

Springs and wire plants: anachronistic defences against Madagascar's extinct elephant birds

William J. Bond^{1,*} and John A. Silander²

¹Botany Department, University of Cape Town, Private Bag, Rondebosch 7701, Republic of South Africa

²Centre for Conservation and Biodiversity, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043, USA

The extinction of large vertebrates in the last few millennia has left a legacy of evolutionary anachronisms. Among these are plant structural defences that persist long after the extinction of the browsers. A peculiar, and controversial, example is a suite of traits common in divaricate (wide-angled branching) plants from New Zealand. Divaricate architecture has been interpreted as an adaptive response to cold climates or an anachronistic defence against the extinct moas. Madagascar, a larger tropical island, also had a fauna of large flightless birds, the elephant birds. If these extinct ratites selected for similar plant defences, we expected to find convergent features between New Zealand and Malagasy plants, despite their very different climates. We searched the southern thickets of Madagascar for plants with putative anti-ratite defences and scored candidate species for a number of traits common to many New Zealand divaricates. We found many Malagasy species in 25 families and 36 genera shared the same suite of traits, the 'wire plant' syndrome, as divaricates in New Zealand that resist ratite browsing. Neither ecologically, nor phylogenetically, matched species from South Africa shared these traits. Malagasy wire plants differ from many New Zealand divaricates in lacking the distinctive concentration of leaves in the interior of shrubs. We suggest that New Zealand divaricates have a unique amalgam of traits that acted as defences and also confer tolerance to cold. We conclude that many woody species in the thickets of southern Madagascar share, with New Zealand, anachronistic structural defences against large extinct bird browsers.

Keywords: evolutionary anachronisms; megafaunal extinction; anti-herbivore defence; *Aepyornis*; divaricates

1. INTRODUCTION

Many large vertebrates have become extinct as humans settled new lands from the Late Pleistocene to the last millennium (Martin & Klein 1984; Burney & Flannery 2005). Their legacy persists in the plants on which they fed. Features such as large fruits and long spines, 'over designed' for the surviving fauna, have been called 'evolutionary anachronisms', leftovers of extinct trophic relationships (Janzen & Martin 1982; Janzen 1986; Barlow 2000). Evolutionary anachronisms are difficult to recognize and to study, especially when there are no extant analogues of the extinct fauna. They may also be diminishing in abundance as direct and indirect effects of the loss of the big vertebrates take their toll on anachronistic species and their adaptations. Here, we provide the first account of anachronistic defences against extinct mega-bird browsers from the island of Madagascar. The defences are convergent with those of many New Zealand plant species. Both islands supported remarkable browser assemblages of large flightless birds, moas (Dinornithidae) in New Zealand and elephant birds (Aepyornithidae) in Madagascar.

Madagascar had a very unusual fauna prior to human settlement some 2000 years ago (Burney *et al.* 2004). Terrestrial herbivores included elephant birds, giant lemurs and giant tortoises but, with the exception of hippos, no

ungulates (Dewar 1984). All of these creatures are extinct. Elephant birds were ratites related to extant ostriches (Struthionidae), emus and cassowaries (Casuariidae), rheas (Rheidae) and kiwis (Apterygidae) and to the extinct moas of New Zealand (Cracraft 1974; Cooper *et al.* 2001). The largest of the estimated 6–12 species of aepyornithids was the elephant bird, *Aepyornis maximus*, estimated to have weighed approximately 450 kg (Amadon 1947) with a browse height of 2–3 m. Madagascar also has an unusual flora with very high levels of endemism (Koechlin *et al.* 1974; Gautier & Goodman 2003). Many plants, particularly in the thicket vegetation of southern Madagascar, have peculiar architectures forming biological landscapes described as bizarre, fantastical and surreal. Iconic among these are the columnar, spiny, cactus-like Didiereaceae and 'bottle' trees (including *Adansonia* spp., *Pachypodium* spp. and *Delonix* spp.; Koechlin *et al.* 1974; Rauh 1995). There are also many non-spiny small-leaved shrubs of diverse ancestry (Grubb 2003).

There were no mammal browsers at all in New Zealand when humans settled the islands approximately 1000 years ago. Moas, the dominant vertebrate browsers, had a dozen species, with the largest weighing approximately 350 kg with a browse height of 2–3 m (Worthy 1990; Worthy & Holdaway 2002). Like Madagascar, New Zealand also has an unusual flora with very high levels of endemism and distinctive plant growth forms (Wardle 1991). These include divaricately branching shrubs, and 'heteroblastic' trees with strikingly different juvenile and adult foliage

* Author for correspondence (william.bond@uct.ac.za).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2007.0414> or via <http://www.journals.royalsoc.ac.uk>.

(Atkinson & Greenwood 1989). Divaricates are characterized by slender but tough branches, wide-angled branching, high orders of branching, small widely spaced leaves and, often, leaves concentrated in the interior of the plant even on non-browsed individuals (Greenwood & Atkinson 1977; Atkinson 1992; Kelly 1994). This combination of traits has been claimed to be unique to New Zealand (Kelly 1994; McQueen 2000). Greenwood & Atkinson (1977) interpreted the divaricate growth form as an anachronistic structural defence against moa browsing. Their hypothesis has been controversial and opposed by proponents of alternative hypotheses related, usually, to climatic factors (McGlone & Webb 1981; McGlone & Clarkson 1993; Day 1998; Howell *et al.* 2002).

Madagascar offers an interesting test of the defence hypothesis. If ratites select for distinctive plant architectures, then Madagascar should have convergent plant traits with New Zealand divaricates, despite its tropical and subtropical climate. There has been only one previous study considering elephant bird herbivory in relation to plant traits. Grubb (2003) compared leaf size of non-spiny plants in the thickets of southern Madagascar with plants from climatically matched ecosystems in Kenya. He noted that spines were rare in Madagascar and that leaves of the thicket species were notably smaller than African species. He rejected climate-related arguments for smaller leaves in Madagascar and suggested that they had evolved in response to elephant bird browsing using, as his model, the small leaves of New Zealand divaricate plants. However, Grubb (2003) observed that divaricate branching was very rare in Madagascar thickets suggesting both convergent and divergent features of plants exposed to ratite browsing.

