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Feathers to Fur

The ecological transformation of Aotearoa/New Zealand

Legacy of avian-dominated plant–herbivore systems in New Zealand

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Abstract: Avian herbivores dominated New Zealand's pre-settlement terrestrial ecosystems to an unparalleled extent, in the absence of a terrestrial mammal fauna. Approximately 50% (88 taxa) of terrestrial bird species consumed plant foliage, shoots, buds and flowers to some degree, but fewer than half these species were major herbivores. Moa (Dinornithiformes) represent the greatest autochthonous radiation of avian herbivores in New Zealand. They were the largest browsers and grazers within both forest and scrubland ecosystems. Diverse waterfowl (Anatidae) and rail (Rallidae) faunas occupied forests, wetlands and grasslands. Parrots (Psittacidae) and wattlebirds (Callaeidae) occupied a range of woody vegetation types, feeding on fruits/seeds and foliage/fruits/nectar, respectively. Other important herbivores were the kereru (Columbidae), stitchbird (Notiomystidae) and two honeyeaters (Meliphagidae). Cryptic colouration, nocturnal foraging and fossil evidence suggest that avian populations were strongly constrained by predation. With the absence of migratory avian herbivores, plant structural, constitutive defences prevailed, with the unusual 'wire syndrome' representing an adaptation to limit plant offtake by major terrestrial avian browsers. Inducible plant defences are rare, perhaps reflecting long-standing nutrient-limitations in New Zealand ecosystems. Evidence from coprolites suggests moa were important dispersers of now rare, annual, disturbance-tolerant herb species, and their grazing may have maintained diverse prostrate herbs in different vegetation types. The impact of moa on forest structure and composition remains speculative, but many broadleaved woody species would likely have experienced markedly reduced niches in pre-settlement time. Several distinctive avian-mediated vegetation types are proposed: dryland woodlands, diverse turf swards, coastal herb-rich low-forest-scrubland, and conifer-rich forests. Since human settlement (c. 750 yrs ago), c. 50% of endemic avian herbivore species or c. 40% overall have become extinct, including all moa, 60% of waterfowl and 33% of rail species. Numerically, avian herbivore introductions (c. 24 taxa) since European settlement have compensated for extinctions (c. 27 taxa), but the naturalised birds are mostly small, seed-eating species restricted to human-modified landscapes. Several naturalised species (e.g. Canada goose, *Branta canadensis*; brown quail, *Coturnix ypsilophorus*) may provide modes and levels of herbivory comparable with extinct species. The original avian and current introduced mammal herbivore regimes were separated by several centuries when New Zealand lacked megaherbivores. This 'herbivory hiatus' complicates comparisons between pre-settlement and current herbivore systems in New Zealand. However, predation, animal mobility, feeding mode, nutrient transfer patterns and soil impacts were different under an avian regime compared with current mammalian herbivore systems. Levels of ecological surrogacy between avifauna and introduced mammals are less evident. Ungulates generally appear to have impacts qualitatively different from those of the extinct moa. Because of New Zealand's peculiar evolutionary history, avian herbivores will generally favour the persistence of indigenous vegetation, while mammalian herbivores continue to induce population declines of select plant species, change vegetation regeneration patterns, and generally favour the spread and consolidation of introduced plant species with which they share an evolutionary history.

Keywords: divaricate; filiramulate; folivory; island ecosystems; plant-herbivore interactions; seed predation

Introduction

The 1989 symposium supplement to the *New Zealand Journal of Ecology* entitled "Moa, mammals and climate in the ecological history of New Zealand" represented a watershed in our thinking about the role of plant herbivores in the development of New Zealand vegetation. Prior to the symposium (held in 1986), avian herbivory was rarely considered a major factor in the

evolution of New Zealand plants and ecosystems (Cockayne 1921). Previous ecological paradigms regarding the levels of avian herbivory, presence of herbivore-resistant features in indigenous plants, and the major historical changes in plant–herbivore systems were challenged at this conference and revised in light of new research. The general consensus in the mid-1980s was that New Zealand terrestrial ecosystems had a long history of significant avian herbivory (Burrows 1989; Clout & Hay 1989), and that in response to this selection pressure many woody and herbaceous plant species appeared to have evolved structural features to deter vertebrate herbivores (Atkinson & Greenwood 1989). Caughley (1989) suggested that recent (i.e. post AD 1850) mammal-dominated herbivore systems had more in common with pre- and early settlement avian-dominated systems than with the 'herbivore hiatus' (c. AD 1450–1850) period following the avian extinctions prior to European introduction of mammals. However, less consideration was given to how the shift in herbivore guilds, from avian to mammal-dominated, might influence conservation management goals and strategies.

In this paper we review generalisations regarding avian herbivory presented at the 1986 symposium, assess their status after a further two decades of research, identify several new themes that need to be considered, and discuss the relevance of past herbivory to current conservation issues regarding the control of introduced mammalian herbivores. The 1986 symposium had a forest focus, which we depart from in order to recognise the breadth of vertebrate herbivory in New Zealand non-forest vegetation types. We also concentrate on herbivory as a disturbance, and largely ignore the role of birds as seed dispersers and pollinators as these are covered by Kelly et al. (2010).

Avian dominance

The dominance of herbivorous birds in New Zealand is striking, yet few authors have tried to explain why such supremacy might have developed on a remote southern archipelago. Evolutionary diversification and speciation of birds in New Zealand into niches typically occupied by mammals elsewhere is generally explained on the basis of the paucity of competing terrestrial mammals during the Cenozoic. However, early Zealandia ought to have contained a mammalian fauna similar to that of eastern Gondwana at the time of complete separation at c. 60 million years ago (Gaina et al. 1998). This included monotremes as well as placental and marsupial representatives (Archer et al. 1985; Godthelp et al. 1992). Currently, fossil evidence exists for only one non-volant, mouse-sized mammal (of unknown taxonomic relationship) from New Zealand during the Cenozoic (Worthy et al. 2006). Recent divergence estimates suggest the presence of several major avian lineages on Zealandia at the time of continental fragmentation (e.g. wrens; Ericson et al. 2002). An explanation for avian dominance must lie in the geographical and ecological history of New Zealand. Flannery (1994) suggests that higher fecundity, mobility and perhaps competitive resistance of birds may have effectively suppressed mammalian diversification and colonisation on a small landmass, especially during the maximum marine transgression in the Oligocene. However, it is possible that the 'land of birds' may be a relatively recent phenomenon, with late Tertiary climate deterioration in the south-west Pacific potentially resulting in the extinction of some fauna (e.g. mammals, crocodiles) in New Zealand (Worthy et al. 2006).

Avian herbivores

Pre-settlement avian herbivores

Since 1986, our understanding of the taxonomy, ecology and distribution of pre-settlement bird species has been substantially advanced through excavation of recently discovered fossil deposits and review of fossil bones in museum collections (e.g. Holdaway & Worthy 1997; Worthy 1998a, b; Worthy & Holdaway 1993, 1994a, 1995, 1996), analyses of coprolites and gizzard contents (Horrocks et al. 2004; Wood 2007a; Wood et al. 2008), stable isotope analyses (e.g. Hawke et al. 1999; Worthy & Holdaway 2002: 212–215; Holdaway et al. 2007), and the development of techniques to investigate ancient-DNA (e.g. Bunce et al. 2003; Huynen et al. 2003; Baker et al. 2005; Haile et al. 2007). Such studies have enabled us to determine the composition of pre-settlement avifaunal communities, distinguish regional faunas, and better understand habitat use and diets, while also providing insights into predator impacts. The following account emphasises the advances made since Atkinson and Millener's (1991) overview of New Zealand avian guilds, and augments the influential work of Worthy and Holdaway (2002).

Herbivore guilds

Worthy and Holdaway (2002) presented a combination of trophic and behavioural avian guilds, differentiating herbivores on the basis of food type (foliage, fruit, nectar), access to the woody vegetation canopy (terrestrial, arboreal), and foraging behaviour (nocturnal, diurnal). While approximately 60 pre-settlement terrestrial bird species fed on plant material to some extent (Table 1), Worthy and Holdaway (2002) confined the dominantly terrestrial herbivore guild to the extinct moa, North Island takahe (*Porphyrio mantelli*), South Island goose (*Cnemiornis calcitrans*), North Island goose (*C. gracilis*), New Zealand coot (*Fulica prisca*), Hodgen's waterhen (*Gallinula hodgenorum*) and Finsch's duck (*Chenonetta finschi*), and the extant kakapo (*Strigops habroptilus*), South Island takahe (*Porphyrio hochstetteri*) and paradise shelduck (*Tadorna variegata*). Other important avian herbivores are assigned to the guilds of arboreal herbivores (kaka, *Nestor meridionalis*; kereru, *Hemiphaga novaeseelandiae*; South Island kokako, *Callaeas cinerea*; North Island kokako, *C. wilsoni*), arboreal–terrestrial herbivores (kakapo; red-crowned parakeet, *Cyanoramphus novaezelandiae*) and arboreal nectarivores (kaka; stitchbird/hihi, *Notiomystis cincta*; bellbird/korimako, *Anthornis melanura*; tui, *Prosthemadera novaeseelandiae*). While guilds form a useful framework for examining ecological functioning of species, individual species often fit in more than one guild, and assigning extinct species to exact guilds can be difficult due to limited evidence of diet (e.g. adzebill, *Aptornis* spp.). Recent advances have helped clarify the diets and ecologies of some pre-settlement avian herbivores.

Moa

Current taxonomy recognises 10 species of moa in six genera (Worthy & Holdaway 2002; with amendments by Bunce et al. 2003; Huynen et al. 2003; Worthy 2005; cf. Tennyson 2010 who recognises nine species). Species range from c. 35 to 250 kg and sexual dimorphism is apparent in several, but most extreme in the two species of *Dinornis*, where females were almost three times heavier than males (Bunce et al. 2003). Recent reviews of moa ecology, coupled with reconstructions of pre-settlement vegetation, point to both habitat and ecological guild segregation or specialisation as

Table 1. Summary of herbivory in the mainland New Zealand avifauna (based on a wide range of literature, with extinct species data from historical observations, fossil evidence, or estimated based on diets of closely related taxa). † = extinct.

