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Apomixis in indigenous New Zealand woody seed plants and its ecological and wider significance: a working hypothesis

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Abstract: Evidence is presented for facultative apomictic seed formation in indigenous hardwood trees, shrubs and lianas in Riccarton Bush, Christchurch, and in indigenous woody species elsewhere in the New Zealand Botanical Region, including its offshore and outlying islands. For the most part, this evidence is based on the formation of abundant mature fruit in female plants isolated from pollen sources, and the subsequent germination of seeds and emergence of seedlings beneath these plants. In a few species, apomixy has been confirmed by cytological techniques. Sexual reproduction occurs in facultative apomicts and genetic diversity is maintained. Apomixis may be widespread among species central to the recovery and management of degraded forests and shrublands, and nationally threatened woody taxa with sparse, local, or restricted distributions. Unequivocal confirmation of the apomixis status hypothesised here and more information on the breeding systems of these species is needed if the extent and ecological role of the phenomenon in the New Zealand indigenous woody flora is to be understood.

Keywords: breeding systems, conservation, ecology, woody plants

Introduction

Apomixis, the asexual formation of seeds, while unknown in gymnosperms, is widespread but uncommon among angiosperms (Bicknell & Koltunow 2004). Apomixis has been described in >400 flowering plant taxa, including representatives of >40 families (Carman 1997), with a distribution pattern suggesting it has evolved many times. Bicknell and Koltunow (2004) suggest that these estimates are very conservative, and that as our understanding grows and methodology improves many more angiosperm taxa will be found to include apomictic representatives.

In this account, apomixis, or asexual reproduction and seed formation, is distinguished from amphimixis, or sexual reproduction and seed formation. A facultative apomict is one where apomixis does not always occur and sexual reproduction, including hybridisation, can also happen. Indeed, it has been suggested that all apomixis in plants is facultative (Savidan 2000) with obligate apomicts being very uncommon (Asker & Jerling 1992), or an artefact of insufficient observation (Savidan 2000).

The focus of plant ecology and conservation biology is overwhelmingly on sexual reproductive strategies and function (Richards 2003) and outcrossing is thought to be of exceptional importance (e.g. Robertson et al. 2011). By comparison, apomixis has been largely ignored by reproductive theoreticians (Richards 2003), sometimes described as an evolutionary 'blind alley' (Stebbins 1950) and it has been claimed that the reproductive characteristics of rare species tend to be biased away from outcrossing and sexual reproduction (Kunin & Gaston 1993).

For the past 43 years, I have been associated with the management and restoration of Riccarton Bush in the inner city of Christchurch. During that time, I have had the rare opportunity to observe, at frequent intervals, the breeding systems, reproductive behaviour, and recruitment of indigenous woody seed plants there. On the basis of these observations I have come to the conclusion that many of the indigenous woody species populations in Riccarton Bush are made up of facultative apomicts and, more broadly, that a substantial number of woody species throughout New Zealand contain facultative apomicts. Apomixis may, in fact, be chronically under-reported in the New Zealand flora.

My working hypothesis is that facultative apomictic seed formation in indigenous woody species is a widespread and important feature of forest successions throughout the New Zealand Botanical Region. In relation to this hypothesis I: (1) briefly discuss apomixis, and how it may be inferred; (2) outline the evidence from Riccarton Bush on which my hypothesis is based; (3) discuss a selection of putatively apomictic species that I, and others, have observed over many years in the light of these criteria; and (4) describe some exemplar sites in which these putative apomicts play a dominant role and that may be used in the future to critically test my hypothesis.

Identification of apomixis and its ecological correlatives

Apomixis is the asexual (uniparental) formation of a seed from the maternal tissue of an ovule and thus obviates the need for meiosis and fertilisation. The exact mechanisms by which apomixis occurs are complex. Most apomictic species rely on prior fertilisation for formation of viable seeds because fertilisation is required for normal endosperm development (pseudogamous), but spontaneous (autonomous) apomixis occurs in some species (Hörandl 2010). Autonomous apomixis has the advantage of assuring reproduction in isolated female individuals. Apomixis is frequently linked with polyploidy (Hörandl 2010).

Observations of isolated female or emasculated plants have been, until recently, the most common (albeit often inconclusive) way of identifying potential apomicts. It was first recorded by observations of a solitary female plant of the perennial, dioecious, woody, native holly *Alchornea aquifolia* (syn. *Caelebogyne ilicifolia*, Euphorbiaceae) of Australia, which continued to form seeds when planted at Kew Gardens, England, as reported by Smith in 1841 (cited by Bicknell & Koltunow 2004). However, as the ploidy level ratio between embryo and endosperm in apomictic seeds differs from sexually reproduced seeds, apomixy can be confirmed via cytology, progeny tests, and DNA based techniques such as DNA Amplified Fragment Length Polymorphism Profiles. In particular, development of flow cytometry has meant rapid survey of populations for the presence of apomictic reproduction is possible (Matzk et al. 2000; Krahulcová & Rotreklová 2010).