Recent experimental studies on extant ratites (emus and ostriches) feeding on New Zealand divaricates have identified specific traits of these and other plant architectures which help confer plant resistance to bird browsing (Bond *et al.* 2004). We set out to test whether the plant species in the thicket biome of Madagascar shared similar traits. Bond *et al.* (2004) showed that divaricate branches of heteroblastic tree species slow feeding rates of emus and ostriches in a manner analogous to the effect of spines on feeding rates of African ungulates (Cooper & Owen-Smith 1986; Milewski *et al.* 1991). Though the birds could meet their daily energy requirements by feeding on adult shoots, they would starve on juvenile shoots owing to the slow feeding rates. However, the nature of effective structural defences against ratites versus ungulate browsers is completely unlike, reflecting their different feeding mechanisms. All extant browsing ratites feed by clamping the beak on a leaf or twig and pulling the head back with a tug or a whiplash action of the head (Bond *et al.* 2004). The birds ingest food whole, swallowing by a 'cranio-inertial' mechanism (Zweers *et al.* 1997) comparable with the 'head-throwing' mechanism of reptiles (Gans 1969). The size of a food item cannot exceed the gape of the beak, so that long food items can only be swallowed by manipulating the long axis parallel with the throat (such as a heron swallowing a fish). Bond *et al.* (2004) identified five structural traits common to juvenile, but not to adult, heteroblastic trees and also to many homoblastic shrub species in New Zealand which reduce feeding rates in ratite browsers. These are as follows:

- (i) small leaves that reduce leaf area lost by plucking,
- (ii) thin twigs that are difficult to clamp and which have

high tensile strength so that they do not break easily when tugged,

- (iii) divaricate (or zigzag) branches that extend when pulled, increasing the distance over which the branch has to be pulled before the force applied breaks off material, and which spring back when released increasing the handling time for the bird, and
- (iv) wide-angled branches that reduce the ability of the animal to swallow larger detached branches because the side shoots exceed gape width at all angles of entry into the beak.

For their experiments with New Zealand divaricate and heteroblastic plants, Bond *et al.* (2004) found that high tensile strength was the key trait reducing stem losses to browsing birds. Stems with low breaking loads were torn off the plants by the clamping and tugging action of emu and ostrich browsing.

Unlike ratites, ungulates shear off leaves and shoots and can chew them up and swallow them. Consequently, high tensile strength and wide-angled branching, key traits for ratite defence, provide no effective defence at all against ungulate browsers (Bond *et al.* 2004). For animals with soft lips, cheeks and mouthparts, thorns are more effective at slowing feeding rates. But thorns are ineffective against birds plucking off leaves with hard beaks (Greenwood & Atkinson 1977). Bond *et al.* (2004) argued that the incompatibility of defences against these different classes of browsers accounts for the absence of 'divaricate' architectures in those parts of the world where ungulate browsers outnumber ratites, such as southern Africa where ostriches account for less than 0.1% of the mean biomass of large vertebrate herbivores in the Kruger National Park (Dean 1997; Owen-Smith & Ogutu 2003).

We encountered plant species in Madagascar with some, or all, of the structural traits characteristic of Bond *et al.*'s (2004) 'anti-ratite' strategy. We scored candidate species for the traits discussed earlier and additional traits hypothesized to have conferred defences against moa browsing in New Zealand (Greenwood & Atkinson 1977; Atkinson & Greenwood 1989; Bond *et al.* 2004). We sampled related species from southern Africa in ecosystems dominated by ungulate browsers but within the natural range of the ostrich (Dean 1997) and scored them for the same set of traits. Traits that diverged from southern Africa but converged with New Zealand would be the best candidates for anti-ratite defences. Plant traits that converged with Africa and diverged from New Zealand are more likely to reflect selection by climate or phylogenetic relatedness. Traits unique to Madagascar would indicate conditions exclusive to the island, including different phylogenetic histories. Unlike New Zealand, Madagascar had other classes of vertebrate browsers, including giant lemurs and tortoises (Dewar 1984; Goodman *et al.* 2003). These may have selected for different kinds of plant defences. Heterophyly on the Mascarene Islands, for example, has been hypothesized to be a structural defence against tortoise browsing (Eskildsen *et al.* 2004; Hansen *et al.* 2004).

2. MATERIAL AND METHODS

(a) *Madagascar*

We sampled thicket vegetation of southwestern Madagascar at a number of sites along a west-east transect from Toliara

Table 1. Traits scored for species sampled in Madagascar and South Africa. (All traits were given a score between 0 and 1. New Zealand (NZ) scores for each trait are listed based on Bond *et al.*'s (2004) study of ratite-resistant plants and/or typical divaricates (Atkinson 1992; Kelly 1994; for more information, see electronic supplementary material, methods).)

trait	definition	NZ score
thin twigs	terminal 50 cm branch with predominantly thin (less than 3 mm) shoots	1
wide-angled branches	terminal 50 cm branch has several side shoots with wide-angled (greater than 70°) branches	1
three-dimensional-angled branching	side shoots branching at different planes from the main axis	1
leaf area	$0.67 \times \text{length} \times \text{width}$ of leaf. Small leaves are ratite resistant	1
inner/outer leaves	most leaves in interior of shrub with fewer leaves on exterior branches	1
high tensile strength	lateral branches unbroken when pulled with a force of approximately 10 kg	1
high lateral displacement	branches displaced by 50 cm or more when pulled	1
zigzag branching	main axis of terminal branches with a distinct zigzag form (figure 1a)	1
heteroblastic	markedly different juvenile and adult leaf size and branch architecture (cf. figure 1c,d). Ten tree species in NZ	1
thorns	presence of spines or prickles on stem (figure 1a). Thorns rare in NZ shrubs (<i>Rubus</i> spp., <i>Discaria toumatou</i>)	0