Family	Species	Status	Broad diet categories
Emeidae	*Anomalopteryx didiformis* (little bush moa)	Endemic †	wood, leaf, fruit, seed
	Emeus crassus (Eastern moa)	Endemic †	leaf, fruit, seed, wood
	Euryapteryx curtus (coastal moa)	Endemic †	leaf, fruit, seed
	E. gravis (stout-legged moa)	Endemic †	leaf, fruit, seed
	Megalapteryx didinus (upland moa)	Endemic †	wood, leaf, fruit, seed
	Pachyornis australis (crested moa)	Endemic †	wood, leaf, fruit, seed
	P. elephantopus (heavy-footed moa)	Endemic †	wood, leaf, fruit, seed
	P. geranoides (Mappin's moa)	Endemic †	wood, leaf, fruit, seed
Dinornithidae	*Dinornis robustus* (South Island giant moa)	Endemic †	wood, leaf, fruit, seed
	D. novaezealandiae (North Island giant moa)	Endemic †	wood, leaf, fruit, seed
Apterygidae	*Apteryx australis* (Southern brown kiwi)	Endemic	leaf, fruit
	A. mantelli (North Island brown kiwi)	Endemic	fruit, leaf
	A. owenii (little spotted kiwi)	Endemic	fruit
Anatidae	*Cygnus atratus* (black swan)	Native	leaf, aquatic plants
	Cnemiornis calcitrans (South Island goose)	Endemic †	leaf, seed, fruit
	C. gracilis (North Island goose)	Endemic †	leaf, seed, fruit
	Branta canadensis (Canada goose)	Introduced	leaf, seed
	Anser anser (feral goose)	Introduced	leaf, seed
	Chenonetta finschi (Finsch's duck)	Endemic †	leaf, seed
	Tadorna variegata (paradise shelduck)	Endemic	leaf, seed
	Hymenolaimus malacorhynchos (blue duck)	Endemic	fruit
	Anas platyrhynchos (mallard)	Introduced	seed, leaf, aquatic plants
	A. superciliosa (grey duck)	Native	seed, leaf, aquatic plants
	Oxyura vantetsi (New Zealand stiff-tailed duck)	Endemic †	aquatic plants
	Biziura delautouri (New Zealand musk duck)	Endemic †	aquatic plants
	Athya novaeseelandiae (New Zealand scaup)	Endemic	aquatic plants
Phasianidae	*Callipepla californica* (California quail)	Introduced	seed
	Synoicus ypsilophorus (brown quail)	Introduced	leaf, seed
	C. novaezelandiae (New Zealand quail)	Endemic †	leaf, seed
	Meleagris gallopavo (turkey)	Introduced	leaf
Rallidae	*Rallus philippensis* (banded rail)	Native	seed, fruit, leaf
	G. australis (weka)	Endemic	leaf, fruit
	Porzana tabuensis (spotless crake)	Native	seed, fruit, leaf, aquatic plants
	Gallinula hodgenhorum (Hodgen's waterhen)	Endemic †	seed, leaf, aquatic plants
	Porphyrio porphyrio (pukeko)	Native	leaf, rhizome, seed, aquatic plants
	P. hochstetteri (South Island takahe)	Endemic	leaf, rhizome, flower, seed
	P. mantelli (North Island takahe)	Endemic †	leaf, rhizome, flower, seed
	Fulica prisca (New Zealand coot)	Endemic †	fruit, leaf, seed, aquatic plants
	F. atra (Australian coot)	Native	fruit, leaf, seed, aquatic plants
Laridae	*Larus novaehollandiae* (red-billed gull)	Native	fruit
Columbidae	*Hemiphaga novaeseelandiae* (New Zealand pigeon)	Endemic	leaf, fruit, flower, shoot
	Columba livia (rock pigeon)	Introduced	seed
	Streptopelia roseogrisea (Barbary dove)	Introduced	seed
	S. chinensis (spotted dove)	Introduced	seed
Cacatuidae	*Cacatua galerita* (sulphur-crested cockatoo)	Introduced	seed, fruit, leaf
	C. roseicapilla (galah)	Introduced	leaf
Psittacidae	*Strigops habroptilus* (kakapo)	Endemic	leaf, seed, fruit, rhizome, wood
	Nestor meridionalis (kaka)	Endemic	fruit, nectar, sap, leaf, seed
	N. notabilis (kea)	Endemic	leaf, fruit, seed, flower, rhizome
	Platycerus eximus (Eastern rosella)	Introduced	nectar, flower, fruit, seed, leaf
	P. elegans (crimson rosella)	Introduced	nectar, flower, fruit, seed, leaf
	Cyanoramphus novaezelandiae (red-crowned parakeet)	Endemic	seed, fruit, leaf
	C. auriceps (yellow-crowned parakeet)	Endemic	fruit, seed, leaf
Cuculidae	*Eudynamys taitensis* (long-tailed cuckoo)	Endemic	seed
Acanthisittidae	*Acanthasitta chloris* (rifleman)	Endemic	fruit
Alaudidae	*Alauda arvensis* (skylark)	Introduced	seed, leaf
Sylviidae	*Bowdleria punctata* (fernbird)	Endemic	fruit
Motacillidae	*Anthus novaeseelandiae* (New Zealand pipit)	Native	seed
Prunellidae	*Prunella modularis* (dunnock)	Introduced	seed
Muscicapidae	*Turdus merula* (blackbird)	Introduced	fruit
	T. philomelos (song thrush)	Introduced	fruit
Pachycephalidae	*Mohoua albicilla* (whitehead)	Endemic	fruit, seed
	M. ochrocephala (yellowhead)	Endemic	fruit, nectar
	M. novaeseelandiae (brown creeper)	Endemic	fruit, nectar
Acanthizidae	*Gerygone igata* (grey warbler)	Endemic	fruit
Monarchidae	*Rhipidura fuliginosa* (fantail)	Native	fruit, nectar

Table 1 continued

Family	Species	Status	Broad diet categories
Eopsaltriidae	*Petroica macrocephala* (tomtit)	Endemic	fruit
	P. australis (robin)	Endemic	fruit
Zosteropidae	*Zosterops lateralis* (silvereye)	Native	fruit, nectar
Notiomystidae	*Notiomystis cincta* (stitchbird)	Endemic	nectar, fruit
Meliphagidae	*Anthornis melanura* (bellbird)	Endemic	nectar, fruit, sap
	Prosthemadera novaeseelandiae (tui)	Endemic	fruit, nectar
Emberizidae	*Emberiza citrinella* (yellowhammer)	Introduced	seed
	E. cirlus (cirl bunting)	Introduced	seed
Fringillidae	*Fringilla coelebs* (chaffinch)	Introduced	seed, fruit
	Cardeulis chloris (greenfinch)	Introduced	seed, fruit
	C. cardeulis (goldfinch)	Introduced	seed, fruit
	C. flammea (redpoll)	Introduced	seed, fruit
Ploceidae	*Passer domesticus* (house sparrow)	Introduced	fruit, seed
Sturnidae	*Sturnus vulgaris* (starling)	Introduced	fruit, seed, nectar
	Acridotheres tristis (myna)	Introduced	fruit, nectar
Callaeidae	*Callaeas cinerea* (South Island kokako)	Endemic †	fruit, leaf?
	C. wilsoni (North Island kokako)	Endemic	leaf, fruit
	Philesturnus carunculatus (saddleback)	Endemic	fruit, nectar
	Heteralocha acutirostris (huia)	Endemic †	fruit
Cracticidae	*Gymnorhina tibicen* (Australian magpie)	Introduced	seed
Paradisaeidae	*Turnagra capensis* (South Island piopio)	Endemic †	fruit, seed, leaf
	T. tanagra (North Island piopio)	Endemic †	fruit, seed, leaf
Corvidae	*Corvus frugilegus* (rook)	Introduced	seed, leaf

the drivers of evolutionary diversification in moa, perhaps in response to changing vegetation patterns and landscapes since the Miocene. The geographic distribution of moa species was analysed by Worthy and Holdaway (2002), who identified at least three distinct assemblages in the South Island during the Holocene: a wet western beech forest assemblage consisting of South Island giant (*Dinornis robustus*) and little bush (*Anomalopteryx didiformis*) moas; an assemblage from the relatively dry eastern forests and scrublands, consisting of South Island giant, eastern (*Emeus crassus*), heavy-footed (*Pachyornis elephantopus*) and stout-legged (*Euryapteryx gravis*) moas; and an assemblage from upland and subalpine areas consisting of South Island giant, crested (*Pachyornis australis*) and upland (*Megalapteryx didinus*) moas (see also Forsyth et al. 2010; and Tennyson 2010, who reviews recent taxonomic changes).

Evolutionary diversification in moa involved the development of sharply contrasting body proportions, as well as morphological diversification, including beak shapes and sizes that reflect adaptation to preferred habitats as well as sexual dimorphism (Worthy & Holdaway 2002; Tennyson & Martinson 2006). In forest, where predation pressure from *Harpogornis* was limited to canopy gaps, tall-statured *Dinornis* was separated from shorter and slender *Anomalapteryx*, yet both had diets high in fibre. In dry eastern forests, scrub and dunelands, where vulnerability to aerial predation increased, a group of gravi-portal species were niche-specialised to diets of coarse fibre (*Pachyornis elephantopus*) and softer tissue (*Euryapteryx* and *Emeus*). Stands of low forest in the east provided predator-buffered habitat for *Dinornis* but not slender *Anomalapteryx*, which would have been out-competed by the other eastern stocky species. Gracile *Megalapteryx* and gravi-portal *P. australis* shared steeper and upland topography, with the former being a specialised soft tissue feeder with agility for predator avoidance in open vegetation, whereas the latter coped with fibrous plant parts and may have been nocturnal.

Our understanding of moa diet has expanded considerably over the last decade. Further direct evidence has been obtained based on analysis of plant remains from moa gizzard contents (Wood 2007a) and desiccated droppings, or coprolites (Horrocks et al. 2004; Wood et al. 2008). Recently, ancient DNA analysis has been used to identify coprolites from several different moa species (Wood 2007b; Wood et al. 2008). Direct evidence of moa diet has now been recovered and analysed for five moa species. Evidence includes plant remains from 24 gizzard content samples and 121 coprolites. Results are summarised in Table 2.

Wood (2007a) analysed gizzard content samples and provided the first direct evidence of diet for heavy-footed moa. The samples included sections of flax (*Phormium tenax*) leaves and clipped twigs up to 8 mm in diameter, revealing the powerful bite force of this moa species. Gizzard content samples from South Island giant moa and eastern moa were also examined. Results supported previous studies (Falla 1941; Gregg 1972; Burrows et al. 1981) that suggested eastern moa fed mostly on fruit and leaves, whereas South Island giant moa was a generalist browser whose diet included a significant woody component.

However, there is some debate over how accurately gizzard content samples reflect the true dietary range of moa species, and it has been suggested that they are likely to be biased towards vegetation in forest/swamp-margin habitat (reflecting preservation sites) or vegetation within reach of a mired bird (Batcheler 1989; Wood 2007a). Recent studies using coprolites have revealed more about the diets of moa in a range of habitat types. Perhaps the most surprising results were the extent to which moa grazed low herbs in some habitats. Horrocks et al. (2004) analysed five coprolites from Takahe Valley, Fiordland, putatively attributed to upland moa. They concluded that this species fed on fibrous, low-calorie twigs and leaves, but that tussockland and lake-edge herbs were also an important diet component. Coprolites from Central Otago and the Dart River Valley, West Otago, identified by ancient DNA analysis as having been deposited by South Island giant moa, heavy-footed moa and upland moa, were examined by Wood et al. (2008). More than half of the plant taxa identified

Table 2. Diet of moa compared to diet of ungulates. Moa diet recorded from plant macrofossils in gizzard and coprolite samples: S, seed, fruit, female cone; C, male cone; L, leaf or petiole; P, pinna; T, twig; B, bark. Uppercase, common (>10) or frequent across samples; lowercase, rare (<10) and/or infrequent across samples. Also shown are whether plant taxa have been recorded being eaten by ungulates, and ungulate diet preference ranking from Forsyth et al. (2002): Y = yes; n = no; + = preferred, 0 = not selected; - = avoided. Symbols in parentheses show no ranking available in Forsyth et al. (2002) but ranked by us from field observation. Blanks indicate no ranking by Forsyth et al. (2002) or the present authors.