Apomictic species usually have sexual relatives that are self-incompatible, obligate outcrossers and often dioecious (Hörandl 2010). While sometimes included with self-fertilisation as a reproductive mechanism, apomixis differs in that it lacks the negative effect of increased homozygosity in the offspring and therefore there is no inbreeding depression. Polyploidy is a common correlate of apomictic plants (Gustafsson 1947).

Apomictic species are invariably perennials and often use vegetative mechanisms for asexual reproductions such as stolons and rhizomes (Bicknell & Koltunov 2004). Apomixis is common in some herbs, especially among members of the Asteraceae and grasses (Asker & Jerling 1992). Apomictic species have better colonising ability, especially of disturbed habitats (Asker & Jerling 1992), and have greater distributional ranges than their non-apomictic sexual relatives (Bierzychudek 1985). Therefore, some are highly successful naturalised invaders of disturbed habitats in New Zealand and elsewhere, e.g. *Taraxacum* spp. (Van Dijk 2003), *Pilosella officinarum* [= *Hieracium pilosella*] (Houliston & Chapman 2004), and *Cortaderia jubata* (Okada et al. 2009). Apomixis has not often been described in woody plants, exceptions being some taxa in the cosexual (both sexes present on the same individual) genera *Crataegus* (Rosaceae) (Muniyamma & Phipps 1979; Dickinson & Phipps 1986), *Amelanchier* (Rosaceae) (Campbell et al. 1987; Burgess et al. 2014), *Sorbus* (Rosaceae) (Hajrudinović et al. 2015) and *Citrus* (Rutaceae) (Koltunow et al. 1995).

Riccarton Bush

Setting

The natural and cultural history and management of Riccarton Bush are discussed by Molloy (1995, 2000) and summarised here. Riccarton Bush (43°31.7′ S, 172°35.7′ E, c. 10 m a.s.l.) is a 7.8 ha remnant of indigenous conifer/hardwood forests within the city of Christchurch. This old-growth stand is representative of a once extensive forest growing on fertile floodplain sediments laid down by the Waimakariri River and smaller local streams. Much of the post-glacial indigenous conifer/hardwood forest that formerly covered the Canterbury Plains, including the site of the present city of Christchurch, was subject to periodic natural and anthropogenic fires. The most recent fire that defines the pre-European boundary of Riccarton Bush is placed, by radiocarbon dating, at 270 years BP, which is in the late Māori period (Molloy & Brown 1995). At present, Riccarton Bush has an almost continuous cover of indigenous plants, forming a coalition of surviving old-growth canopy trees, such as *Dacrycarpus dacrydioides*, *Elaeocarpus hookerianus*, *Elaeocarpus dentatus*, *Hoheria angustifolia* and *Sophora microphylla* (all species not known to be apomictic) and large, putatively apomictic lianas such as the dioecious *Passiflora tetrandra*, *Rubus schmidelioides* and *Muehlenbeckia australis*, and the cosexual *Parsonsia heterophylla*, with a dense understory and ground layer of seral indigenous woody species, mostly putative apomicts (see below).

Evidence for and extent of apomixis

My suspicion that apomixis may form an important part of the reproductive strategy of woody plants in Riccarton Bush was first aroused by the observation of abundant fruit set in female plants growing there of the indigenous dioecious species *Coprosma robusta*, *Melicytus ramiflorus*, *Pittosporum tenuifolium*, *Pittosporum eugenioides*, *Myrsine australis*, *Griselinia littoralis*, *Pseudopanax arboreus*, *Pseudopanax crassifolius*, *Schefflera digitata*, *Plagianthus regius* subsp. *regius*, and the gynodioecious *Carpodetus serratus*. Almost every flower in an inflorescence formed a mature fruit in these species. Copious crops of fruit were observed regularly on isolated female plants of the same species cultivated at Landcare Research, Lincoln, the Christchurch Botanic Gardens and its satellite Mona Vale, and in private gardens, including my own. In every case, fruit set was followed by the germination of seeds and emergence of seedlings, often in abundance, beneath their respective seed trees.

A large solitary female tree of the indigenous *Alectryon excelsus* subsp. *excelsus* was planted in Riccarton Bush in the 1950s (formerly naturally present). This putative apomict does not flower every year, but when it does, it sets ample fruit that has resulted in abundant seedling and juvenile offspring beneath its canopy and dispersed through other parts of the Bush. I have noted similar behaviour of this taxon in degraded forests within its natural range, e.g. in valley floor forests of nearby Banks Peninsula.

