. Spectrometric analyses showed that the distinctive colour patches associated with each spine would have been particularly conspicuous to birds, who are sensitive to bright (achromatic) visual signals. Paleoecological records indicate that the maximum browsing height of the tallest moa species was approximately three metres. So the sudden shift to leaves that are ordinary in size, shape and colour at approximately three metres roughly coincides with a height refuge from bird browsers.

These results are important for two reasons. First, they provide one of the first quantitative examples for crypsis in plants. Second, they illustrate that plants can alternate colour-based defensive strategies during ontogeny, switching from being cryptically coloured as seedlings, to aposomatically coloured as juveniles and ultimately colour-undefended as adults, once they grew above the reach of the putative browser. Many animals switch colour-based defensive strategies during ontogeny. Fadzly et al. show evolu-

So why is *P. crassifolius* so unusual looking? A recent study suggests that browsing birds may have selected for its unusual appearance. Prior to human arrival, New Zealand lacked native land mammals (except for two species of bat) and instead was home to giant, flightless birds called moa. Because birds lack teeth and cannot chew, they must swallow leaves whole, by first placing them in their bill and then snapping their head forward to orient them
tion might sometimes favour a similar colour-based strategy in plants.

**New Zealand Mistletoes**

Rather than referring to a single phylogenetic lineage, the term ‘mistletoe’ refers to a polyphyletic group of plants that have evolved parasitic lifestyles independently.21,22 There are two main phylogenetic lineages of mistletoes: the family Loranthaceae, which evolved in the Southern hemisphere, and the family Viscaceae, which evolved in the northern hemisphere.23,24 Both lineages have since dispersed out of their native hemispheres and many geographic locales now house members of both families.

Australasia is home to an unusually high diversity of Loranthaceous mistletoes, which show varying degrees of host specialisation; some species are found on only a single host species, while other exploit a large number of different host species. Several previous observers have noted that Australian mistletoes often resemble their hosts with striking accuracy. Possums (order Phalangeriformes) are important, arboreal browsers in Australian forests and many host trees are heavily defended chemically. If Australian mistletoes have evolved to mimic their hosts morphologically, possums may confuse them with their chemically defended hosts.25,26

A similar situation may occur in New Zealand. Some Viscaceous mistletoes, such as *Korthalsella salicornioides* (A. Cunn) Tiegh., parasitise shrubs and small trees and often look remarkably similar to their preferred hosts (Fig. 2). Common herbivores such as insects might therefore have difficulties distinguishing mistletoes from chemically defended hosts. On the other hand, Loranthaceous mistletoes in New Zealand look quite different from their preferred hosts. One difference between families that may explain their apparent differences in host resemblance is that Viscaceous mistletoes attack mostly small-statured hosts, while Loranthaceous species usually attack taller trees. Therefore, if New Zealand mistletoes have evolved to resemble their preferred hosts, the putative herbivore may have attacked small-statured hosts preferentially. Although it is difficult to pinpoint which herbivore this might be, one obvious candidate is moa.

**Scree Plants**

Approximately 15 million years ago New Zealand began a period of very rapid tectonic uplift, which transformed New Zealand into a mountainous archipelago characterised by extensive areas of alpine habitat. Alpine habitat does not support forest and is instead inhabited by herbs, tussocks and short-statured shrubs. Alpine areas in New Zealand also contain a distinctive type of rocky habitat called ‘scree slopes’, which occur on especially steep, alpine terrain. Scree slopes are demanding places for plants to grow, because the soil surface is comprised of large rocks that are moving continuously down slope. Although these rocks move slowly, over the course of a perennial plant’s lifespan this movement acts to separate vegetative plant parts from their root systems. Numerous plant species from a wide range of phylogenetic backgrounds have adapted to this harsh habitat by producing stems that connect above- and below-ground tissues by continuously elongating as vegetative plant parts are pulled down-slope away from their root systems.