Reference (with moa genera covered)	Falla (1941): *Emeus, Dinornis*	Gregg (1972): *Dinornis, Euryapteryx, Emeus*	Burrows et al. (1981): *Dinornis*	Horrocks et al. (2004): *Megalapteryx?*	Wood (2007): *Dinornis, Emeus, Pachyornis*	Wood et al. (2008): *Dinornis, Pachyornis, Megalapteryx, Euryapteryx*	Plant eaten by ungulates	Ungulate diet preference
Gymnosperm								
Prumnopitys taxifolia	S	S, L, C	S, L		S, L		y	-
Dacrycarpus dacrydioides		T			L		y	-
Phyllocladus sp.		l		L			y	-
Podocarpus spp,		L			L		y	-
Gymnosperm						s, l	y	(-)
Dicotyledon								
Nothofagus spp.				S, l			y	-
Nothofagus menziesii						l	y	-
Plagianthus regius			s, T, b				y	
Hoheria/Plagianthus					t		y	
Elaeocarpus hookerianus			s		S		y	0
Carpodetus serratus			s		S		y	0, -
Pennantia corymbosa			s		S		y	0
Pseudopanax ferox			S, l				n	
Pittosporum sp.		S			s		y	+, 0
Myoporum laetum	S						y	-
Melicope simplex		S					y	-
?*Aristotelia*?*Pseudopanax anomolus*				L			y	(-)
Coprosma spp.		S	S	L	S	S, L	y	0
Coprosma rhamnoides	S	S					y	0
Coprosma rotundifolia		S	S				Y	(-)
Coprosma cuneata					s		y	(-)
Coprosma sp. cf. *microcarpa*			S		s		y	(-)
Coprosma sp. cf. *robusta*			S				y	+
Coprosma petriei						S	n	(-)
Coprosma wallii					s		n	
Corokia cotoneaster		S			S		y	0
Coriaria plumosa						S	y	(-)
Melicytus sp.						s	y	(+)
Myrsine divaricata			S, L		l		y	0
Muehlenbeckia spp.			S				y	0
Muehlenbeckia australis	S						y	0
Muehlenbeckia axillaris						S	n	(-)
Rubus spp.		S, T, L	S, L, T		S	s, T	y	0,-
Calystegia sepium					s		n	
Tetrapathaea tetrandra			s				n	
Clematis sp.			s				y	+, 0
cf. *Androstoma* [*Cyathodes*] *empetrifolia*					s		n	(-)
Leptospermum scoparium			L		S		y	-
Lophomyrtus obcordata			s				y	-
Hebe sp.						l	y	(-)
Hebe cf. *pimeleoides*					L		y	(-)
Olearia virgata			T				n	(-)
Olearia sp.					T	s	y	+, -
Teucridium parviflorum			s				n	
Gaultheria crassa						S	y	(-)
Pimelea sp.			s				y	(-)
Euphrasia sp.				L			y	(-)
Ranunculus sp.						S	y	(-)
Ranunculus gracilipes					S	S	y	(-)
Nertera sp.	s						y	+, -
Carmichaelia	s	T				s	y	(+)
cf. *Einadia allanii*	s				S	S	n	(-)
Einadia triandra	s				S	S	n	(-)
Chenopodium sp. cf. *allanii*			S				n	(-)
Colobanthus sp.					s	S	y	(-)
Lagenifera pumila						S	n	(0)
Pratia angulata						S	Y	-
Ceratocephala pungens						S	n	(-)
Myosurus minimus subsp. *novae-zelandiae*						S	n	(-)
Myosotis pygmaea var. *pygmaea*						s	y	(-)

Table 2 continued

Reference (with moa genera covered)	Falla (1941): Emeus, Dinornis	Gregg (1972): Dinornis, Euryapteryx, Emeus	Burrows et al. (1981): Dinornis	Horrocks et al. (2004): Megalapteryx?	Wood (2007): Dinornis, Emeus, Pachyornis	Wood et al. (2008): Dinornis, Pachyornis, Megalapteryx, Euryapteryx	Plant eaten by ungulates	Ungulate diet preference
Oxalis exilis						S	y	-
Urtica incisa						S	y	-
Gonocarpus aggregatus						S	y	(-)
Leucopogon fraseri						L, S	y	(-)
Wahlenbergia pygmaea						S	y	(-)
Monocotyledon								
Poaceae				L		s		
Carex sp.		S	l, s	S		S	y	-
Carex secta		S	S	S			n	(-)
Cordyline australis		S			s		Y	+
Phormium tenax		S, L		L			Y	+
Baumea [Cladium] sp.		S					N	(-)
Eleocharis sp. cf. acuta					S		N	(-)
Juncus sp.						S	y	-
Isolepis sp.		s					n	(-)
Gaimardia sp.	s						n	(-)
Unidentified grass/sedge			L					
Fern								
Polystichum vestitum					P		y	+, -
Bryophytes								
Unidentified sp.			l	L		l	y	

in these coprolites grow to <30 cm in height, including herbs as small as *Ceratocephala pungens* and *Wahlenbergia pygmaea*. These represent feeding in the understorey of sparse shrubland (Central Otago), valley-floor grassland and early-successional communities associated with rockfalls (Dart River Valley).

Current sources of evidence (both direct analysis of coprolites and gizzard content, and indirect interpretations of moa skull morphology) indicate that, at the broadest level, *Dinornis*, *Anomalopteryx*, *Megalapteryx* and *Pachyornis* were capable of consuming coarse-fibre, whereas *Emeus* and *Euryapteryx* preferred soft-textured foods (Burrows et al. 1981; Batcheler 1989; Worthy & Holdaway 2002: 198–204; Horrocks et al. 2004; Wood 2007a; Wood et al. 2008). Furthermore, the frequent co-occurrence of herbaceous and woody plant material in the diet of South Island giant, heavy-footed, upland and eastern moas suggests a combined grazing–browsing feeding ecology for at least some species (Wood 2007a; Wood et al. 2008). This supports Holdaway's (1989) suggestion that adult moa had a low-quality, high-volume diet that included a diverse range of plant taxa, partly to avoid large doses of toxins from particular plant species, but also because they had a large trace element requirement, and their diet changed during growth to exploit plants of varying heights. Currently, insufficient evidence exists for determining levels of dietary variation between males and females of moa species. However, this might be expected to have existed in some instances, particularly in *Dinornis*, where females were significantly larger than males.

Other avian herbivores

Compared with moa, other terrestrial avian herbivores are less diverse and usually restricted by habitat or mobility. The greatest number of species and diversity occurred in the herb-feeding waterfowl and rails, which in New Zealand do not undergo seasonal migrations offshore. The waterfowl included flightless geese (*Cnemiornis* spp.), the flightless Finsch's duck and paradise shelduck. These birds fed on turf

and swards adjoining water bodies that would have offered refuge from predators.

Unpublished data from putative Finsch's duck coprolites indicate the species was dominantly herbivorous, and isotopic analysis of Finsch's duck bones reveals that in some regions it fed beneath dense canopy (Worthy & Holdaway 2002). Excavations in Central Otago rock shelters have uncovered v-shaped coprolites (Wood 2007b), similar in size and shape to droppings of the Australian wood duck (*Chenonetta jubata*). These are attributed to the closely related Finsch's duck, which was abundant in Central Otago prior to human settlement (Worthy 1998a). Initial examination suggests the coproplites are comprised mostly of grasses (Wood 2007b).

Five rail species also occupied a wide range of vegetation, perhaps alternating between grassland and forest seasonally, as takahe do in Fiordland today (Lee & Jamieson 2001). Major woody plant defoliators were limited to parea (*Hemiphaga chathamensis*) on the Chatham Islands (Powlesland et al. 1997); kereru (Clout et al. 1995), kakapo (Atkinson & Merton 2006; Butler 2006; Wilson et al. 2006) and kokako (NI, SI) (Powlesland 1987), which occurred throughout New Zealand. Their diets included foliage and fruits/seed of most broadleaved shrubs and trees, and occasionally ferns. The kakapo has the broadest dietary range of plant parts and species of any extant avian herbivore. It consumes leaves, roots, fruits, and seeds, of ferns, grasses, forbs, shrubs and trees. Currently, the kakapo appears to be the only avian herbivore to feed on the sclerophyllous leaves of *Dracophyllum* and the poisonous (at least for mammals) leaves and seed of *Coriaria*.

Temperate grasslands worldwide have a long evolutionary history and, in potentially forested regions, are usually maintained by large grazing mammals in association with fire (Craine & McLauchlan 2004). In New Zealand, biotic mechanisms for maintaining natural grasslands were limited, although takahe, kakapo, quail (*Coturnix novaezelandiae*) and moa would have grazed grasses, eaten seeds and browsed shrubs in these communities, while also foraging in adjoining forest.

Currently, within native grassland, avian herbivores generally eat grass seeds but show strong preferences for different plant parts and species. For example, takahe feed on immature leaf meristems while kakapo crush and digest the oldest portion of the leaf lamina, even when feeding on the same plant species (*Chionochloa rigida, Celmisia petriei*) in Fiordland (Lee & Jamieson 2001; Butler 2006). Both herbivores feed on leaves of *Carex, Schoenus* and *Carpha*, but overall there is surprisingly little overlap in diet.

Extreme inter-annual variability in reproduction among several New Zealand plant-feeding birds has now been linked to periodic heavy flowering of dominant tree species. Kakapo breeding tracks heavy rimu (*Dacrydium cupressinum*) fruiting in southern New Zealand (Harper et al. 2006), and breeding in some populations of kaka relies on availability of *Nothofagus* seed (Wilson et al. 1998). Both these parrots are usually seed predators of the masting species. Takahe feed heavily on the seeds and flowering-tiller bases of *Chionochloa* species when available in mast years, and this increase in food availability has a positive effect on breeding, due to increased clutch size and fledging success (Hegg 2008).