Pigeonwood (*Hedycarya arborea*) was not recorded in Riccarton Bush by Armstrong (1870), or subsequent authors, but recently seven young plants from 40 cm to 1.8 m tall have been located in different parts of Riccarton Bush and are almost certainly dispersed by the New Zealand pigeon or kererū (*Hemiphaga novaeseelandiae*) from the planted forest of mixed indigenous conifer/hardwood species established in the Christchurch Botanic Gardens in the early 1930s. Four plants of *Hedycarya arborea,* sourced from Queen Charlotte Sound, were planted in the Botanic Gardens in 1957, and since then spread widely throughout this planted forest, which also supports a resident breeding population of the New Zealand pigeon that regularly visit nearby Riccarton Bush in search of food.

Figure 1. Aerial image of the Riccarton Bush protected area, showing the planted exotic trees in the grounds of Riccarton House to the right, and the old growth canopy trees and recovery of indigenous understorey plants of Riccarton Bush to the left (© Terraview International Limited 2010).

We have confirmed levels of apomictic and amphimictic seed formation in a female-biased population of the indigenous dioecious shrub *Coprosma robusta* in Riccarton Bush using flow cytometry (Heenan et al. 2003).

The progeny of the putative apomicts have played a significant role in the spectacular recovery of Riccarton Bush following past disturbances and the revised management practices put in place since 1974 (Fig.1; see also Molloy & Wildermoth 1995).

A number of other species in the endemic or indigenous New Zealand flora have been shown to be apomictic. Apomixy has been demonstrated at low levels in a cultivated plant of the dioecious shrub *Coprosma waima* (Rubiaceae) and reported evidence of apomictic seed formation in cultivated plants of the indigenous dioecious shrubs *Coprosma parviflora*, *Coprosma robusta* and *Coprosma serrulata* (Heenan et al. 2002). The majority are prominent in successions, most having effective fruit dispersal, rapid seed germination, relatively fast growth rates, and ability to reproduce vegetatively from basal or stem sprouts following damage (for further evidence of these traits in New Zealand forest trees see Wardle 1991; Burrows 1994, 2006). It should also be noted that these putative apomicts are often, though not exclusively, associated with disturbed habitats and fertile soils derived from nutrient-rich parent materials such as basic volcanic rock, schists, limestones, alluvium and colluvium. Hair (1966) suggested that *Pomaderris* (Rhamnaceae) were likely candidates, a supposition later confirmed by Harvey and Braggins (1985) who documented apomixis in *Pomaderris phylicifolia* and *Pomaderris hamiltonii* via emasculation studies and cytology. No endemic or indigenous dicotyledonous herb is known to be apomictic. Hair (1956) showed *Agropryum scabrum*, a grass present in New Zealand, to be apomictic via cytological evidence and breeding studies, but it is now thought to be introduced.

Indigenous woody seed plants in Riccarton Bush presumed to be facultative apomicts are listed in Table 1, together with other New Zealand species suspected or confirmed as being so, along with plant growth form, breeding systems, dispersal and pollination modes, chromosome numbers and successional status.

The putative apomicts suggested or confirmed here are indigenous trees, shrubs and lianas, most being small-statured trees or shrubs and a number favour seral or forest marginal habitats. They are predominantly dioecious, occasionally gynodioecious, and include only two cosexuals (*Pomaderris* spp.). Apomixis appears to be widespread in *Coprosma* (as hypothesised by Heenan et al. 2002) and other species-rich dioecious genera such as *Melicytus*, *Pittosporum* and *Pseudopanax*. Aside from *Coprosma* and *Streblus*, all are entomophilous. *Plagianthus* has wind-dispersed winged seeds, but all the rest have bird-dispersed fruit or seeds. Most can reproduce by vegetative means, especially following damage.

I list in Table 1 confirmed polyploids (pers. comm. Murray Dawson 2018) but the relatively high chromosome numbers of most of the rest suggest some ancient polyploid events involving paleodiploid ancestors with low basic numbers. This provides some support for the claim that polyploidy is a common correlate of apomictic plants (Gustafsson 1947), although the reasons for this association remain unclear (Bicknell & Koltunow 2004).

Selected putatively apomictic species

Hedycarya arborea

Pigeonwood, *Hedycarya arborea*, is endemic to New Zealand, reaching its south-eastern limit on Banks Peninsula where it is

Table 1. Indigenous woody seed plants in Riccarton Bush presumed to be facultative apomicts. Breeding systems from Webb et al. (1999), other literature, and my own observations gathered over many years. Chromosome numbers from Dawson (2008). Breeding system: D = dioecism; G = gynodioecism; H = hermaphroditism; Seeds or fruit: F = fleshy; N = non-fleshy. Pollination mode: A = anemophily; E = entomophily. Growth habit: T = tree; S = shrub; L = liana. Notes: The dry leathery capsules of *Pittosporum* burst open to expose black seeds immersed in a sticky fluid and dispersed by birds. Similarly, the dry capsules of *Melicope simplex* open to release black shiny seeds on threadlike attachments and dispersed by birds.

