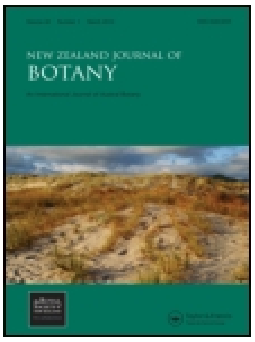

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The endemic tree *Corynocarpus laevigatus* (karaka) as a weedy invader in forest remnants of southern North Island, New Zealand

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Abstract Native species can display invasiveness even in their natural systems. *Corynocarpus laevigatus* (Corynocarpaceae), karaka, is a tree species apparently native to the north of the North Island, New Zealand, with a history of human cultivation further south, where it appears to be outcompeting other native tree species. Invasiveness was assessed by comparing vegetation in paired plots with and without karaka at 14 sites in forest remnants in the lower half of the North Island. Potential to spread was estimated via dispersal and recruitment patterns around parent trees. Karaka has several "weedy" characteristics. Most seed falls near the parent, but recruitment apparently improves outside the shady canopy, resulting in concentric invasion rings. Compared with nearby non-karaka plots, karaka plots have fewer non-karaka trees, lower abundances of seedlings of other woody species, and slightly higher numbers of exotic species. Karaka appears to be homogenising vegetation, through reduction in herb cover and increase in shrub cover and probably eventual replacement of canopy trees. With its range anthropically extended, management of karaka's invasiveness appears necessary in lower North Island, South Island, and the Kermadec and Chatham Islands, involving elimination or control, depending on local cultural values.

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Keywords competition; *Corynocarpus laevigatus*; ethnobotany; invasion; forest regeneration; fragment; homogenisation; New Zealand; remnant; seedling; weed; woody

INTRODUCTION

A weed species is generally considered to be an exotic species naturalising in a system in which it has no (recent) history of occupation, and so causing management concern (Williams & West 2000). Such species potentially have serious effects on pre-existing vegetation (e.g., Groves & Burdon 1986; Drake et al. 1989; Williamson 1996). However, a species does not need to be exotic to become ecologically "out of balance" (Carr 2001), although something in its ecosystem has to change as a result of anthropic activities before its responses can reasonably be considered weedy. Native species have become weedy following human modification of the environment in Victoria, Australia, including species native to Victoria itself (Carr 2001). In New Zealand, the liane *Muehlenbeckia australis* is aggressive around the edges of Manawatu, lower North Island, forest remnants, within its natural range (M. Greenwood pers. comm; GLR pers. obs.), and a number of other native species display weediness (Williams & West 2000).

A New Zealand "weedy native" species is *Corynocarpus laevigatus* J.R.Forst. & G.Forst. (Corynocarpaceae), an endemic tree called karaka by the first (Maori) settlers to the New Zealand mainland, wairarapa by Moriori (Shand 1896), and latterly kopi by Chatham Islanders. Several reports indicate its potential weediness. Esler (1974) recorded that karaka increased in lowland forest remnants of the Manawatu after stock were removed. In the adjacent Horowhenua district, Duguid (1990) noted that karaka had "increased in bush remnants and

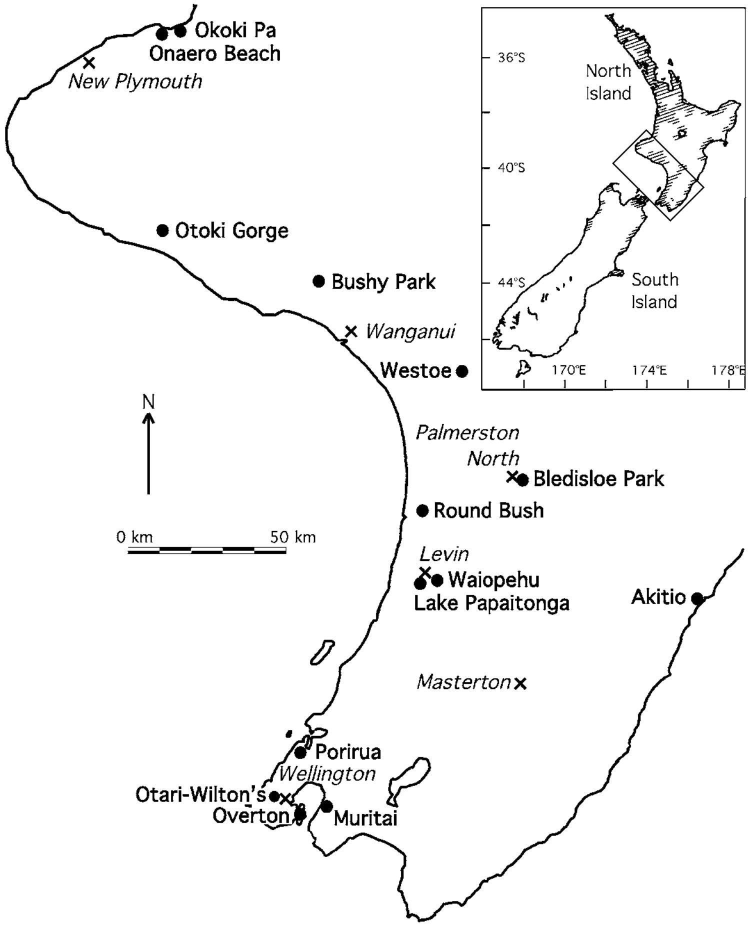


Fig. 1 Location of the fourteen areas sampled for karaka and non-karaka plots (●) in relation to major urban areas (×, italics). Hatching, distribution of karaka according to Sawyer et al. (2003).