Evidence from predator-accumulation deposits and bone damage of prey (Worthy & Holdaway 1994b, 1996, 2002; Worthy & Zhao 2006) suggests strong predator-driven influences on herbivore foraging activity. This idea is reinforced when we consider the cryptic colouration, nocturnal or crepuscular feeding habits, and innate avoidance behaviours demonstrated by many native avian herbivores. The pre-settlement suite of avian predators included Haast's eagle (*Harpagornis moorei*), Eyles' harrier (*Circus eylesi*), NZ falcon (*Falco novaseelandiae*) (Seaton et al. 2008), laughing owl (*Sceloglaux albifacies*), morepork *(Ninox novaeseelandiae)* and possibly the adzebill. All except the eagle must have been active across habitats ranging from dense conifer forests to open grasslands. The eagle may have been more restricted to open, low-growing vegetation (Scofield & Ashwell 2009). Vegetation physiognomy rather than forest type appears to influence avian community composition (Worthy & Holdaway 2002), perhaps through increased predation pressure in low-statured vegetation types.

Avian herbivore extinctions

Human settlement of New Zealand over the last 750 years (Wilmshurst et al. 2008) precipitated a cascade of avian extinctions (Tennyson 2010), caused primarily by hunting and ongoing predation by introduced mammals, particularly rodents (*Rattus* spp.), mustelids (*Mustela* spp.) and possums (*Trichosurus vulpecula*) (Worthy & Holdaway 2002), exacerbated in some cases by habitat loss (Duncan et al. 2002). The result has been extinction of c. 50% of the major avian herbivores, including virtually all large flightless species (Fig. 1). Moa were clearly the major herbivore drivers of woody vegetation composition and structure, joined by waterfowl and rails in open herb-dominated habitats. Numerically, the greatest loss of species has been from forest and woodlands, particularly amongst shoot, foliage, fleshy fruit and seed feeders (Fig. 1). Most of these extinctions occurred within the first two hundred years of human settlement (late 13th century) (Holdaway & Jacomb 2000; Tennyson & Martinson 2006). This led to a substantial temporal gap in herbivore activity. The release of terrestrial ecosystems from intense avian herbivory affected not only plant removal and dispersal, but also the deposition and cycling of nutrients, and the intense reworking of litter and upper soil layers.

Naturalised avian herbivores

European settlement in the late 18th century saw the deliberate introduction of common avian species from the northern hemisphere and Australia (Thomson 1922; McDowell 1994). Species that established successfully were those released in large numbers that came from environments similar to those found in New Zealand (Duncan et al. 2002). Twenty seven of these were herbivorous species (Table 1). Columbidae (pigeons and doves), Phasianidae (turkeys, pheasants, partridges), Fringillidae (finches) and Emberizidae (buntings) are all represented by at least two species. Although similar in number to the indigenous avian species lost, the feeding modes and habitat preferences of the naturalised avifauna are strikingly different. Overall, there is a predominance of volant birds that feed on seed, small fleshy fruits and occasionally foliage
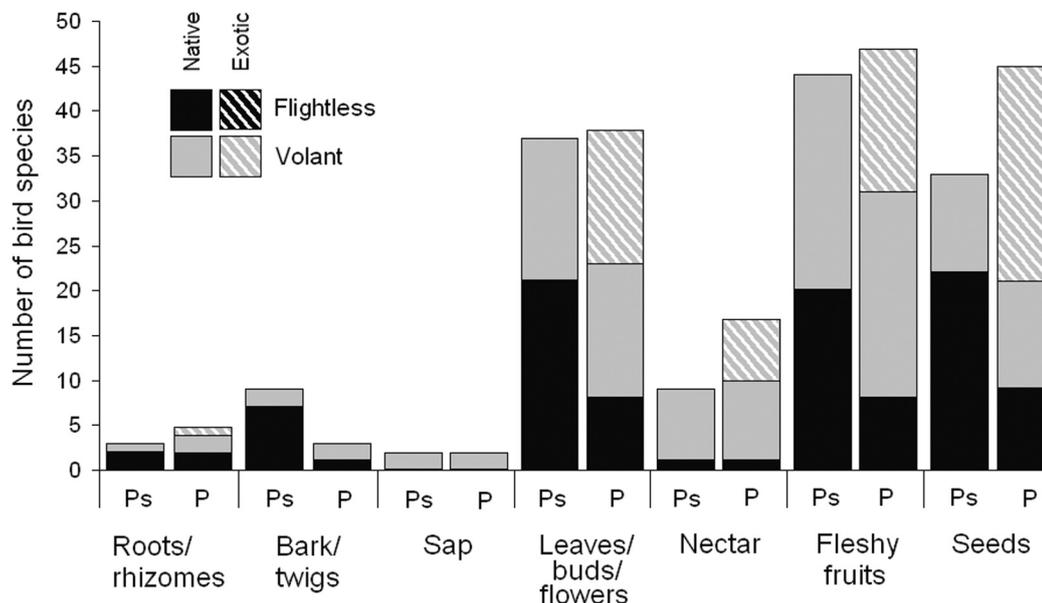

Figure 1. Comparison of herbivorous avifauna composition between pre-settlement (Ps) and Present (P).

and nectar, and that most frequently occur in agricultural and urban landscapes. The latest bird distribution data (Robertson et al. 2007) show that the most widespread (>50% occurrence) naturalised bird species are seed and/or fruit eaters: (blackbird, *Turdus merula*; chaffinch, *Fringilla coelebs*; house sparrow, *Passer domesticus*; yellowhammer, *Emberiza citrinella*; goldfinch, *Carduelis carduelis*; greenfinch, *C. chloris*; redpoll, *C. flammea*). Other seed eaters (rock pigeon, *Columba livia*; California quail, *Callipepla californica*) are also common (c. 40% occurrence), while the most widespread foliage eaters are Canada and feral goose (*Branta canadensis*; *Anser anser*) (c. 25% occurrence). The role of native vegetation in maintaining populations of these species is poorly understood, because most are relatively mobile, more abundant in areas of human settlement, and favour seeds from naturalised plant species (Williams & Karl 1996). Nevertheless, the naturalisation process has provided some surrogacy for extinct birds. For example, Canada goose and feral goose are probably adequate surrogates for the extinct geese (*Cnemiornis* spp.), at least around water bodies, and the California quail and brown quail (*Coturnix ypsilophorus*) may compensate for the loss of the endemic quail. Similarly, the Australian coot (*Fulica atra*) may partially fill the role of the extinct New Zealand coot. However, avian introductions have not restored the guilds of terrestrial shoot browsers and fruit dispersers (Fig. 1) that were major functional groups amongst birds prior to human settlement.

Avian herbivore impacts

Plant adaptations to avian herbivory

Atkinson and Greenwood (1989) discussed four major growth characteristics found in indigenous plant species that they considered a response to moa herbivory: spiny tussocks, mimicry, reduced visual apparency and divarication. Surprisingly, most of these features have received little attention since first suggested as adaptations against avian herbivores, and only divarication has been explored in detailed studies. Mimicry and cryptic colouration amongst juvenile phases of many woody species are notable features of New Zealand woody plants and deserve further examination. Batcheler (1989) suggested that winter-deciduous and poisonous plants in New Zealand also developed to reduce moa herbivory, a view largely based on the stature and co-occurrence of such plants in open habitats with moa. Neither of these features is particularly common or distinctive in the New Zealand flora, and deciduousness is more likely a phenotypic response to local associations of cold climate and nutrient-rich soils (McGlone et al. 2004) that facilitate net carbon gain and seasonal loss of leaves.

Wire plants

Traditionally, researchers in this field have focused on divarication, the distinctive small-leaved, narrow-stemmed, highly-branched habit exhibited by many New Zealand shrub species and the juvenile phases of some tree species. However, divarication is merely a subset of an architectural syndrome characteristic of many New Zealand woody plants. Wardle (1991) suggested the term 'filiramulate' to emphasise the slender wiry twigs that may be highly branched, zigzagging, or merely flexuous, with small leaves and buds, and long internodes. Divarication is one manifestation of this form. Adaptive explanations need to account for the complete spectrum of filiramulate species.

Using domesticated ratites (emu, *Dromaius novaehollandiae* and ostrich, *Struthio camelus*), Bond et al. (2004) demonstrated that divarication functions to reduce leaf and particularly stem offtake rates by herbivores that characteristically tug vegetation, to levels below those needed for the birds' daily energy requirements. In contrast, rates of leaf and shoot removal on non-divaricate shoots by ratites provided more than enough energy for daily requirements. Bond et al. (2004) emphasised small, dispersed leaves on thin, widely-branched, strong, elastic stems as the key features of the divaricate habit selected by sustained ratite browsing, and reflecting the birds' distinctive clamping and tugging action. Plant remains from moa gizzard contents (Burrows et al. 1981; Wood 2007a) and nesting material (Wood 2008) indicate that the beaks of some species could cut stems 5–8 mm in diameter (and possibly 15 mm; Wood 2007a). Therefore, moa may not have been constrained as effectively as emu and ostriches, which are not major browse feeders. Nevertheless, a comparison of juvenile and adult shoot architecture in a range of indigenous heteroblastic species shows both higher tensile and shear strength in the divaricate shoots, suggesting that this growth form also impaired a bird's ability to cut through small stems (W.G. Lee unpubl. data). Support for the generalised wire plant syndrome (emphasising the functional significance of the filiramulate habit) as a structural defence against large bird browsers comes from studies in Madagascar, where the natural herbivore fauna also included large, now extinct, ratites; in Madagascar's case, the elephant birds (Aepyornithidae). Bond and Silander (2007) discovered that many Malagasy plant species in 25 families and 36 genera shared the same suite of traits as divaricates in New Zealand (small leaves; tough, thin, wiry branches; wide-angled branching; and high lateral displacement of branches resulting in springiness). However, these traits were not seen to the same extent in phyllogenetically matched species from South Africa, where mammalian herbivory predominates.

McGlone et al. (2004) have highlighted the concurrence of deciduousness and divarication, with 41% (11 species) of New Zealand's deciduous species having divaricating juvenile or adults forms. They suggest that both deciduousness and divarication represent parallel strategies for maximising carbon gain in response to seasonally stressful climatic conditions on nutrient-rich soils, as suggested by their co-occurrence in forests on alluvial frost flats. The high nitrogen levels in foliage of these species (Lee & Johnson 1984) may well attract herbivores, but according to McGlone et al. (2004) it is primarily a response to climo-edaphic conditions. While we agree with their interpretation for the evolution of deciduous plants in New Zealand, the evidence for the role of climate in the development of the divaricate habit, though widely investigated in recent decades, is not compelling. McGlone and Webb (1981) proposed that divarication arose during the Pleistocene to protect growing points and foliage from wind, desiccation and frost. However, in experimental studies of congeners or juveniles versus adults with contrasting habit, none of these factors has been shown to consistently or strongly distinguish divaricate from other growth forms (e.g. Kelly & Ogle 1990; Bannister et al. 1995; Darrow et al. 2001). Day (1998) suggested that divaricate architecture was highly plastic depending on light conditions, and might improve irradiance capture in deep shade by opening up of the canopy structure, and in open habitats by avoiding photoinhibition. Gamage and Jesson (2007) recently demonstrated that heteroblastic species, including divaricates, exhibit few structural or morphological adaptations for tolerating low irradiance levels. Christian et

al. (2006) grew divaricate and non-divaricate congeners under a range of irradiance levels and measured plant traits that influence light capture. Structural (non-photosynthetic tissue) support costs in divaricates were large, and more than four times those of non-divaricates. The authors concluded that such a difference in carbon expenditure would probably not be compensated for by enhancement in net canopy photosynthesis attained from avoidance of photoinhibition. Howell et al. (2002) contended that by shielding their leaves within a screen of outer branches, divaricate shrubs reduce their vulnerability to cold-induced photoinhibition. However, Lusk (2002) pointed out that the measured response by Howell et al. (2002) was not consistent across all tested species and that acclimation rather than adaptation was a alternative plausible interpretation for the photosynthetic response. From their comparative study, Bond and Silander (2007) suggested that cage-like architectures with interior foliage found in some New Zealand plants, and their absence in Madagascan wire plants, indicate that foliar protection may be important for shrubs growing in the open in a temperate climate.