Species	Gender	Fruit type	Pollination mode	Growth habit	Chromosome number: 2n unless otherwise indicated	Polyploid	Successional status	Fruit set confirmed in isolated female or emasculated hermaphrodite	Confirmed apomixis
Alectryon excelsus subsp. *excelsus*	D	F	E	T	32	No	Forest	Yes	No
Aristotelia serrata	D	F	E	T	28	No	Seral	No	No
Carpodetus serratus	G	F	E	T	30	No	Seral & forest	No	No
Coprosma areolata	D	F	A	S	22 (N)	Possibly	Seral & forest	No	No
Coprosma crassifolia	D	F	A	S	132	Yes	Seral & forest	No	No
Coprosma parviflora	D	F	A	S	132	Yes	Seral & forest	No	Yes
Coprosma propinqua	D	F	A	S	44	Possibly	Seral	Yes?	No
Coprosma robusta	D	F	A	T	44	Possibly	Seral	No	Yes
Coprosma rotundifolia	D	F	A	S	44	Possibly	Seral & forest	No	No
Coprosma serrulata	D	F	A	S	NA	Yes	Subalpine	No	Yes
Coprosma waima	D	F	A	S	44	Possibly	Forest	No	Yes
Corynocarpus laevigatus	G	F	E	T	44-46	No	Forest	Yes	No
Griselinia littoralis	D	F	E	T	36	No	Seral & forest	Yes	No
Hedycarya arborea	D	F	E	T	57 (N)	Yes	Forest	No	No
Melicope simplex	D	N	E	S	36	No	Forest	No	No
Melicytus ramiflorus	D	F	E	T	32	No	Seral & forest	No	No
Meryta sinclairii	D	F	E	T	48	?	Seral & forest	Yes	No
Muehlenbeckia australis	D	F	E	L	20	No	Seral	Yes	No
Muehlenbeckia complexa	D	F	E	L	20	No	Seral	No	No
Myrsine australis	D	F	E	T	46	No	Seral & forest	No	No
Passiflora tetrandra	D	F	E	L	12 (N)	Yes	Forest	No	No
Pennantia corymbosa	D	F	E	T	50	No	Seral & forest	No	No
Pittosporum eugenioides	D	N	E	T	24	No	Seral & forest	No	No
Pittosporum tenuifolium	D	N	E	T	24	No	Seral & forest	No	No
Plagianthus regius subsp. *regius*	D	N	E	T	42	No	Seral & forest	No	No
Pomaderris hamiltonii	H	N	E	S	36	Yes	Seral	Yes	Yes
Pomaderris phylicifolia	H	N	E	S	36	Yes	Seral	Yes	Yes
Pseudopanax arboreus	D	F	E	T	48	No	Seral & forest	No	No
Pseudopanax crassifolius	D	F	E	T	48	No	Seral & forest	No	No
Rubus schmidelioides	D	F	E	L	28	Yes	Seral & forest	No	No
Schefflera digitata	D	F	E	T	24	No	Seral & forest	No	No
Streblus heterophyllus	D	F	A	T	14 (N)	No	Forest	No	No

a relatively common tree in modified conifer/hardwood forest up to about 500 m above sea level (Wilson 2013). *Hedycarya arborea* is dioecious, entomophilous, fleshy fruited, and has a very high as yet unresolved somatic number of very small chromosomes that requires further study (see Table 1; also de Lange & Murray 2002). Its seeds germinate readily and seedlings grow relatively rapidly. In addition, vigorous basal stem sprouts are a feature of most plants from saplings to mature trees. All these features make it a prime candidate for facultative apomixis, although we lack as yet confirmation.

Corynocarpus laevigatus

Known as karaka or New Zealand laurel on the mainland, and kopi in the outlying Chatham Islands, *Corynocarpus laevigatus* is of particular interest as a putative apomict in view of its much debated taxonomic status, origin and natural distribution, widespread translocation and cultivation by Polynesian seafarers and settlers, and its subsequent invasion of disturbed and semi-natural forests, both in the New Zealand Botanical Region and further afield.