(Tulear) to Tolagnaro (Fort Dauphin) in protected areas and other relatively undisturbed sites. At each site, we sampled woody species with relatively small leaves (usually less than 20 mm × 20 mm), and some or all of the five traits identified by Bond *et al.* (2004) as anti-ratite defences. Candidate species were scored for all of these and several additional traits (table 1). Larger-leaved species, whose foliage would be readily accessible to bird browsers, were noted but not scored. We did not use divaricate indices (Atkinson 1992; Kelly 1994) because these were designed to quantify a qualitative 'archetype' of the 'typical' New Zealand divaricate, independent of function. Neither Kelly's nor Atkinson's indices include tensile strength, the key trait for preventing shoot loss to ratite browsing (Bond *et al.* 2004). In addition to the qualitative species trait survey, we took quantitative trait measurements on four heteroblastic tree species, i.e. with different adult and juvenile leaf forms and branch architectures. The methods are described in the electronic supplementary material.

(b) South Africa

We compared plant traits of Malagasy thicket species with African analogues. The thicket biome of Madagascar resembles the subtropical thickets of southern Africa physiognomically and ecologically (Vlok *et al.* 2003) with many shared phylogenetic lineages (Grubb 2003; Cowling *et al.* 2005). We sampled a spectrum of thicket biome types in southern Africa from the eastern Cape of South Africa (Sundays River Valley, Fish River Valley) to thicket and savannah vegetation in Zululand in the northeastern corner of South Africa and semi-arid shrublands with some thicket affinities in the western Cape region (Agter Cedarberg) of South Africa. The South African study areas differ from each other in rainfall amount (250–650 mm) and seasonality (Cedarberg, winter rainfall; eastern Cape, all year rainfall and Zululand, summer rainfall). Climate diagrams are provided in the electronic supplementary material.

The African study areas also differ in extant and historical mammal assemblages (Skead 1980, 1987). The Addo Elephant Park, part of the eastern Cape study area, has had high densities of elephants (*Loxodonta africana*) for the last 50 years with an additional presence of black rhinoceros (*Diceros bicornis*) and large numbers of kudu (*Tragelaphus strepsiceros*). The Zululand study areas included game parks (Hluhluwe–Umfolozo, Ndumo) with large herds of smaller antelope (mixed

feeders: impala (*Aepyceros melampus*) and nyala (*Tragelaphus angasi*); browsers: kudu, bushbuck (*Tragelaphus scriptus*) and giraffe (*Giraffa camelopardalis*) in addition to elephant and black rhinoceros. Historically, the Cedarberg area had a different suite of ungulate species (eland (*Taurotragus oryx*) and springbok (*Antidorcas marsupialis*) being common) and, probably, a low density of elephant and black rhinoceros (Skead 1980). Ostriches are present in all three study areas with greatest relative importance (biomass) in the arid shrublands of the west (Cedarberg; Milton *et al.* 1994).

In each study area, we selected woody plant species for trait analysis using similar criteria to Madagascar. Sampling was restricted to smaller-leaved woody species (smaller target for browsers) though with a larger minimum size (approx. 40 × 40 mm) than Madagascar because leaf sizes were generally larger. In addition to the general ecological comparison of thicket species, we also compared phylogenetically related taxa by sampling species from 15 genera and 1 family (African *Portulacaria* now included in Didiereaceae; Applequist & Wallace 2003) found in both Madagascar and southern African thickets (Cowling *et al.* 2005). Where genera had more than one species in the African study areas, we sampled those species with the smallest leaves. A total of 109 species in 32 families and 65 genera were sampled in South Africa (electronic supplementary material, table 2).

3. ANALYSES

To help define trait differences between the Malagasy and African plants, we applied a classification tree analysis to the data. This is a non-parametric method analogous to discriminant function analysis, which assigns samples to a group (e.g. Madagascar, South Africa) according to the values of predictor variables (Breiman *et al.* 1984; De'ath & Fabricius 2000). The analysis begins with the whole dataset, in this case, all the African and Malagasy species sampled, and then progressively splits samples into smaller groups using the best predictor variable at each hierarchical step. The aim of the analysis is to assign each sample (species) to one of the pre-defined groups (sampling area) using the available predictor variables (e.g. leaf size, tensile strength, etc.). The results resemble a taxonomic key with a hierarchical binary decision tree assigning samples to successive groups. We used the Classification Trees module

in STATISTICA v. 7.0 with a C&RT split selection method, Gini measure of goodness-of-fit and FACT style direct stopping rule set at a smallest group size of 5% of the sample set ($n=155$ taxa). Besides identifying the best predictor variable and its value at each split, the analysis also identifies the overall importance of predictor variables (scaled from 0 to 100). This is analogous to assessing the importance of a variable in a multiple regression analysis by its overall contribution to all possible regression models, rather than its selection for a single 'best model' (Burnham & Anderson 2002; StatSoft 2004).

As a test of phylogenetic constraints on plant form, we calculated the difference between trait values for Malagasy and African species within each of the 16 shared lineages. Where more than one species in a genus was sampled in one or both areas, differences between mean values were calculated. As a conservative measure of trait differences, we also calculated the difference between the maximum trait value for any African species (most similar to New Zealand divaricates) and the minimum trait value for Malagasy species (least similar to New Zealand divaricates). If trait values are a legacy of common ancestry, rather than a product of different selection pressures, then there should be no difference (difference value = 0) between Malagasy and African members of a clade. We used a univariate t -test of the null hypothesis that mean values for the 16 comparisons should be zero for each trait.