Overall, climate-related explanations for divarication and heteroblasty have received little experimental support. Irrespective of alternative functions, we believe there is strong evidence for divaricate or filiramulate plants being part of the wire-plant syndrome – an unusual structural defence against large browsing birds. The traits involved are carbon-based constitutive (i.e. permanent and present before any browsing event) rather than inducible (i.e. temporary and only activated after first browsing) defences, and usually associated with fertile soils. The wire-plant syndrome primarily reduces shoot loss, and is functionally analogous to spines on many African woody species foraged by mammals. Only very long (>10 cm) and dense spines deter ratite feeding on plants (W.G. Lee pers. obs.), and this may explain why spines are rarely found in woody plants selected by avian herbivores (Bond & Silander 2007). Atkinson and Greenwood (1989) suggested multiple long spines on herbaceous *Aciphylla* evolved to deter ratite browsing. Ratite extinctions in New Zealand and Madagascar have left wire plants as a functional anachronism.

Foliage as fruit syndrome

Janzen (1984) proposed that small herbaceous plants with nutritious foliage and small, dry, inconspicuous fruits were dispersed inadvertently when grazed by large ungulates. He saw the process as a highly evolved dispersal mechanism, particularly for plants that occupied ephemeral or ruderal habitats where herbaceous vegetation was in a state of arrested succession as a result of browsing, grazing and trampling animals. Coprolites reveal small herbs were important in the diet of moa in eastern South Island (Wood et al. 2008). The seeds of *Ceratocephala pungens*, *Colobanthus* sp., *Einadia triandra*, *Myosotis pygmaea*, *Myosurus minimus novae-zelandiae*, *Oxalis exilis*, *Ranunculus* spp. and *Wahlenbergia pygmaea* were common in coprolites and all fit the Janzen (1984) plant-trait–habitat syndrome. *Ceratocephala* and *Myosurus* have nutrient-rich foliage (>4% N) (W.G. Lee unpubl. data) and they persist where the faeces of sheep and rabbits are concentrated, such as at stock camps and holding paddocks (Rogers et al. 2007a). Further, 50 (63%) of the 79 species of non-composite herbs of rare or threatened status in dryland ecosystems are small and short-statured, produce numerous, dry, inconspicuous seeds, and occupy ephemeral or ruderal habitats or sites with extreme soil chemistry (Rogers et al. 2005: Appendix 4). Given the apparent dependence of *Ceratocephala*

and *Myosurus* on dispersal and habitat mediation by ratites, the role of large grazers may have much greater relevance to the current threatened herbaceous and subshrub flora than previously thought (Rogers et al. 2007a).

Compensatory growth

In most plants, fitness declines consistently as the intensity of herbivory increases, but McNaughton (1983) demonstrated that some plants can compensate for herbivory up to some level before fitness declines, and a minority actually have improved fitness (i.e. over-compensation) under low levels of herbivory. Initially the concept of over-compensation was controversial (Belsky et al. 1993), but there is increasingly supportive evidence from controlled experiments (Agrawal 2000). Birds (and mammals) feeding on foliage of woody plant species in New Zealand rarely stimulate vegetative growth, or initiate new shoot production. New Zealand woody species can resprout new shoots following experimental removal, but recovery times are exceedingly slow. Bee et al. (2007) found diameter growth rates (1.2 mm yr^{-1}) of saplings of species in western Fiordland were half the lowest rate recorded in comparable studies globally, and shoot recovery times for 60% (of foliage) clipped plants was almost 2 years. We are aware of only one record of an induced response: following heavy possum browsing of adult shoots in its canopy, the small heteroblastic tree *Pittosporum turneri* reverted to juvenile filiramulate resprouts (C. Ecroyd pers. comm. 2008).

However, in the takahe we do have an example of an avian herbivore that appears to induce compensatory growth to the extent that feeding has negligible consequences for plant performance. This large, flightless rail wanders through the alpine grasslands removing tussock tillers and feeding on the undifferentiated basal portion. The discarded lamina fraction near the tussock enables the number and source of the tillers to be identified. Takahe typically remove less than 10% of the tiller complement in any one tussock, and this is readily replaced in *Chionochloa pallens* within a growing season (Mills et al. 1989). There is no evidence of over-compensation by any tussock species, and compensatory responses may be limited to *Chionochloa* species on nutrient-rich sites.

Avian-induced vegetation types

Most ecologists envisage avian herbivores influencing plant habit rather than vegetation physiognomy or composition. However, Worthy and Holdaway (2002) suggest that vegetation structure actually determines faunal composition and distribution, but they did not explore the mechanistic basis for this interaction. Caughley (1989: 8) stated that "a plant-herbivore system is not simply vegetation suffering the misfortune of animals eating it. Rather it is an interactive system with massive feed-back loops between the dynamics of the plants and the dynamics of the animals". In support of this, there is increasing evidence that some of our vegetation types were herbivore induced, especially where abiotic extremes also constrained plant growth. We identify four vegetation types that appear to have originated in a landscape dominated by avian herbivores, frequently, but not invariably, associated with abiotic stresses such as seasonal drought, salt deposition and submergence.

Dry woodland

Vera (2000) pictured pre-civilisation forests of Europe as a shifting patchwork of communities (localised grassy glades, scrub, and tall woodland with grass and herb understoreys)

that was maintained principally by large grazing mammals. An analogous landscape, but induced by large bird browsers, may have been widespread in the eastern South Island during the Holocene. Palaeobotanical data (e.g. McGlone & Moar 1998; Wood & Walker 2008) and extant vegetation relicts indicate that low forest, woodland and scrub dominated the dry basins and hill slopes of the eastern South Island. Small-leaved angiosperms in the genera *Olearia*, along with *Kunzea*, *Discaria*, *Coprosma*, *Ozothamnus*, *Hebe*, *Melicytus*, *Carmichaelia*, *Sophora* and *Corokia*, were prominent on higher-fertility soils, while the conifers *Phyllocladus alpinus* and *Halocarpus bidwillii* dominated glacial outwash and lower-fertility soils (Rogers et al. 2005:53). We suggest that the rich herbaceous component of eastern dryland floras (e.g. Druce 1993) points to a diverse array of pre-settlement micro-sites for low-stature herbs and short fast-growing grasses. Indeed, a pollen diagram from Otago's Idaburn Basin has high pollen frequencies of several diminutive herbs (some rarely seen in contemporary dryland communities or pollen rains) (McGlone & Moar 1998). These herbs included *Colobanthus*, *Raoulia*, *Taraxacum magellanicum* and Brassicaceae. Abundant, small-grained Poaceae pollen also points to a conspicuous presence of drought-tolerant grass genera such as *Festuca*, *Poa*, *Rytidosperma*, *Dichelachne* and *Elymus*. Further, lianes of the genera *Muehlenbeckia*, *Rubus*, *Calystegia*, *Carmichaelia*, *Parsonsia*, *Helichrysum* and *Clematis* were an important component of wire plant communities of the eastern South Island. We suggest that large-bodied birds, particularly the stoutly-built, eastern moa guild, played a major role in maintaining open understoreys and a patchwork of small glades within the low forest, woodland and scrub of the eastern South Island (Rogers et al. 2005). In New Zealand, large browsing and grazing birds may even have induced sparsely-wooded, herb-rich vegetation in particular circumstances, creating an equivalent of the savannah, prairie and steppe vegetation elsewhere, but with distinctive features such as a low frequency of fire.

Turf swards

Lloyd (1981) was the first to recognise the high frequencies of diminutive plants across many dicotyledonous genera in New Zealand, in contrast to the accepted trend towards increased size and woodiness in island plants. Over 20% of indigenous vascular plants occur in turf swards less than 50 mm tall associated with ephemeral wetlands that extend from the coast to the alpine zone (Johnson & Rogers 2003). Unlike similar vegetation types in the northern hemisphere, New Zealand turfs of ephemerally-wet and other environments have abundant small dicotyledonous herbaceous species, mixed with grass and sedge and other monocot (e.g. *Juncus, Triglochin*) forms. Virtually all of these communities have strong abiotic constraining factors (e.g. salt winds limiting woody encroachment in maritime turfs; winter inundation and summer drought limiting tall vegetation development in ephemeral wetlands; snow-lie preventing tussock encroachment in snow bank communities). Such communities would persist in core areas in the absence of avian grazers, but their extent (outside of those in the alpine zone), compositional diversity, and habit convergence are certainly facilitated by avian grazers, particularly waterfowl. The long-term interaction of grazers with these communities results in a dense, diverse turf of small-leaved, short-lived, often rhizomatous and succulent, angiosperm species. Analogous communities, comprising similar plant genera, have been described from Australia,

where they are associated with intense grazing by marsupials (Pharo and Kirkpatrick 2006),

Coastal low forest and shrubland

Predator-free offshore islands, such as the Snares (Warne 2003), and relict mainland populations provide an indication of the scale and intensity of disturbance from ground- and burrow-nesting seabirds on the soils and vegetation of pre-settlement mainland New Zealand (for mainland small petrels see Worthy & Holdaway (1996)). Feedback relationships between breeding seabirds and trees on islands can produce cycles of bird occupation with catastrophic vegetation collapse followed by bird abandonment and tree recruitment (Gillham 1961). However, offshore islands have limitations when used as indicators of pre-settlement seabird–vegetation systems because (1) many were not exposed to trampling by ratite and other birds that would collapse burrows and disturb ground nests, and (2) there was a greater diversity of predatory raptors and flightless birds such as weka (*Gallirallus australis*) and adzebill preying on mainland nests, Yet, given that 150 000 Hutton's shearwaters (*Puffinus huttoni*) now occupy a tiny fraction of their former range, it may be no exaggeration to suggest that there were once hundreds of millions, if not billions, of burrow-breeding petrels on the mainland (McGlone et al. 1994; Worthy & Holdaway 2002). Nevertheless, topographical relief providing take-off opportunities in combination with friable soils for burrowing would constrain the mainland pattern of burrow-breeding seabirds (e.g. Hawke 2003).