The species is endemic to New Zealand and is the southernmost member of an ancient, isolated, south-west Pacific genus of five distinct species (e.g. Philipson 1987; Molloy 1990; Wagstaff & Dawson 2000), with a history in New Zealand dating back to the Early Miocene about 20 MYA (DA Lee, Geology Department, University of Otago, pers. comm.), based on fossil fruit impressions comparable with the mature fruit and reticulate fibrous endocarp of *C. laevigatus* (cf. Campbell 2002; Figs. 1&2; Kirk 1889, Plate 88). *Corynocarpus laevigatus* has a high, probably derived, chromosome number of 2n = 46 (Dawson 1997), is gynodioecious (Garnock-Jones et al. 2007), apparently entomophilous, and female plants with empty anthers (staminodes) produce ample quantities of large fleshy fruit following flowering. Copious crops of fruit are produced by female plants, and poor to nil fruit by hermaphrodite plants (Moore 1986; Garnock-Jones et al. 2007; pers. obs.). The fruit is dispersed by the New Zealand and Chatham Island pigeon (parea, *Hemiphaga chathamensis*), or falls from trees resulting in dense carpets of seedlings beneath female trees and little else. The seeds germinate readily and seedlings grow rapidly when away from the influence of parent trees on frost-free, well drained fertile sites protected from strong winds, forming deep-rooted fast-growing saplings which begin to flower when about 10 years old. It has the ability to reproduce vegetatively from basal stem sprouts after crown damage.

From its natural habitat in northern New Zealand, *C. laevigatus* was translocated by early Polynesian seafarers and settlers to coastal and inland districts in the North Island and northern South Island, some northern offshore islands such as the Three Kings, and outlying islands such as the Chathams and Kermadecs and cultivated as a much valued tree crop (Molloy 1990). Over time, *C. laevigatus* has spread naturally from many translocation sites into nearby disturbed indigenous forest remnants that it is now almost impossible to distinguish original from culturally induced stands with certainty (cf. Cockayne 1958; Leach & Stowe 2005). In some localities this putative apomict is described as a weedy invader (e.g. Costall et al. 2006).

Griselinia littoralis

Widely known as broadleaf, *Griselinia littoralis* is a shrub to tree of variable form and stature, occurring throughout New Zealand as a frequent component of lowland to montane conifer/hardwood forests, montane and subalpine beech forests, and subalpine low forest, shrubland and wetland, as well as across a range of successional communities, particularly on sites recovering from fire or logging.

Griselinia littoralis is dioecious, entomophilous, produces fleshy fruit, and has a relatively high, probably derived, chromosome number of 2n = 36. Although comparatively short in stature, *G. littoralis* is long-lived and notable on fertile sites for the large girths it can achieve by its ability to withstand fire and continue to grow from basal stem sprouts. Female plants, including isolated trees, produce large quantities of fruit that are dispersed by birds, giving rise to abundant fast-growing seedlings.

Under the heading '*Griselinia littoralis* bush', Wardle (1991) described and illustrated several examples of conifer/hardwood and beech forests disturbed by fire and milling in eastern South Island, followed by secondary successions involving *Griselinia littoralis*, and other putative apomicts such as *Aristotelia serrata*, *Carpodetus serratus*, *Melicytus ramiflorus*, *Myrsine australis*, *Plagianthus regius* subsp. *regius*, *Pittosporum eugenioides*, *Pittosporum tenuifolium*, *Pseudopanax arboreus*, *Pseudopanax colensoi* var. *colensoi* and *Pseudopanax crassifolius*.

Of special interest are the dense enclaves of *Griselinia littoralis* within beech forests that have been disturbed by early anthropogenic fires (Wardle 1991, Fig. 8.7), often on soils containing recent beech charcoal (Molloy et al. 1963). The recovery of beech forest on these sites is principally by marginal migration of beech from existing beech forest, and is very slow and apomixis may have permitted these *Griselinia littoralis* enclaves to become semi-permanent. *Griselinia littoralis* also forms stands on former lowland to montane conifer/hardwood sites as confirmed by buried charcoals, or surface and buried wood.

Coprosma propinqua

This species, in its several forms, occurs throughout New Zealand in a range of habitats from high rainfall, warm climate, estuarine and freshwater wetlands to semi-arid, frosty, drought-prone, rupestral sites. *Coprosma propinqua* is probably the most widespread and common indigenous shrub, best known as a prominent member of primary or secondary 'grey scrub' (*sensu* Meurk et al. 1987; Wardle 1991); a uniquely New Zealand woody plant community of divaricating shrubs (see below). *Coprosma propinqua* is dioecious, anemophilous, produces fleshy fruit dispersed by birds leading to numerous seedlings, and has a high, probably derived, chromosome number of 2n = 44.

A cultivated, strictly female plant of *C. propinqua* was reported by Wardle (1971) as regularly producing a full crop of drupes in his Christchurch garden, which in turn resulted in many seedlings beneath it. Initially he considered apomixis a possibility, but noted that some seedlings resembled F1 plants of the hybrid *C. propinqua* x *C. robusta*. Others were similar to F2 seedlings, with some resembling the mother plant. *Coprosma propinqua* is uncommon in Christchurch gardens, but *C. robusta* is frequently cultivated, often as a hedge plant, and volunteers readily. Airborne pollen of *Coprosma* was counted from a microscope slide exposed within the canopy of Wardle's cultivated plant. From this he concluded that *C. propinqua* 'is efficient, but undiscriminating in its anemophily'. This situation is replicated in Riccarton Bush where F1 hybrids between the common *C. robusta* and the uncommon *C. propinqua* occur, with seedlings of hybrids and those representing both parents

apparent. As noted in my introduction, both apomictic and amphimictic seed production have been confirmed in the population of *C. robusta* in Riccarton Bush (Heenan et al. 2002), so that sexual reproduction, including hybridisation, can also occur with a level of apomixis in both species.