4. RESULTS

(a) Wire plants

Many thicker species in Madagascar had the combination of small leaves, tough, thin, wiry branches, wide-angled branching and high lateral displacement of branches (springiness), which deter ratite browsing. For convenience, we will refer to such plants as 'wire plants' rather than divaricates from which they differ in several ways. We recorded more than 50 species in 36 genera distributed across 25 families with the wire plant syndrome (electronic supplementary material, table 1). In addition, we found heteroblastic trees with strikingly different juvenile and adult forms in species of *Terminalia* (Combretaceae), *Albizia* and *Acacia* (Fabaceae), *Poupartia* (Anacardiaceae) and *Alluaudia* (Didiereaceae). Several wire plants are shown in figure 1.

Comparisons of branches of the four heteroblastic species reveal the characteristic features of wire plants that occur in juvenile plants but not in adults: thin twigs, smaller leaves, wider-angled branches and high tensile strength (actually high breaking load; figure 2). Mean diameter of test shoots was 2.54 mm for adult and 2.01 mm for juvenile shoots. Despite the thicker adult stems, 63% of adult shoots broke ($n=19$) compared with 20% of juvenile shoots ($n=24$) when a force up to 10 kg was applied. These features of juvenile branches, together with high lateral displacement, also emerge as contrasts in the analyses of the survey data from Madagascar and Africa.

Mean trait values for the Madagascar samples are compared with African samples in table 2. The Malagasy species differ most from the African species in the following traits: (i) high tensile strength, (ii) wide-angled branching, and (iii) high lateral displacement. African samples had two to three times more spiny species than Madagascar. In contrast, zigzag branching (figure 1a) was common (25% of

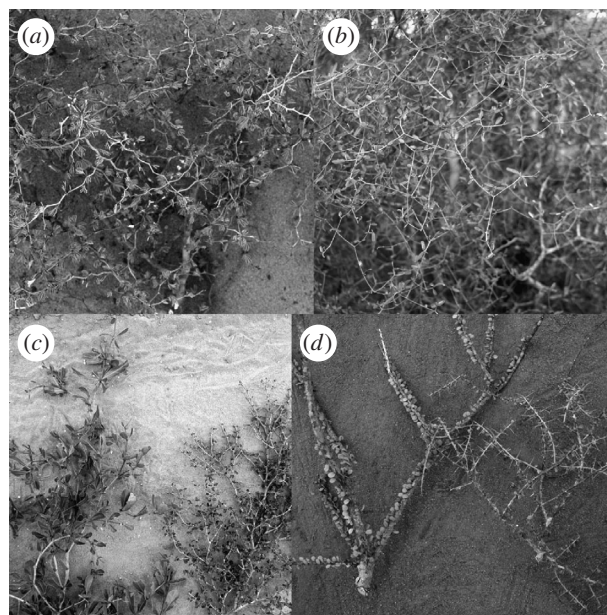


Figure 1. Examples of Malagasy wire plants and spines. (a) *Acacia delicatula* with zigzag branching and very reduced spines, (b) *Croton* sp. resembling New Zealand divaricate with thin tangled branches, (c) heteroblastic *Terminalia* with, left, adult branch (>3 m), right, juvenile branch (<2 m) and (d) heteroblastic *Alluaudia humbertii* with, left, adult branch (>3 m), right, juvenile (<2 m).

the sample) in Madagascar but rare in African species and only weakly developed (not as wide-angled) where it did occur (e.g. *Gymnosporia polyacantha*, *Asparagus racemosus*).

Results for the classification tree analysis of Malagasy wire plants versus African species are shown in table 3. Most of the Malagasy species (41 out of 45 species) were separated from African taxa by lateral displacement greater than 0.9 and tensile strength greater than 0.25. One African species, *Carissa tetramera*, was classified with the core Malagasy species by these criteria and two Malagasy species (*Croton* sp. and *Terminalia ulexoides*) with high lateral displacement, but low tensile strength were classified with a small group of African species. Both species strongly resemble New Zealand divaricates in having tangled, wide-angled branching. Three less springy Malagasy species (lateral displacement less than 0.9) were distinguished from African species by thin twigs (greater than 0.65), small leaves (greater than 0.5) and high tensile strength (greater than 0.75). The classification tree was less successful at discriminating between species among the three African study areas. Most of the arid shrubland species had thin twigs, small leaves and low tensile strength (table 3). Eastern Cape and Zululand thickets and savannah species had thicker stems and many Zululand species had large leaves (table 3). The importance value of predictor variables of the overall classification tree were as follows (100 = most and 0 = least important): thin twigs 100; tensile strength 74; leaf class 70; lateral displacement 69; wide-angled branching 61; three-dimensional branching 52; spines 45; zigzag branching 34; heteroblastic 31; and inner-outer canopy dimorphism 21. A classification tree analysis for Madagascar versus all African sites combined gave the same selection criteria (lateral displacement greater than 0.9, tensile strength greater than 0.25) for the majority of wire plants (42 out of 47 species), but the importance value of the variables differed in this reduced