Vegetation dynamics in conifer-rich forests

The success of many indigenous conifer species, especially *Podocarpus totara, Dacrycarpus dacrydioides, Prumnopitys taxifolia* and *P. ferruginea*, on relatively fertile soil derived from alluvial, colluvial and volcanic processes has long been considered anomalous, since conifers worldwide generally are restricted to low-productivity soils, a reflection of their inability to compete with faster-growing angiosperms (Bond 1989). Feeding and soil and litter scarification by large avian herbivores may have created a competitive advantage and expanded niche for conifers through increased irradiance as shrub vegetative cover was reduced and by removing dense ground cover. Coomes et al. (2005) demonstrated that deep shade (e.g. from tall ferns) restricts regeneration opportunities for conifers in relatively productive New Zealand forests. The resource-adapted conifers in our forests may be the product of a long history of interaction with ground-dwelling avian herbivores that maintained a relatively open understorey on productive soils. If the above hypothesis is correct, then extinction of moa by the early 14th century should have caused a shift in the vegetation dynamics of these forests. An expansion of ferns, broadleaved shrubs and small trees in the understorey, and an associated decrease in irradiance, would have disadvantaged conifers, resulting in a regeneration gap that should have lasted several centuries until the introduction of ungulates. The presence of a conifer regeneration gap has been a seminal controversy in New Zealand's forest ecology (Wardle 1991). Forest vegetation dynamics in New Zealand during the Holocene have been largely driven by multi-scaled disturbances associated with earthquakes (Wells et al. 2001), floods (Duncan 1993), cyclones (Martin & Ogden 2006), volcanic activity (Leathwick & Mitchell 1992) and natural fires (Ogden et al. 1998; Rogers et al. 2007b). Such disturbances are reflected in cohort establishment on the disturbed sites following canopy collapse. These geologic and climatic

processes strongly influence forest canopy composition and demography, masking the more subtle and secondary effects of herbivores. Thus, detecting any vegetation signature created by the extinction of avian herbivores is difficult, and likely only to be found in long-lived, tall mixed beech-podocarp forests on tectonically stable landforms.

Avian species and ecosystem processes affecting herbivory

Seabirds, via non-autochthonous supply of nutrients, may have been key drivers of productivity and food-web structure in terrestrial plant communities across much of New Zealand during the Quaternary (Worthy & Holdaway 2002). Nutrients deposited by seabirds are undoubtedly incorporated into the wider ecosystem (Hawke & Holdaway 2005; Holdaway et al. 2007), and definitely drive ecosystem processes on small offshore islands (e.g. Mulder & Keall 2001; Fukami et al. 2006), including the composition of invertebrate faunas (Towns et al. 2009). However the extent of seabird activity on mainland areas may have been limited, particularly by topography, substrate conditions, predators and inter-annual changes in food abundance in aquatic environments. Even on offshore islands with no mammalian predators, colonies of burrowing seabirds and ground-nesting birds are only occupied seasonally and are restricted to certain habitats including take-off sites and those with free-draining, friable soils. Also, on these islands, seabird burrowing density declines with altitude (>65 m a.s.l.) and beneath dense (>50 stems ha^{-1}) woody vegetation (Roberts et al. 2007). Seabird distribution on the mainland is now severely modified by mammalian predation. Pre-settlement distribution can be reconstructed in part by the occurrence of fossil bones, cadmium-rich soils and evidence of burrows. Petrel and shearwater colonies were generally concentrated near the coast, although bones accumulated by predators have been found at inland sites (Worthy & Holdaway 1996). Gannets, gulls and shags were likely to have preferred coastlines, steep headlands, or braided riverbeds, with potential for take-off. Populations of nesting seabirds are sensitive to fluctuations in marine food resources largely driven by climate factors (Mills et al. 2008), so distributions would have varied over time.

Terrestrial avian herbivores are often overlooked as sources of nutrient enrichment in ecosystems. They may not have attained the high local densities of seabird colonies, and phosphorus and nitrogen levels in droppings are usually less than a third of those in seabird guano (Lee unpub. data), but their impacts may have been more pervasive than seabirds across the landscape, concentrating nutrients at resting and feeding sites. However, it is puzzling that nutrient augmentation by birds, both seabirds and herbivores, in terrestrial ecosystems appears to have had little impact on the ecophysiology of indigenous plants. They retain exceedingly low intrinsic relative growth rates compared with naturalised species from other countries (King and Wilson 2006).

Avian and mammalian herbivores: similarities and differences

Nowadays, introduced mammalian herbivores dominate most terrestrial ecosystems, but there are at least three situations where it is possible to compare the feeding of herbivorous birds and mammals in similar habitats: takahe and red deer (*Cervus elaphus*) in Fiordland; kokako and possums in podocarp forest in the central North Island; and waterfowl and sheep (*Ovis aries*) or lagomorphs (*Oryctolagus cuniculus* and *Lepus europaeus*) on coastal and inland turfs, South Island.

Takahe and red deer

The alpine summer ranges of takahe and red deer overlap in the Murchison Mountains, eastern Fiordland. Diet studies indicate both share preferences for tall tussock species *Chionochloa pallens* and *C. rigida* (Mills & Mark 1977). However, their modes of feeding are quite different; takahe remove the tillers, eat the basal meristematic portion, and discard the lamina, whereas deer graze the laminas and generally leave basal parts of the leaf intact. Among the larger *Celmisia* species, takahe feed exclusively on the leaf bases of *C. petriei*. This species is generally ignored by red deer. They favour *C. verbascifolia*. Overall, red deer selectively remove palatable herbs from grasslands, and, at moderate densities, induce short swards. Takahe, in contrast, feed preferentially on very few herbaceous species, and rarely cause structural or compositional shifts. In winter, both herbivores are restricted to shrubland and forest at lower elevations where there is negligible overlap in diet. Takahe feed almost exclusively on the starch-rich rhizomes of the summer-green fern *Hypolepis millefolium*, which are largely below ground and therefore inaccessible to deer. However, deer may indirectly encourage *Hypolepis* establishment by removing other understorey ferns and broadleaved shrubs. Red deer densities in the Murchison Mountains peaked at 11 deer km^{-2} (Parkes et al. 1978), representing an animal biomass of c. 1100 kg km^{-2}. In contrast, population densities of takahe across the Murchison Mountains average less than 1 bird km^{-2} or 2-3.5 kg km^{-2}.

Kokako and possums

Kokako and possums co-occur in central North Island podocarp–hardwood forests, where chick and egg predation by possums and ship rats (*Rattus rattus*) primarily limits kokako populations. Leathwick et al. (1983) and Fitzgerald (1984) undertook comparative studies of diets of these largely arboreal herbivores (although they used different assessment techniques – kokako feeding observations and possum faecal pellet analysis). Their findings suggest that kokako and possums share a preference for particular plant parts (leaves, flowers and fruits), and certain broadleaved species (e.g. *Melicytus ramiflorus*, *Pseudopanax arboreus* and *Schefflera digitata*). The two herbivores eat the full range of fruit seasonally available in the forest, but there is less overlap for leaves, with conifer and epiphyte foliage forming a larger proportion of the diet of kokako than that of possums. Possums also consume much foliage of the canopy dominants *Beilschmiedia tawa* and *Weinmannia racemosa*, which are rarely eaten by kokako. However, possum diet beyond the central North Island is known to include conifer foliage and young fruits (e.g. *Podocarpus hallii*, *Libocedrus bidwillii*). Sustained possum browse is known or suspected to kill adult trees (e.g. *Metrosideros robusta, Fuchsia excorticata*) and mature epiphytic plants (e.g. Loranthaceous mistletoes), although its impact is variable between regions, tree populations and even between individual trees (Payton 2000). While some kokako feeding involves defoliation (e.g. when they eat scale insects from *Schefflera digitata* leaves; Clout & Hay 1989), this is not known to kill trees. However, possums occur at much higher density (typically 3–11 per hectare in podocarp–hardwood

forest – c. 9-33 kg km^{-2} ; Efford 2000) than kokako (1 pair per 4–10 hectares – c. 1-2.25 kg km^{-2}) (Innes et al. 2006).

Waterfowl and sheep, rabbits and hares

Sheep and lagomorphs frequently graze maritime turfs and ephemeral wetlands, often in seasonal association with grazing ducks or geese, most commonly paradise shelducks, Canada geese and feral geese. Canada geese and sheep are a common combination in pastures adjoining lakes in New Zealand's eastern South Island where birds congregate outside of their breeding season. Dry matter consumption per animal is similar for Canada geese and sheep (Win 2001), and animal densities on pasture near lakes may be comparable. We are unaware of comparative studies of avian and mammalian feeding modes in these habitats, but our observations indicate that both groups graze the turf intensively, to less than 2 cm in height. This type of feeding reduces competition from exotic pasture grasses, which may help to maintain the native plant component of the turfs. Currently, the impact of avian grazers and small mammals on pasture and native turf communities cannot be distinguished, although where sheep hooves break the turf canopy, exotic herbs and grasses may invade. The realised niche of these turfs, over much of their environmental range, appears to be extended by grazing, as that suppresses grass and sedge invasion.

Moa and mammals

It has long been suggested that the widespread presence of deer restores a large-vertebrate browsing and grazing influence to New Zealand terrestrial ecosystems, following the demise of the moa. Atkinson and Greenwood (1989) provided the first comparative analysis of moa and ungulate herbivory, identifying qualitative (diet range, habitat range), quantitative (feeding mode, digestive processes, foraging behaviour), and ecological impact differences between the two groups. They suggested that deer have a broader diet and habitat range than moa, although in the lowland, on nutrient-rich soil, they considered the effects of both herbivore groups might be similar. Can we now provide a more substantive comparison of moa and ungulate impacts?

Diet

Increasing information on moa diet, primarily from gizzard remains and coprolites, indicates that very few of the plant taxa consumed by moa are also preferred by ungulates (Wood et al. 2008) (Table 2); the majority of species eaten by moa were neither selected, nor avoided, according to the classification of Forsyth et al. (2002). Indeed, we suggest that most of the herbs consumed by moa are also avoided by other herbivorous mammals such as lagomorphs and possums. Although deer browse bark and small-diameter twigs of palatable shrubs and trees, moa consumed a much wider range of fibrous plants and plant parts, including leaves of the fibrous monocot *Phormium tenax* (Burrows et al. 1981; Wood 2007a). Red deer target plant species that have low foliar fibre and relatively high foliar N contents (Forsyth et al. 2005). Plants with these traits may not be represented in moa gizzard contents and coprolites because of differential digestibility and detection, or their comparatively low abundance in pre-human plant communities, although this is unlikely.

Atkinson and Greenwood (1989: 90) posited that mammalian teeth would allow greater bite size, and therefore greater intake rates, than would a moa bill with its pulling and cutting action, as demonstrated by Bond et al. (2004)

using extant ratites. Moa regularly consumed a range of fleshy fruits, with very small and endocarp-protected fruits appearing in gizzards and coprolites. Fruits are rarely taken directly by ungulates, although there are few studies of seeds present in droppings. In contrast, ungulates frequently consume and damage bark of select woody species, a feeding action unreported for ratites.