Meryta sinclairii

The puka, *Meryta sinclairii*, provides a striking example of the link between apomixis and the rapid colonisation of degraded forest habitats by secondary successions of woody plants. As reported by Godley (2006), the endemic *Meryta sinclairii* is found wild only on the offshore Hen and Chickens and Three Kings Islands, and not on the mainland of New Zealand. It is a species with tropical affinities, along with several others in these islands.

Meryta sinclairii is dioecious, produces fleshy fruit, and is entomophilous with a high, probably derived, chromosome number of $2n = 48$ (Dawson 2008); traits characteristic of some other putative apomicts already discussed. From observations carried out over several years on a cultivated isolated female tree in Wellington, Godley (2006) noted that each year this tree 'regularly produced a good crop of fruit. And each year, as the gardener told me, seedlings came up under this tree'. From these observations, Godley suspected that female trees of *Meryta sinclairii* can produce seeds without pollination, adding the comment 'Biologists call this apomixis'. However, in contrast to other putative woody apomicts discussed here, *Meryta sinclairii* appears to lack the capacity to resprout after damage.

Exemplar sites

There are several situations in New Zealand where disturbance and pre-existing forest composition have resulted in vegetation communities with a high concentration of putative apomictic trees, lianas and shrubs. One of these, regenerating subcanopy communities in lowland forests, has been discussed above using the example of Riccarton Bush. Others include the grey scrub communities of the eastern South Island; and shrub and forest communities of offshore and outlying islands.

Eastern South Island

Large areas of the eastern South Island are covered in scrub to low forest which includes numerous species but prominently *Aristotelia fruticosa*, *Coprosma crassifolia*, *Coprosma intertexta*, *Coprosma propinqua*, *Coprosma rigida*, *Coprosma tayloriae*, *Coprosma virescens*, *Corokia cotoneaster*, *Discaria toumatou*, *Myrsine divaricata*, *Melicytus alpinus*, *Muehlenbeckia complexa* and *Olearia odorata*, and the lianas *Clematis mārata, Muehlenbeckia australis*, and *Rubus schmidelioides* (Fig. 4). Where this community occurs within South Island pastoral lands, its spread could have been enhanced by the presumed capacity of many of its component species to produce seed apomictically, by their positive response to the aerial application of phosphatic fertiliser to stimulate the growth of associated pasture plants, and by their capability to resprout following fires (cf. Burrows 1994; Wiser et al.1997).

The Otago Lakes area is the best documented of these grey scrub areas. Present distribution of indigenous forest in the Upper Clutha district of Otago, and the Holocene history of fires in this district, have been described in detail by Wardle (2001a, b), and more broadly earlier by Molloy et al. (1963). The fertile

soils of this area are derived from nutrient-rich schistose parent materials. Today, tall beech (Nothofagaceae) forest is present from the valley floors to the upper tree limit in the higher rainfall north-western headwaters feeding Lakes Wanaka, Hawea and Wakatipu, with fire-induced vegetation dominating southwards and eastwards down the rainfall gradient, apart from isolated pockets of relict beech forest in topographic refugia protected from fires. On the north-west facing slopes above the Makarora River and Lake Wanaka (44°18´ S, 169°10´ E, 600–1500 m a.s.l.), fire-induced vegetation consists of extensive areas of bracken (*Pteridium esculentum*) maintained by repeated burning; small seral stands of *Kunzea robusta* (de Lange 2014; not suspected of being apomictic), an erect small tree with spreading branches; and *Kunzea serotina* (de Lange 2014), a short-statured, fastigiate shrub that forms semi-permanent stands on the dry frosty terraces between Hawea and Wanaka, and the dry hillsides at Bendigo (Burrell 1965; Wardle 2001a). However, successional hardwood communities are vigorously colonising unburnt bracken and are dominated by the putative apomicts *Aristotelia serrata*, *Carpodetus serratus*, *Coprosma lucida*, *Griselinia littoralis, Myrsine australis*, *Pittosporum tenuifolium*, and *Pseudopanax crassifolius*. Other species less likely to be apomict, such as the cosexual *Coriaria arborea* and the monocot tree *Cordyline australis*, take a prominent part in the successions (Fig. 2). *Prumnopitys taxifolia* and other native conifers once occurred on lower slopes above these lake edges in a zone of mixed conifer/beech/hardwood forest that flourished prior to anthropogenic fires (Holloway 1954; Wardle 2001a, b). The reinstatement of these original forests, which at one time covered a large part of eastern South Island (Molloy et al. 1963), is likely to be very slow, if achieved at all, in the absence of reliable conifer and other seed sources, and some of these successional hardwood communities may become semi-permanent.