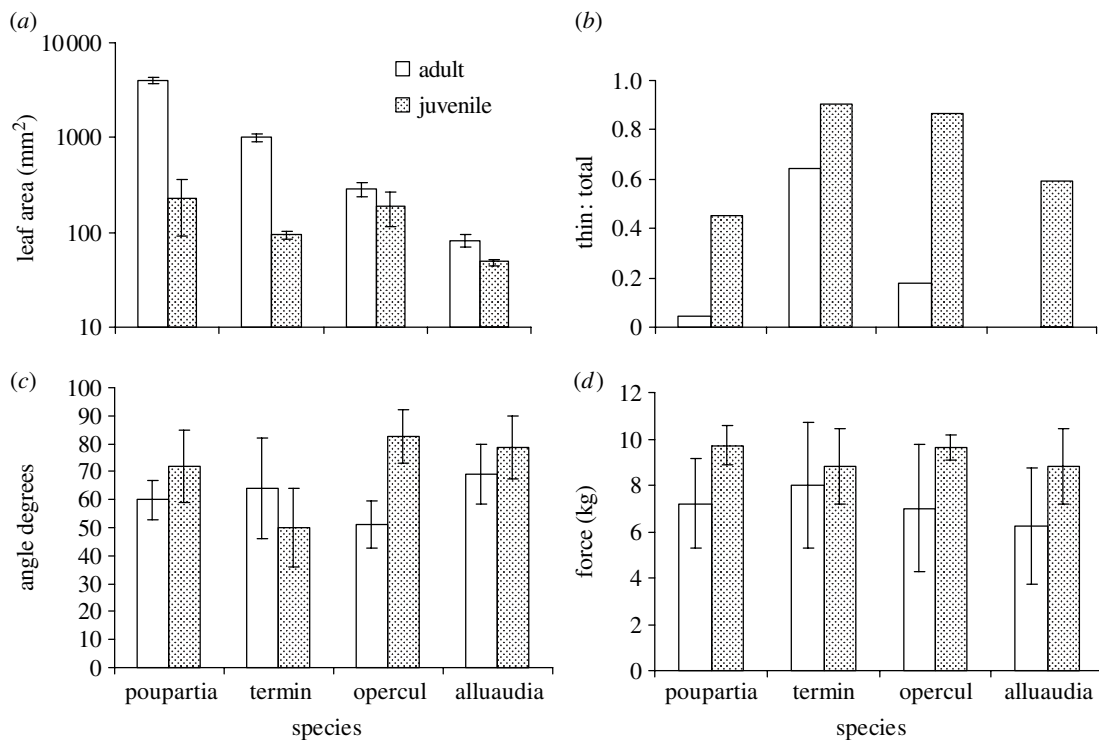


Figure 2. Comparison of traits in juvenile (shaded) and adult branches of *Poupartia minor*, *Terminalia seyringi*, *Operculicarya decaryi* and *A. humbertii*. (a) leaf area, log mm², (b) ratio of thin (less than 3 mm in diameter) branches to total branch length in a 50 cm sample shoot, (c) branch angle and (d) breaking load–tensile force required to break off a sample shoot. A maximum force of 10 kg was applied. Error bars are standard deviations from the mean.

Table 2. Mean trait values (with s.d.) for species sampled from Madagascar and three study areas in South Africa. (The percentage of species in each sample that were spiny or with zigzag main axes is also given. Values range from 0 to 1 with large values indicating, respectively, high tensile strength, high lateral displacement, wide-angled branches, thin twigs, branches angled in all dimensions and leaves concentrated in the interior of a plant (electronic supplementary material, methods).)

trait	Madagascar		East Cape thicket		Cedarberg shrubland		Zululand savannah and thicket	
	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
<i>N</i> spp.	48		42		19		48	
tensile strength	0.90	0.27	0.22	0.36	0.08	0.25	0.24	0.38
lateral displacement	0.98	0.10	0.15	0.28	0.51	0.36	0.20	0.35
wide-angle branches	0.85	0.23	0.36	0.40	0.38	0.43	0.38	0.36
thin twigs	0.73	0.24	0.30	0.34	0.86	0.18	0.31	0.31
three-dimensional branch angles	0.70	0.35	0.89	0.23	0.87	0.27	0.97	0.14
leaf size	0.56	0.20	0.54	0.33	0.81	0.30	0.30	0.29
inner/outer leaves	0.07	0.20	0.00	0.00	0.00	0.00	0.01	0.06
thorns (%)	12.5		33.3		31.6		45.8	
zigzag (%)	25.0		10.0		0.0		2.0	

analysis. Tensile strength was the most important variable discriminating Malagasy species from African ones (100) followed by lateral displacement (83), wide-angled branching (65) and thin twigs (39).

Table 4 shows mean differences between Malagasy versus African species within each of 16 clades (15 genera and 1 family). Four traits were significantly different in analyses comparing both the mean and the minimum differences between genera with more than one species. Wire plants in Madagascar had significantly greater lateral displacement of branches, higher tensile strength, wider-angled branches and thinner twigs than their African counterparts. They also had smaller leaves

than most of their African relatives. It is interesting to note that several Malagasy clades had flattened branches whereas their African counterparts had more three-dimensional branching (table 4); this is in contrast with New Zealand divaricates, which have complex three-dimensional branch architecture. It should also be noted that for every trait, some of the paired comparisons showed no difference between island and mainland species. For example, high breaking load was a feature of both African and Malagasy species of *Acacia* and *Dichrostachys*, although the African species all had much stouter branches than their thin-stemmed Malagasy wire plants relatives.

Table 3. Results of a classification tree analysis presented in the form of a dichotomous key. (The first split is based on the trait 'lateral displacement' with values greater than 0.9 (54 species) or less than 0.9 (101 species). For species with a value greater than 0.9, the next split is on the trait 'tensile strength' with values greater than 0.25 nearly all assigned to Madagascar. The study area column indicates the number of species in the terminal groups in Madagascar (M), and African study sites (C=Cedarberg, EC= eastern Cape thicket, Z=Zululand savannahs and thickets).)

		study area			
		M	C	EC	Z
lateral displacement greater than 0.9	tensile strength greater than 0.25	41			1
	tensile strength less than 0.25	2	4	1	5
lateral displacement less than 0.9	thin twigs greater than 0.65				
	leaf class greater than 0.5				
	tensile strength greater than 0.75	3			
	tensile strength less than 0.75	0	12	4	1
	leaf class less than 0.5	0	2	1	6
	thin twigs less than 0.65				
	leaf class greater than 0.15				
	thin twigs greater than 0.4	1	1	13	3
	thin twigs less than 0.4			16	15
	leaf class less than 0.15			6	17
	total	47	19	41	48