In summary, the present evidence is that moa consumed a wider range of the flora than ungulates, including more fibrous, herbaceous and nutritionally-poor woody elements. However, the diet range of ungulates has not been examined extensively using droppings. Fruit consumption by moa and debarking by ungulates were important differences between the two groups.

Population density

We expect that moa densities in New Zealand were comparable to extant ratite densities elsewhere (0.15–<2 individuals km^{-2}, emu - Poplel et al. 1991; ostrich - Campbell & Borner 1995; cassowaries - Moore 2007; rhea - Barri et al. 2009; cf. Caughley 1989; Holdaway & Jacomb 2000; Gemmell et al. 2004), suppressed in part by aerial and terrestrial avian carnivores. We are in broad agreement with the evaluation by Forsyth et al. (2010) of estimates of moa density; they concluded moa density at the time of human settlement was around 0.3 or 0.6 individuals km^{-2}.

Worthy and Holdaway (2002: 209) also thought ungulate densities were likely to be higher than those of moa because of ungulate's superior cellulose-digesting capacity and their herding behaviour. Moa, in contrast, probably moved about singly or in small family groups. Nugent and Fraser (2005) suggested a national average density for red deer in forest of about 3–4 km^{-2}, in areas where they are regulated by hunting. However, densities during the early eruptive phase, several decades after their colonization, would have peaked at more than 30 animals km^{-2}, prior to severe food limitation. We therefore suggest that previous (and probably extant) densities of ungulates were far greater than likely densities of moa, a conclusion supported by a global comparison of population densities in natural communities of mammals and birds across a range of body sizes (Silva et al. 1997) and by the independent analyses of Forsyth et al. (2010).

Landscape utilisation

The mobility of large ratites may have been constrained by topography, with access between feeding and roosting areas facilitated by a tracking system. However, according to Tennyson & Martinson (2006), upland and crested moa were upland and steepland specialists. In general, quadripeds will be able to utilise steeper sites than those accessed by heavy-bodied bipeds. Australian cassowaries (*Casuarius casuarius*) are limited by steep terrain and favour tracks between ridge and valley-floor feeding sites (Mack 1995). We envisage moa showing similar mobility patterns. Ungulates and possums have exposed plant communities of steep terrain (other than cliffs) to vertebrate herbivory as a selection force for the first time. Indeed, Rogers and Walker (2002) showed 38% of New Zealand's threatened and uncommon plants occur on coastal and inland cliffs below the treeline, and in many instances vertebrate herbivory is a significant threat (Dopson et al. 1999).

Vegetation patterns and processes

Table 3 summarises our view of the major differences between

Table 3. Herbivores and vegetation changes in New Zealand during pre- and post- settlement phases. Major drivers of vegetation pattern and process are listed with responses by each biome.

Period	Pre-Settlement Holocene to c. 1450 AD	Post-Maori and Pre-European c. 1450 to c. 1850	Post-European c. 1850 to present day
Major drivers	Climate, soils, earthquakes, cyclones and avian herbivores	**New drivers:** fire, absence of large herbivores	**New drivers:** mammalian herbivores, indigenous habitat destruction, invasive weeds
Biome Response			
Forest	Mosaic understorey and canopy reflecting interactions of natural disturbance and local zones of concentrated avian grazing; arrested early succession patches supporting areas of low-growing forbs; widespread conifer regeneration; variable understoreys of sparse and clusters of wire plants, cryptic, and unpalatable shrubs, often protecting broadleaved species. Numerous inaccessible sites with diverse dense broadleaved shrub and fern flora.	Forests largely eliminated in dry eastern areas by fire. Elsewhere expansion of understorey broadleaved tree and shrub species, and ferns in most forest types. Forest consolidates across semi-arid environments, out of areas topographically protected from fire.	Depletion of forest understorey structure by eruptive populations of ungulates, with removal of diverse palatable shrub and fern species; residual regeneration of conifers; sharpened transition zones between woody and simplified non-woody communities.
Scrub	Small-leaved scrub widespread with broadleaved species in thickets, gullies, and other inaccessible sites.	Broadleaved component expanded into all scrub, and attenuated forest/scrub/grassland ecotones with other major vegetation types in response to relaxed herbivory.	Spread of sclerophyllous (largely fire-induced), aromatic, spiney or cage-canopied scrub species, especially into modified grassland during 20th century.
Grassland	Grasslands dominated by short ephemeral grasses and prostrate herbs, with tall tussocks limited to outcrops, bluff systems, wetlands, and alpine zone.	Fire-facilitated expansion of first short then tall tussock grassland, with marked decrease of fire-sensitive woody components and widespread rise in dominance of Sphagnum.	Conversion of tall-tussock grassland into short-tussock grassland with increasing incidence of shrubs and herbs with browsing-resistant traits.
Herbfield	Extensive low-growing riparian and inter fluvial herbfields.	Tall herbfield and graminoid expansion commensurate with decreases in avian herbivore densities.	Removal of tall herbs and close grazing creates zone of low-growing herbs, displaced by exotic pasture species in areas of low abiotic stress.
Wetlands	Diverse woody and tall monocot-dominated wetlands with large adjoining areas dominated by turf systems.	Fire removes woody species, local expansion of many tall graminoid and restiad components.	Grazing creates high residual exotic herbaceous weed communities, occasionally invaded by browse-resistant shrubs and trees.

the impacts of moa and deer on vegetation dynamics in New Zealand. We suggest that moa effects on vegetation patterns and processes were uneven across the landscape, reflecting local differences in diversity and density of animals. Aggregations, comprising clusters of relatively small groups of moa, would have been concentrated by vegetation quality and quantity, and predation risk. Moa would have favoured areas of naturally high soil fertility in all vegetation types. These nutrient-rich soils in the pre-settlement landscape were created by tectonically-induced landslides, colluvial activity off glacially over-steepened slopes, and periodic flooding along riparian zones, with the relative level of enrichment reflecting the natural nutrient status of the watershed rock types. The greatest number of moa genera appears to have ranged in warmer, eastern, low-rainfall areas, in habitats affiliated with limestone (Worthy & Holdaway 2002).

In forests, following tree-fall from wind-throw or landslides, concentrated grazing and nutrient enrichment by moa could have maintained early successional stages dominated by small herbs, until, at some time, the encroachment of herbivore-resistant wire plants and unpalatable woody species would have reduced grazing quality. However, these more browse-avoiding and browse-tolerant shrubs and trees would have eventually enabled the establishment of broadleaved species and canopy dominates, once herbivores were physically excluded. Such interactions between herbivores and forest communities would have produced a mosaic of transient vegetation types based on differential herbivore use. In flood plain forests, similar processes could have occurred, with herbivores reducing understory development and delaying successional rates. Shrublands would have been similarly dominated by herbivore-resistant species, with palatable species restricted to inaccessible sites. Shrubland may have been less extensive because of intense moa activity, including soil scarification on non-forested areas, which would have favoured short, fast-growing grasses and forbs. Analogous processes may have restricted slow-growing, long-lived *Chionochloa* tussock grasslands, and the development of tall herbaceous vegetation

zones around wetlands, both vegetation types displaced by herbivore-induced sward and turf communities.

The transition from avian, especially moa, to ungulate herbivory in New Zealand involved several centuries when large herbivores were absent from terrestrial ecosystems (Table 3). However during the herbivore gap, widespread burning by Polynesian settlers also transformed this herbivore-naive vegetation, creating novel non-forest communities largely without parallel in the pre-settlement era. This involved widespread depletion of woody components in grasslands and wetlands, and the destruction of forests in eastern South Island areas. European pastoralism has continued to use burning to manage vegetation, but intensified the grazing and introduced many grazing-tolerant exotic grasses. It is in these divergent ecological contexts that we have to compare the effects of moa and ungulates.

Atkinson and Greenwood (1989: 92) observed that "for the most part, introduced browsing mammals are acting as a new influence on vegetation and, in many places, are depleting its structure and composition compared with that of pre-Polynesian New Zealand". This statement requires careful evaluation because strongly moa-mediated vegetation types had long disappeared from the landscape by the time ungulates arrived. Numerous studies (see Forsyth et al. 2010) show the widespread floristic depletion of New Zealand forests in the presence of ungulates, but the issue here is whether or not these impacts are greater than what would have occurred under pre-settlement avian herbivory.

From our comparative analysis, ungulates appear to have greater densities, feeding efficiency, and mobility, compared with moa, and consequently have probably simplified and decimated forest understorey vegetation over larger areas and to a greater extent. Moreover, the presence of ungulate species, such as sika deer (*Cervus nippon*), that have superior ability to digest low quality herbage appears to lead to canopy regeneration failure in *Nothofagus* forests (Husheer et al. 2006), an effect which moa would have been unlikely to achieve. Although some wire plants with dense, caged canopies are relatively resistant to ungulate browsing, many of the woody species with avian herbivore-resistant features have succumbed. Outside of forests, ungulate herbivory is creating scrubland vegetation dominated by spiney, aromatic, or cage-canopied species, with noticeable losses of large herbs. In fire-induced tall tussock grasslands in montane and lowland zones, ungulate grazing can favour short sward grasses which may be compositionally analogous to moa-induced grassland communities. However, there was also no pre-human avian equivalent of the footprint pressure of today's cattle (*Bos taurus*) (Duncan & Holdaway 1989) or ungulates in general (Forsyth et al. 2010). Ungulate hooves can be especially damaging on moist soils.

We conclude that present-day ungulate impacts create a far greater number of niche-restricted indigenous plant species than were ever present during the time of the moa.

Changing herbivore guilds and conservation management

Conservation goals

The rapid demise of moa (Holdaway & Jacomb 2000) and most other large terrestrial avian herbivores after human contact (Tennyson & Martinson 2006) created a period of at least three centuries when New Zealand forests were effectively without large vertebrate herbivores. As noted by Caughley (1989), this interregnum would have created a new vegetation dynamic, largely unconstrained by herbivory, but regionally modified by Polynesian fires (Table 3). During the period when herbivore pressure was removed or at least severely reduced, we suggest there was a significant expansion of broadleaved species and ferns in forest understoreys, and similar increases in large herbs in those grasslands where fire was rare. It was this vegetation that greeted European settlers during the late 18th and early 19th centuries, and which became the baseline from which conservation goals were derived during most of the 20th century. The vertebrate herbivore-free vegetation paradigm was embraced in conservation legislation, which at the time of the last symposium (1986) emphasised protecting ecosystems in their pre-1840 state. Nowadays, however, biodiversity protection goals for most public conservation land recognise the dynamic character (e.g. disturbance, succession, climate change) of communities, and the impossibility (and undesirability) of trying to replicate communities found at a fixed point in the past. The goal of the New Zealand Biodiversity Strategy (DOC & MfE 2000) focuses on sustaining biodiversity pattern ("a full range" and "all species and subspecies") rather than some historic state, and maintaining or restoring biodiversity processes (a "healthy functioning state") in order to protect both biodiversity pattern (the full diversity of genes, species, communities, habitats and ecosystems, and landscapes) and the ecological and evolutionary processes that sustain this pattern.