Offshore islands

The cultural history, vegetation, flora, fauna, and detailed records of change on the offshore Three Kings Islands are well documented, especially for Great Island, the largest in the group (Baylis 1948, 1951; Bellingham et al. 2010). According to Baylis (1948), Great Island was originally covered by *Meryta sinclairii* forest close to the sea, and elsewhere by mixed coastal forest dominated by species found in coastal forests on the nearby North Auckland mainland and adjacent islands. Local endemics were probably dominant on stony soils and in exposed situations, and some were present as subdominants in tall coastal forest. On Great Island especially, this vegetation was almost entirely destroyed by the fires and cultivations of the Polynesian settlers who occupied the islands from the early 1600s until about 1840. Following their departure, some regeneration occurred but may have been retarded by the goats and pigs left on the island by the departing settlers. By that time, *M. sinclairii* had disappeared from Great Island and had not reappeared by 1899 when goats were re-introduced to provide food for shipwrecked sailors. Goats subsequently increased in such numbers that forest regeneration was halted and in most places the vegetation was dominated by the Three Kings endemic *Kunzea triregensis* (de Lange 2014). In 1946, all goats on Great Island were destroyed because of the threat they posed to the extinction of plants and animals peculiar to the Island. The response was instantaneous, and by the end of 1947, a year later, seedlings of the original forest dominants were evident, including those of *M. sinclairii* which, according to Baylis (1948), 'must have been carried by birds from other

Figure 2. Lower slopes of the McKerrow Range above the delta of the Makarora River, Lake Wanaka, showing the early stages of hardwood succession on land previously maintained in bracken fern by repeated burning (Photo: Brian Molloy 2006).

Figure 3. The Chatham Island robust entity of *Muehlenbeckia australis*, forming a dominant cover to the virtual exclusion of other woody plants, South East Island (Photo: Jeremy Rolfe 1985).
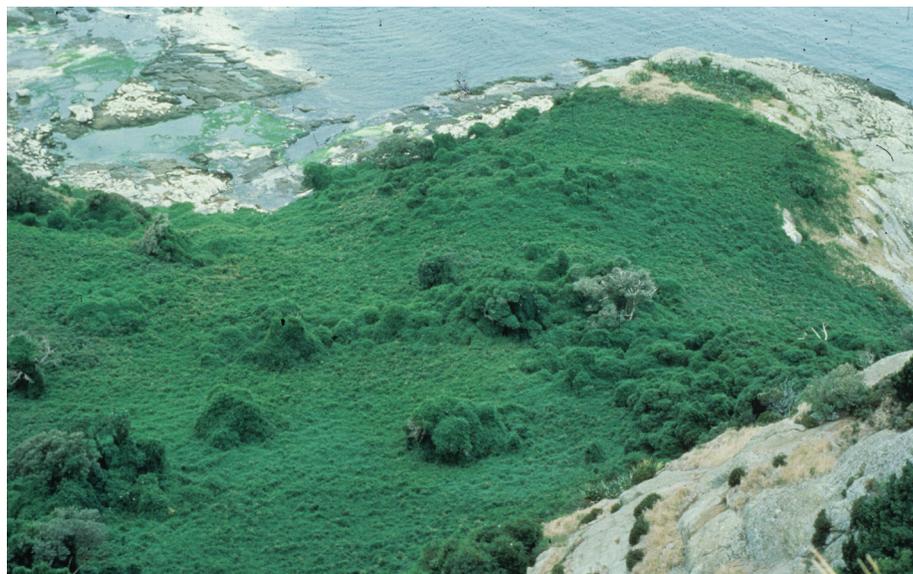
Figure 4. Large community of grey scrub of *Coprosma propinqua* and associated shrubs and lianas, on fertile skeletal schistose soils above Waikerikeri Creek, Dunstan Mountains, Otago (Photo: Brian Molloy 2007).

Figure 5. Dense stand of *Meryta sinclairii*, with its characteristic large leafy canopy, on the east face of the ridge between North-West Bay and South-East Bay, Great Island, Three Kings Group (Photo: Anthony Wright 1982).

islands of the group', in particular North-East and South-West Islands, where both he and Cheeseman (1891) recorded *M. sinclairii* in pure stands in places. In 1951, seedlings of *M. sinclairii* were common on slopes facing South-East Bay, with North-East and South-West islands as the main seed sources, and red-billed gulls (*Larus novaehollandiae*) the principal carriers (Baylis 1951). Thirty-six years after the removal of goats, dense stands of *M. sinclarii* had returned to Great Island (Fig. 5), although Baylis (1951) did not consider pure stands a stable climax there, even close to the sea.