Table 4. Comparison of mean trait differences between phylogenetically paired Malagasy and African species. (Values greater than 0 indicate that the Malagasy species had higher lateral displacement, greater tensile strength, wider-angled branches, thinner twigs and smaller leaves than their African relatives. Statistical test=univariate *t*-test of the H_0 that the mean difference=0. Statistics are calculated for differences between mean trait values for each clade in each area. Mean2 and p_2 are calculated for differences between minimum Malagasy and maximum African trait values for each clade. Clades compared: *Acacia*, *Albizia*, *Brachylaena*, *Cadaba*, *Carissa*, *Commiphora*, *Croton*, *Dichrostachys*, *Didiereaceae* (*Decarya*, *Alluaudia*, *Portulacaria*), *Diospyros*, *Grewia*, *Mundulea*, *Poupartia* (= *Sclerocarya*), *Rhigozum*, and *Terminalia*.)

trait	mean	s.d.	<i>t</i> -value	<i>p</i>	mean2	p_2
lateral displacement	0.74	0.34	8.68	0.000	0.63	0.000
tensile strength	0.63	0.41	6.24	0.000	0.48	0.001
wide-angled branch	0.48	0.43	4.48	0.000	0.30	0.022
thin twigs	0.40	0.36	4.46	0.000	0.23	0.043
zigzag branches	0.26	0.45	2.31	0.036	0.22	0.089
leaf size class	0.21	0.28	2.98	0.009	0.08	0.315
heteroblastic	0.20	0.38	2.08	0.055	0.12	0.232
inner-outer leaves	0.04	0.13	1.33	0.203	0.03	0.333
spines	-0.13	0.47	-1.07	0.300	-0.16	0.237
three-dimensional branching	-0.20	0.36	-2.28	0.037	-0.28	0.014

5. DISCUSSION

Many species from the southern thickets of Madagascar share the distinctive wire plant suite of traits: slender, wiry, wide-angled, springy branches with small leaves. Other than a single species, *C. tetramera*, there were no analogous growth forms in thicket and savannah biomes in southern Africa. Nor are the traits a phylogenetic legacy from African ancestors. The strongest resemblance is to New Zealand divaricate plants, thousands of kilometres away, with a very different temperate climate, and belonging to a south temperate flora with very different phylogenetic histories. One of the few features the islands had in common was the presence of large flightless bird browsers (Dewar 1984; Worthy & Holdaway 2002). The trait characteristics of wire plants are the same as those identified experimentally as reducing browse losses to extant ratites in New Zealand

plants (Bond *et al.* 2004). Madagascar and New Zealand appear to have convergent plant defence syndromes against extinct mega-bird browsers. As in New Zealand, the wire plant syndrome is particularly remarkable in heteroblastic tree species owing to the widely divergent juvenile and adult branch architectures (figure 1). The contrast between heteroblastic acacias in Madagascar and Africa is very revealing. Juvenile forms of heteroblastic Malagasy acacias have long, lax, zigzag branches with tiny spines (figure 1). Juvenile forms of heteroblastic African acacias have very large spines, reduced leaves, and rigid heavily ramified branches which act as cages (Milewski *et al.* 1991; Archibald & Bond 2003).

Though we found the wire plant form in some 25 families and 36 genera, our study was preliminary and our list is probably far from complete. If, as Grubb (1992) noted,

structural defences are most common in semi-arid and nutrient-rich ecosystems, then we would expect to find wire plants in the drier deciduous forests of western Madagascar but not in the humid forests of the central plateau and the east. We also found many large-leaved species which are not wire plants in the Malagasy thickets, mostly trees (e.g. members of *Adansonia*, *Androya*, *Cedrelopsis*, *Croton*, *Delonix*, *Diospyros*, *Entada*, *Grewia*, *Gyrocarpus*, *Maerua*, *Salvadora*, *Salvadoropsis*, *Strychnos*, *Uncarina*). A few small-leaved shrubs with brittle branches and acute-angled branches were also locally common (e.g. *Polycline*, *Zygophyllum*). It seems probable that pristine Malagasy thickets contained a mix of edible, structurally defended plants, chemically defended plants and some undefended palatable species. The loss of the birds, and the introduction of mammals with utterly different feeding modes, may be having profound and continuing effects on species composition in these plant communities.

(a) *Wire plants and divaricates in New Zealand*

The Malagasy wire plants do not only show striking convergence in several traits, but they also differ in important ways from New Zealand divaricates. These differences are illuminating in the light of long-standing controversies on the functional significance of divaricate branching (Greenwood & Atkinson 1977; McGlone & Webb 1981; Atkinson & Greenwood 1989; McGlone & Clarkson 1993; Kelly 1994). We found very few shrubs with leaves concentrated in the interior of the canopy. This distinctive feature of many divaricates has been interpreted as a defensive trait (reducing access of browsers by a 'cage' effect), an inbuilt frost shelter reducing exposure of leaves to the cold night sky (McGlone & Webb 1981; Kelly & Ogle 1990), or, most recently, as a canopy architecture that reduces photoinhibition of cold leaves exposed to bright sunlight (Howell *et al.* 2002; Christian *et al.* 2006). The absence of the trait in Madagascar, with its tropical climates, is consistent with the climate-related hypotheses and not with the browse defence arguments. Unlike mammal defences, Malagasy wire plants often have lax forms and do not make cage-like architectures. We suggest, therefore, that many New Zealand divaricates have a unique amalgam of traits that (i) conferred resistance to moa browsing and also (ii) provided protection of leaves from climate extremes for shrubs growing in the open in a south temperate climate.