Substrate colour matching seems to occur in a wide range of other plant species inhabiting permanently rocky habitat. Perhaps the best-known example is the genus Lithops, which grows in the rocky deserts of Southern Africa and rightly deserves its common name ‘stone plant’, given their remarkable resemblance to rocks and small pebbles. Like New Zealand scree plants, the ‘stone plant’ syndrome is not restricted to this genus, and many species from a range of phylogenetic backgrounds appear to have converged on this distinctive appearance. Other notable examples of cryptically coloured plants inhabiting rocky habitats are

![Figure 2. Korthalsella salicornioides infecting Leptospermum scoparium.](image-url)
A Hypothesis

Under what conditions is crypsis a viable defensive strategy in plants? Several conditions are necessary: (1) Plants need to be preyed upon by visually orientated herbivores. If a plant’s main herbivores locate plants using olfactory or tactile cues, visual...
mimicry would obviously be ineffective. (2) Plants need to be habitat specialists, such that they grow in environments that provide a consistent visual background. Plant species that utilise a wide range of habitats lack a specific background that they can evolve to resemble, which would likely inhibit the evolution of crypsis, unless species were locally adapted to different habitats. (3) Plants must be short-statured, such that they grow in close physical proximity to the visual background generated by their preferred habitat. By definition, an object is cryptic because it resembles its background. So when a plant grows away from a background that it resembles, it loses any effect of crypsis. (4) The preferred habitat must be unpalatable. If the visual background of a preferred habitat were itself palatable, for instance when mistletoes parasitize palatable hosts, there would be no adaptive benefit to resembling it. Under these four circumstances, crypsis appears to be a viable defensive strategy in plants. Although there is little evidence to support this hypothesis to date, this may be due to a lack of investigative effort rather than realism.

**A Methodological Framework to Test for Crypsis**

How does one test the hypothesis that a plant is cryptically coloured? The most obvious way is to conduct an experiment by manipulating the plant’s colour and offering it to herbivores. An experimental approach is the only way to provide a direct link between plant colour and herbivore damage. Unfortunately, this might not always be possible. There are numerous obstacles to designing effective experiments in ecology.29 One such barrier to experimental tests of plant crypsis is an absence of appropriate techniques to manipulate the colour of plants leaves. In the case of New Zealand, another serious problem is that an important group of herbivores is now extinct, which makes a direct experimental approach impossible. Ambiguity concerning putative herbivores may also be the rule rather than an exception. Some researchers have argued that this situation applies to most plants across the globe:

“Living organisms are beautifully built to survive and reproduce in their environments. Or that is what Darwinians say. But actually it isn’t quite right. They are beautifully built for survival in their ancestor’s environments… Since modern man has drastically changed the environment of many animals and plants over a time scale that is negligible by evolutionary standards, we can expect to see anachronistic adaptations everywhere.” (Richard Dawkins, quoted by30).

Many scientific disciplines, such as astrophysics, geology and palaeontology, suffer from an inability to conduct manipulations as a regular part of scientific inquiry. Similarly, experimentmentation is beyond the reach of most questions in biogeography, because most biogeographic phenomena operate on spatial and temporal scales that are too large to manipulate. Instead, biogeographers rely on observations and indirect hypothesis testing, in much the same way as astrophysicists, geologists and palaeontologists. However, biogeographers have developed a useful methodological tool that can be used to good effect under these circumstances.

‘Null models’ are pattern-generating algorithms that simulate biological patterns in the absence of a structuring process.31,32 Simply put, null models test hypotheses by comparing field observations to randomised expectations. Although they are powerful tools for identifying patterns in field observations, they cannot be used to precisely identify the processes responsible for them.

By providing a means to test whether a plant shows an unusual likeness to the appearance of its preferred habitat, null models can provide the foundations for a research program on plant crypsis. Qualitative judgements based on human vision are insufficient to identify cryptic plants, because the human eye differs markedly from most herbivores, but see ref. 33. Apparently cryptic colour patterns could also arise by chance relatively easily. A plant whose colour is determined solely by physiological processes could easily disperse by chance into an environment that is coloured similarly.

To test whether a scree plant is cryptically coloured, null models can be used to redistribute a population of such plants across a range of alpine habitats. Differences between the spectral properties of leaves and each alpine habitat can then be calculated to establish whether scree plants are less conspicuous in their preferred habitat relative to other potentially suitable habitats. Similarly, null model simulations can be used to simulate the distribution of mistletoes among potential host species. The conspicuousness of observed mistletoe-host species combinations, both in terms of morphology and reflectance spectra,34,35 can then be compared to all other potential mistletoe-host species combinations. If observed species combinations are less conspicuous than what would be expected by chance pairings of mistletoes and their hosts, one can conclude a cryptic pattern exists. Null model comparisons also can be recalculated according to the visual systems of different types of herbivores,36 to test whether results change from the perspective of different types of herbivores.

While this approach cannot establish whether herbivores would actually overlook a plant, it can be used to establish whether a plant is especially inconspicuous. This is a powerful insight and an important first step in testing the crypsis hypothesis. By providing a means to test for a cryptic pattern, null models can lead the way to understanding whether plants sometimes hide from predators.

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References