Facultative apomixis may well form part of the reproductive strategy of other dioecious endemic and indigenous woody plants on Great Island such as *Alectryon excelsus* subsp. *grandis*, *Coprosma macrocarpa* subsp. *macrocarpa*, *Coprosma rhamnoides*, *Melicope ternata*, *Melicytus* aff. *ramiflorus*, *Myrsine oliveri*, *Passiflora tetrandra*, *Pittosporum fairchildii*, *Streblus smithii*, and the rarities *Elingamita johnsonii* and *Pennantia baylisiana*.

Outlying islands

The tree flora of the outlying Chatham Islands has few species, and no conifers. Leaving aside the tree ferns and the palm *Rhopalostylis* aff. *sapida*, 15 small to larger hardwood tree species are indigenous to the Chatham Islands, and 14 considered endemic, including two recently described species, *Myoporum semotum* and *Olearia telmatica* (de Lange et al. 2011).

From the exposed coast inland, the Chatham Island lowland or maritime forest, such as it is today after much disturbance by Polynesian and European settlers, is dominated by the cosexual *Olearia traversiorum* and *Corokia macrocarpa*, the dioecious putative apomicts *Myrsine chathamica*, *Melicytus chathamicus*, *Coprosma chathamica*, *Plagianthus regius* subsp. *chathamicus*, and the naturalised putative apomict *Corynocarpus laevigatus* has spread rapidly as an invasive. Like most of their counterparts in mainland New Zealand, these putative apomicts have the ability to resprout after disturbance, with female plants producing abundant fruit and seedlings, which in turn can lead to their local dominance, especially

the clonal, near-endemic, *Myrsine chathamica*.

Remaining stands of the endemic and indigenous tree species are best seen on the well-drained fertile coastal sands of the northern and eastern coasts, extending inland as scattered stands on older dunes enriched by windblown sands, gradually decreasing in numbers in a transition zone of mixed sand and peat, finally giving way to heath-like low forest or shrub communities on deep peat formerly dominated by the peat-forming and highly flammable cosexual *Dracophyllum arboreum* and its litter (Wright 1959). The above putative apomictic species also occur, albeit in lesser numbers, on enriched colluvium and alluvium derived from schistose, volcanic and limestone rocks in the northern parts of Chatham Island, and on the southern tableland and its steep gullies and coastal cliffs, notably in the Te Awatapu slumped area.

There is presumptive evidence also for apomictic seed production in the following woody species: the dioecious undershrub or small tree *Piper excelsum* subsp. *excelsum*, common in maritime forest stands released from animal grazing and browsing; the locally abundant dioecious sand coprosma *Coprosma acerosa*, and the gynodioecious sand daphne *Pimelea villosa*; the dioecious *Coprosma propinqua* var. *martinii*, especially on enriched riparian sites around Lake Huro; the dioecious *Leptecophylla robusta* forming successional heath-like communities following the burning of *Dracophyllum arboreum*; and the local robust form of the dioecious liana *Muehlenbeckia* aff. *australis*, frequently seen in forest and shrubland remnants, forming a near-monoculture to the virtual exclusion of other woody species on South East Island (Fig. 3). Female plants of all these species produce copious quantities of fruit and abundant seedlings in the absence of grazing and browsing animals and repeated burning.

Conclusion

The hypothesis I propose here for facultative apomixis being a common reproductive strategy among trees, shrubs and lianas in New Zealand is largely based on the observation of

abundant fruit set in female plants isolated from pollen sources and the subsequent germination of seeds and emergence of seedlings beneath the fruiting plants. There is an inherent bias towards dioecious species in this approach as it is more difficult to assess apomixy in hermaphrodite, monoecious or gynodioecious plants without extra evidence. And further, with the exception of a handful of species, my examples are putative only and await unequivocal confirmation through breeding system and cytological evidence as advocated by Nogler (1984). Notwithstanding this reservation, there is good reason to suggest that facultative apomixis – which permits a range of sexual interactions – may be far more prevalent among indigenous New Zealand woody seed plants than previously thought. Future studies should be extended to other indigenous woody species and genera, especially dioecious taxa, but also those with gynodioecious and hermaphroditic breeding systems.

The putative woody apomicts appear to have the significant ecological trait of rapid colonisation of disturbed habitats similar to apomictic herbs which have been shown to be successful colonists of disturbed sites, e.g. *Taraxacum* spp. (van Dijk 2003) and *Pilosella officinarum* (=*Hieracium pilosella*) (Houliston & Chapman 2004). Knowledge about apomixis status may be of potential benefit for the management of existing forest remnants and the design and management of restoration projects. As pointed out by Heenan et al. (2003), the extent of apomixis and sexual reproduction in individual plants and populations is also likely to have important implications for species conservation, in particular for those species with sparse, small, or fragmented populations.

Acknowledgements

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