6. CONCLUSIONS

Evolutionary anachronisms are difficult to identify and challenging to study. Nowhere is this better exemplified than in New Zealand where debate over the function of divaricate branching has continued for decades. Yet, as Janzen (1986) noted, 'vegetation cannot be understood solely through a consideration of contemporary physiology, weather, and interactions with contemporary native animals'. In Madagascar and elsewhere, we also need to consider the selective forces generated by extinct megafauna. In this study, we did so by exploring trait convergence in different climatic and faunal settings. Our results show convergence in plant architectural traits between New Zealand divaricates and Malagasy wire plants despite the very different climate and phylogenetic origins of the vegetation. In contrast, Malagasy wire plants showed striking divergence

from southern African thicket species despite similar climates and shared phylogenetic origins. Their absence in Africa is consistent with the incompatibility of structural defences against both ratite and ungulate browsers. Based on our analyses, we interpret the wire plant syndrome as an anachronistic structural defence against browsing by extinct elephant birds. The defence has evolved repeatedly in many lineages in Madagascar.

We thank Joel Ratsirarson, Jeannin Ranaivonasy, Pierre-Jules (Coca) Rakotomalaza and Rachel Prunier, in Madagascar, and Winifred Bond and Matt Waldram, in South Africa, for their invaluable field assistance. Cynthia Jones, Steve Goodman, Margaret Rubega, Carl Schlichting and Bob Dewar provided critical comment on an earlier version of the manuscript. W.B. was funded by the University of Cape Town and the National Research Foundation of South Africa. J.S. and W.B. were also supported by a grant from the University of Connecticut.

REFERENCES

- Amadon, D. 1947 An estimated weight of the largest known bird. *Condor* **49**, 159–164. (doi:10.2307/1364110)
- Appelquist, W. L. & Wallace, R. S. 2003 Expanded circumscription of Didiereaceae and its division into three subfamilies. *Adansonia* **25**, 13–16.
- Archibald, S. & Bond, W. J. 2003 Growing tall vs. growing wide: tree architecture and allometry of *Acacia karroo* in forest, savanna, and arid environments. *Oikos* **102**, 3–14. (doi:10.1034/j.1600-0706.2003.12181.x)
- Atkinson, I. A. E. 1992 A method for measuring branch divergence and interlacing in woody plants. DSIR Land Resources Technical Record, vol. 86, p. 19. Lower Hutt, New Zealand: DSIR Land Resources.
- Atkinson, I. A. E. & Greenwood, R. M. 1989 Relationships between moas and plants. In *Moas, mammal and climate in the ecological history of New Zealand* (ed. M. R. Rudge). *New Zeal. J. Ecol.* **12**(Suppl.) 67–96.
- Barlow, C. 2000 *The ghosts of evolution*. New York, NY: Basic Books.
- Bond, W. J., Lee, W. G. & Craine, J. M. 2004 Plant structural defences against avian browsers: the legacy of New Zealand's extinct moas. *Oikos* **104**, 500–508. (doi:10.1111/j.0030-1299.2004.12720.x)
- Breiman, L., Friedman, J. H., Olshen, R. A. & Stone, C. J. 1984 *Classification and regression trees*. Monterey, CA: Wadsworth & Brooks/Cole Advanced Books & Software.
- Burney, D. A. & Flannery, T. F. 2005 Fifty millennia of catastrophic extinctions after human contact. *Trends Ecol. Evol.* **20**, 395–401. (doi:10.1016/j.tree.2005.04.022)
- Burney, D. A., Burney, L. P., Godfrey, L. R., Jungers, W. L., Goodman, S. M., Wright, H. T. & Jull, A. J. T. 2004 A chronology for late prehistoric Madagascar. *J. Hum. Evol.* **47**, 25–63. (doi:10.1016/j.jhevol.2004.05.005)
- Burnham, K. P. & Anderson, D. R. 2002 *Model selection and inference a practical information-theoretic approach*, 2nd edn. New York, NY: Springer.
- Christian, R., Kelly, D. & Turnbull, M. T. 2006 The architecture of New Zealand's divaricate shrubs in relation to light adaptation. *New Zeal. J. Bot.* **44**, 171–186.
- Cooper, S. M. & Owen-Smith, N. 1986 Effects of plant spinescence on large mammalian herbivores. *Oecologia* **68**, 446–455. (doi:10.1007/BF01036753)
- Cooper, A., Lalueza-Fox, C., Anderson, S., Rambaut, A., Austin, J. & Ward, R. 2001 Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. *Nature* **409**, 704–707. (doi:10.1038/35055536)
- Cowling, R. M., Proche, S. & Vlok, J. H. J. 2005 On the origin of southern African subtropical thicket vegetation. *S. Afr. J. Bot.* **71**, 1–23.