What role does mammalian herbivory have in conservation management?

The range of mammalian herbivores in indigenous vegetation in New Zealand is shifting plant species and trait assemblages, favouring unpalatable plants with sclerophyllous and aromatic leaves, dense, highly branched canopies, or spines. Small, ground-hugging plants that grow below the level at which large herbivores can bite are also generally favoured (Table 3). Tolerance of mammalian herbivores and ongoing dispersal by such herbivores for some indigenous fleshy-fruit-producing plants (Williams et al. 2000) will maintain the realised niche of a subset of indigenous plants, but even after several centuries of mammalian occupation no vegetation communities demonstrate equilibrium with resident browsers. Overall, mammalian herbivore impacts are very different from the effects of former avian herbivores, and, moreover, mammals will inevitably consolidate the presence of naturalised plant species with which they share an evolutionary history (Table 3).

In several situations, conservation managers have been advocates for ongoing mammalian herbivory, particularly to foster conifer regeneration in forests, maintain grasslands by truncating successional processes, and protect turf communities by preventing dominance of introduced weed species. In forest ecosystems, terrestrial mammalian herbivores (e.g. deer, goats) do not prefer eating indigenous gymnosperms (Forsyth et al. 2002), although possums do eat several species (e.g. *Podocarpus hallii, Libocedrus bidwillii*). Depletion of the forest understorey through removal of broadleaved shrubs and some ferns favours regeneration of relatively shade-tolerant and unpalatable conifers (Coomes et al. 2005). However, this effect is variable across the landscape and several ferns are also unpalatable, often increasing in abundance with moderate deer use and affecting recruitment of some canopy dominants. In some contexts, increasing conifer representation in forests

may be an important conservation goal, e.g. in projects that aim to support large populations of kereru, or boost kakapo fecundity. In such situations the retention of low numbers of deer may be an option.

The widespread tall- and short-tussock grasslands of the eastern South Island that developed after forest and shrubland clearance following extensive fires by humans since the 13th century are often perceived as communities induced by feral (e.g. rabbits, hares) and domestic (e.g. sheep, cattle) grazers. Although mammalian grazing has been a filter in the origin of these communities, it has been fire that has primarily created their physiognomy and herbaceous character. Nowadays, with the decrease in fire frequency, it is grazers that limit the establishment of a continuous tussock cover and the return of woody species (Walker et al. 2009). Grazing is often advocated to suppress invasion of woody (e.g. *Pinus contorta*), forb (e.g. *Hieracium pillosella*) and grass (e.g. *Agrostis capillaris*) weeds, and there is some evidence for these effects locally (Lord 1990). However, the widespread incursion of all these weeds, even in areas with intensive grazing histories, suggests that grazing may affect the rate of invasion rather than the ultimate outcome at the landscape scale. The problem mammalian grazers present as a management tool for biodiversity protection relates to the collateral damage caused on indigenous plants by ongoing grazing, and the way grazers decrease cover generally, thereby making the vegetation more vulnerable to occupation by any new grazing-tolerant invasive exotic (and native) species that becomes established. Clearly, vegetation types that originated via grazing (and fire) will require ongoing grazing for maintenance (Lord 1990), assuming they are in equilibrium or steady-state, but as conservation end-points these communities may be achievable only at a local scale where grazing can be easily manipulated. In seral grasslands, even in the absence of mammalian grazers, woody species will expand, initially from local seed sources comprising grazing-tolerant natives and exotics (Walker et al. 2009).

Another system where mammalian grazers may maintain dominance of indigenous species is the turf communities associated with ephemeral wetlands. Early results from exclosures (i.e. fence plots that exclude all vertebrate grazers) show that *Agrostis capillaris*, *Trifolium repens* and *Hieracium pilosella* increase their cover in periodically inundated zones when grazers are excluded. Mammals (e.g. rabbits, hares and sheep) facilitate the spread of exotic species (via seed dispersal and the creation of establishment sites) and partially control it (via herbivory). However, they also restrict the return of indigenous tussock and woody vegetation in surrounding habitat. It is possible that exotic incursions following grazing removal may be set back by prolonged inundation events in these habitats. Avian grazers could fulfil a similar role in controlling invasion by exotics, without the negative effects on adjoining indigenous vegetation.

What role do naturalised avian herbivores have in conservation management?

The vegetation of New Zealand developed over millions of years in the presence of birds and it is unlikely that any ecosystem components would be seriously disadvantaged by naturalised herbivorous birds, apart from the impact of imported avian diseases. Atkinson (1988) advocated that we consider the intentional introduction of avian guild replacements for extinct taxa, in order to restore key functional processes in New Zealand ecosystems. Internationally this has been taken up more recently in conservation biology by those arguing for

the 're-wilding' of landscapes in North America by species either functionally or taxonomically closely related to the extinct Pleistocene megafauna (Donlan et al. 2005, 2006). While raising many issues about identifying, breeding and managing these new species in modern landscapes, the re-wilding perspective does broaden our conservation vision beyond the often depressingly large task of saving species and stopping ecosystem declines (Caro 2007). Under New Zealand's current biosecurity regulations it is probably unrealistic to expect permits to be granted to import species new to New Zealand to address conservation goals, even if we could agree on what those species might be. However, we could utilise many of the naturalised bird species already present, foster their population growth, and accept them as part of a natural Holocene re-wilding experiment that may partially compensate for the human-induced avian extinctions of the past millennia.

Conclusions

Since the 1986 symposium on "Moa, mammals and climate in the ecological history of New Zealand", our understanding of avian herbivores has expanded considerably. The composition of the pre-settlement avifauna is now well established, and new techniques are revealing aspects of the diet and habitat use of the extinct species. The basic perspectives advanced at the first symposium continue to have support. Avian herbivores, mostly folivores and frugivores, dominated terrestrial ecosystems. They were constrained by aerial and ground predators, but utilised habitats up into the alpine zone. Greatest diversity characterised the browser/grazer guilds, with moa showing considerable dietary plasticity, depending on habitat, and divergent morphological adaptations to either high-fibre-browser or soft-tissue-grazer food. Increasing attention is being given to avian herbivores that favoured turf communities associated with ephemeral wetlands and coastal areas occupied by c. 20% of our vascular flora. The legacy of avian herbivores can be perceived in the composition and structure of some of our vegetation types, in the growth habit of plant species, and in the predominance of fleshy-fruit-producing woody species.

Extinctions decimated the guild of large-terrestrial-browsers, and weakened all other groups of avian herbivores. Ecologically, mammalian introductions are not effective substitutes for lost avian species, although in specific contexts there may be similarities between avian and mammalian herbivores. Native birds in general continue to decline, particularly forest-dwelling herbivores (Innes et al. 2010), and many introduced avian herbivores are considered game-birds and culled because of their impacts on pastoral farming. The conservation imperative for protective management of indigenous birds is higher than ever, and is strongly supported by the increasing recognition of special avian-selected features in the plants, vegetation and ecosystems of New Zealand. Advances in reconstructing avian ecosystems as functional substitutes for what has been lost are likely to shift conservation management towards approaches that embrace all naturalised avian species, irrespective of their country of origin.

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the issues covered in this paper. Shortly before his death in December 2008, he kindly agreed to review this manuscript, responding: "My general comments reflect my own prejudices on the topic, and are probably out of order, but I'm going to make them anyway!" It was these "prejudices", as he modestly calls them, on the history and character of New Zealand vegetation that inspired and challenged new avenues of ecological research, and gave aspects of our ecology an international profile. We also acknowledge the pioneering work of Ian Atkinson and Michael Greenwood, who in their synthesis at the 1986 symposium thoughtfully articulated a new paradigm for herbivory in New Zealand. We thank Ian Atkinson, Matt McGlone, Peter Bellingham and several anonymous referees for improving the clarity and content of manuscript. WGL acknowledges funding from the New Zealand Foundation for Research, Science and Technology (C0 9X0503). The Department of Conservation and Landcare Research supported the publication of this special issue.

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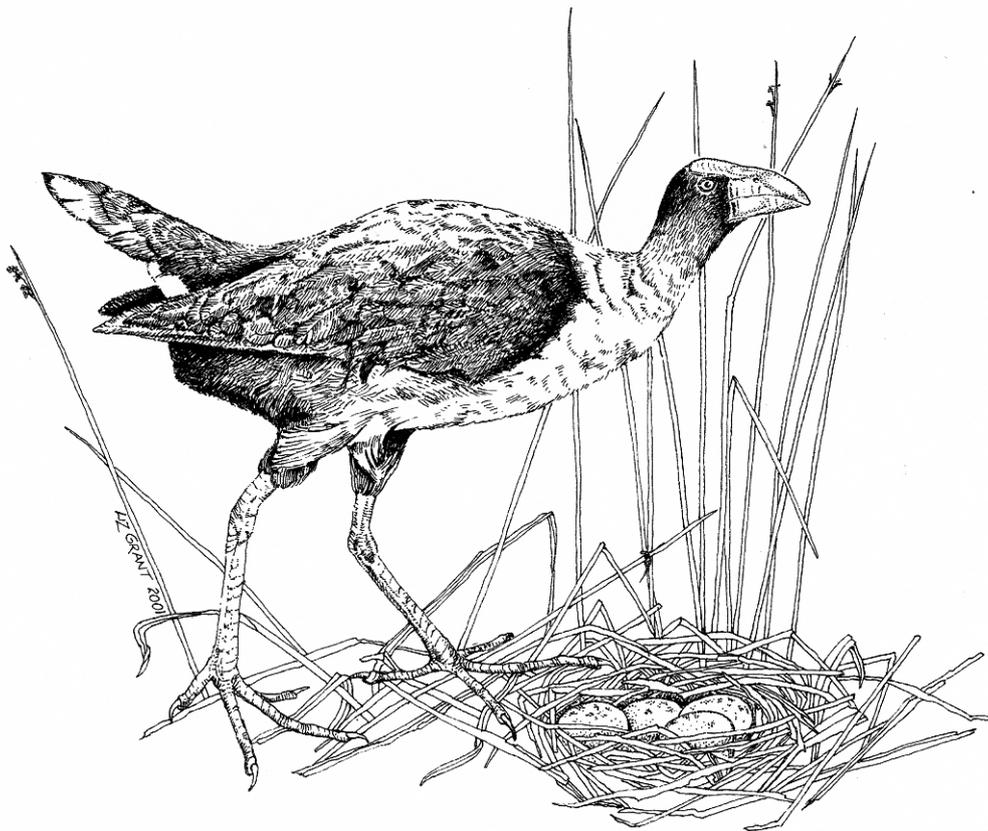
The herbivorous native pukeko, drawn by Liz Grant (http://www.artbyliz.co.nz/) for the cover of NZ J Ecology 25(1) 2001.