- Cracraft, J. 1974 Phylogeny and evolution of the ratite birds. *Ibis* **116**, 494–521.
- Day, J. S. 1998 Light conditions and the evolution of heteroblasty (and the divaricate form) in New Zealand. *New Zeal. J. Ecol.* **22**, 43–54.
- De'ath, G. & Fabricius, K. E. 2000 Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* **81**, 3178–3192. (doi:10.2307/177409)
- Dean, W. R. J. 1997 Family Struthionidae: ostrich. In *The atlas of southern African birds*, vol. 1 (eds J. A. Harrison, D. G. Allan, L. G. Underhill, M. Herremans, A. J. Tree, V. Parker & C. J. Brown). Non-passerines, pp. 2–3. Johannesburg, Republic of South Africa: Birdlife South Africa.
- Dewar, R. E. 1984 Extinctions in Madagascar: the loss of the subfossil fauna. In *Quaternary extinctions: a prehistoric revolution* (eds P. S. Martin & R. G. Klein), pp. 574–593. Tucson, AZ: University of Arizona Press.
- Eskildsen, L. I., Olesen, J. M. & Jones, C. G. 2004 Feeding response of the Aldabra giant tortoise (*Geochelone gigantea*) to island plants showing heterophylly. *J. Biogeogr.* **31**, 1785–1790. (doi:10.1111/j.1365-2699.2004.01092.x)
- Gans, C. 1969 Comments on inertial feeding. *Copeia* **4**, 855–857. (doi:10.2307/1441816)
- Gautier, L. & Goodman, S. M. 2003 Introduction to the flora of Madagascar. In *The natural history of Madagascar* (eds S. M. Goodman & J. P. Benstead), pp. 229–249. Chicago, IL: The University of Chicago Press.
- Goodman, S. M., Ganzhorn, J. U. & Rakotondravony, D. 2003 Introduction to the mammals. In *The natural history of Madagascar* (eds S. M. Goodman & J. P. Benstead), pp. 1159–1187. Chicago, IL: The University of Chicago Press.
- Greenwood, R. M. & Atkinson, I. A. E. 1977 Evolution of the divaricating plants in New Zealand in relation to moa browsing. *Proc. New Zeal. Ecol. Soc.* **24**, 21–33.
- Grubb, P. J. 1992 A positive distrust in simplicity—lessons from plant defenses and from competition among plants and animals. *J. Ecol.* **80**, 585–611. (doi:10.2307/2260852)
- Grubb, P. J. 2003 Interpreting some outstanding features of the flora and vegetation of Madagascar. *Perspect. Plant Ecol. Evol. Syst.* **6**, 125–146. (doi:10.1078/1433-8319-00046)
- Hansen, I., Brimer, L. & Mølgaard, P. 2004 Herbivore-detering secondary compounds in heterophyllous woody species of the Mascarene Islands. *Perspect. Plant Ecol. Evol. Syst.* **6**, 187–203. (doi:10.1078/1433-8319-00077)
- Howell, C. J., Kelly, D. & Turnbull, M. T. H. 2002 Moa ghosts exorcised? New Zealand's divaricate shrubs avoid photo-inhibition. *Funct. Ecol.* **16**, 232–240. (doi:10.1046/j.1365-2435.2002.00613.x)
- Janzen, D. H. 1986 Chihuahuan desert nopaleras: defaunated big mammal vegetation. *Ann. Rev. Ecol. Syst.* **17**, 595–636. (doi:10.1146/annurev.es.17.110186.003115)
- Janzen, D. H. & Martin, P. S. 1982 Neotropical anachronisms: the fruits the gomphotheres ate. *Science* **215**, 19–27. (doi:10.1126/science.215.4528.19)
- Kelly, D. 1994 Towards a numerical definition for divaricate (interlaced small-leaved) shrubs. *New Zeal. J. Bot.* **32**, 509–518.
- Kelly, D. & Ogle, M. R. 1990 A test of the climate hypothesis for divaricate plants. *New Zeal. J. Ecol.* **13**, 51–61.
- Koechlin, J., Guillaumet, J.-L. & Morat, P. 1974 *Flore et végétation de Madagascar*. Vaduz, Germany: J. Cramer Verlag.
- Martin, P. S. & Klein, R. G. (eds) 1984 *Quaternary extinctions: a prehistoric revolution*. Tucson, AZ: University of Arizona Press.
- McGlone, M. S. & Clarkson, B. D. 1993 Ghost stories: moa, plant defenses and evolution in New Zealand. *Tuatara* **32**, 1–21.
- McGlone, M. S. & Webb, C. J. 1981 Selective forces influencing the evolution of divaricating plants. *New Zeal. J. Ecol.* **4**, 20–28.
- McQueen, D. R. 2000 Divaricating shrubs in Patagonia and New Zealand. *New Zeal. J. Ecol.* **24**, 69–80.
- Milewski, A. V., Young, T. P. & Madden, D. 1991 Thorns as induced defenses—experimental evidence. *Oecologia* **86**, 70–75. (doi:10.1007/BF00317391)
- Milton, S. J., Dean, W. R. J. & Siegfried, W. R. 1994 Food selection by ostrich in southern Africa. *J. Wildlife Manage.* **58**, 234–248. (doi:10.2307/3809386)
- Owen-Smith, N. & Ogotu, J. 2003 Rainfall influences on ungulate population dynamics. In *The Kruger experience: ecology and management of savanna heterogeneity* (eds J. T. du Toit, K. H. Rogers & H. C. Biggs), pp. 310–331. Washington, USA: Island Press.
- Rauh, W. 1995 *Succulent and xerophytic plants of Madagascar*. Mill Valley, CA: Strawberry Press.
- Skead, C. J. 1980 *Historical mammal incidence in the Cape Province. The western and northern Cape*, vol. 1. Cape Town, Republic of South Africa: CDNEC, Cape Provincial Administration.
- Skead, C. J. 1987 *Historical mammal incidence in the Cape Province. The eastern half of the cape Province including the Ciskei, Transkei and East Griqualand*, vol. 2. Cape Town, Republic of South Africa: CDNEC, Cape Provincial Administration.
- StatSoft, Inc. 2004 STATISTICA (data analysis software system), version 7. See <http://www.statsoft.com>.
- Vlok, J. H. J., Euston-Brown, D. I. W. & Cowling, R. M. 2003 Acocks' valley Bushveld 50 years on: new perspectives on the delimitation, characterization and origin of subtropical thicket vegetation. *S. Afr. J. Bot.* **69**, 27–51.
- Wardle, P. 1991 *Vegetation of New Zealand*. Cambridge, UK: Cambridge University Press.
- Worthy, T. H. 1990 An analysis of the distribution and relative abundance of moa species (Aves: Dinornithiformes). *New Zeal. J. Zool.* **17**, 213–241.
- Worthy, T. H. & Holdaway, R. N. 2002 *The lost world of the moa*. Bloomington, IN: Indiana University Press.
- Zweers, G. A., Berge, J. C. V. & Berhoudt, H. 1997 Evolutionary patterns of avian trophic diversification. *Zoology* **100**, 25–57.