[was] now shading out other vegetation beneath its heavy canopy". Gabites (1993, p. 42) noted it spreading into Wellington bush areas, appearing in the Wellington Botanical Gardens (in native forest areas) after 1875 (Gabites 1993, p. 97). Sawyer et al. (2003) reported that there were "several places where aggressive regeneration of karaka is leading to replacement of existing plant communities by stands of karaka", including the important conservation reserve of Kapiti Island where karaka formed "dense thickets" after elimination of vertebrate pests. It is also colonising and establishing populations in several Manawatu forest remnants (P. R. van Essen & M. Greenwood pers. comms; Greenwood 2004). Thus, karaka may be invasive even in its own country, a situation which we examine here.

Corynocarpus laevigatus occurs in coastal and lowland forest of northern North Island, coastal regions of the lower North Island and northern South Island, and down the dry east coast to Banks Peninsula (Fig. 1), as well as in the Kermadec Islands and Chatham Islands (Sawyer et al. 2003; Stowe 2003). It grows 15–20 m tall, has large (to 30 cm long), thick, elliptic-oblong, glossy leaves, and prolific production of large, orange drupes usually around 30–40 mm long (van Essen & Rapson 2005) and up to 63 mm (Platt 2003), which are conspicuous in late summer and autumn (Salmon 1993; Sawyer et al. 2003). As a genus *Corynocarpus* is taxonomically isolated by characters such as its petaloid scales and discrete nectaries (Philipson 1987). Currently it is placed in the Cucurbitales, in the monogeneric family Corynocarpaceae, which probably evolved in the palaeotropics (Wagstaff & Dawson 2000). The ancestral taxon had two independent southward radiations, one to New Guinea, Solomon Islands, Vanuatu, and Australia (Queensland and northern New South Wales), and the other to New Caledonia, where the endemic species *C. dissimilis* is closely related to *C. laevigatus*, and on to the New Zealand region (Molloy 1990; Wagstaff & Dawson 2000; cf. Stevenson 1978).

Fossils of fruits resembling karaka have been found in a Miocene deposit 5–24 million years old in a deltaic coastal ecosystem in eastern Southland, South Island (Campbell 2002). Karaka is relatively frost-intolerant (Molloy 1990), and firmly coastal in the South Island, though it can survive as far south as Dunedin when planted (Bannister et al. 1996). Thus, it was probably eliminated from southern New Zealand during glacial periods, to survive only in the northern North Island or offshore islands. Karaka pollen does not preserve well (Macphail & McQueen 1983) and is poorly recorded by palynological studies, although palynology led Mildenhall (1980) to suggest that it arrived as late as the Quaternary. Byrami et al. (2002) and Wilmshurst et al. (2004) have recorded karaka pollen, the latter from deposits up to 300 years old, during an early period of Maori planting.

Karaka drupes were widely used by Maori as a food source, the dry flesh for immediate consumption, while the kernels, called kopia by Maori, or Maori peanut or karakaranut by Europeans (Anon. 1988; Sawyer et al. 2003), could be stored. Lengthy preparation of kernels was required to remove the neurotoxin karakin (Skey 1871; Best 1942; Bell 1974), an especial danger to children, as was the stringent treatment thereof (Skey 1871; Best 1942). However, Platt (2003) suggested that the real toxin was a seed-borne fungus, as animals do eat the fruits (Mitcalfe 1969; Stevenson 1978; Anon. 2004; cf. Connor 1977), which seldom persist under a parent tree even in an ungrazed area (GLR pers. obs.). The value of karaka as a source of food and medicine (Macdonald 1973, p. 99) was such that it was deliberately planted at pa sites (naturally defensible positions fortified with earthworks and/or stockades) and other areas used by Maori (e.g., Molloy 1990; Salmon 1993; Sawyer et al. 2003; Stowe 2003). Early European records indicate substantial groves of karaka in many areas of New Zealand in the nineteenth century. A once extensive grove near Massey University, Palmerston North, was established by descendents of the Aotea canoe (Anon. 1988). Beckett (1963) reported a grove 6 ha in extent near Red Rocks, Wellington, about 1890, and McFadgen (1963) a grove 0.8 km long in the Wainuiomata valley near Wellington in 1859. Thus, Maori greatly altered the natural distribution of karaka within New Zealand.

Maori folklore states that karaka was brought to New Zealand from their ancestral homeland of Hawaiki (Best 1942), and at least two "introductions" are recorded, one in the Aotea canoe (Smith 1913) about AD 1350, from an island called Rangituhua (equated with Sunday/Raoul Island in the Kermadec Islands group; Best 1942, p. 45) to Patea River banks, south Taranaki (Houston 1965), and one in the Nukutere canoe from which karaka were sown at Waioeka, Bay of Plenty (Best 1925, p. 91). Karaka may have originated in the Kermadec Islands, as oral history suggests (Buck 1949, p. 46, 63), to be transferred thence to New Zealand, but karaka has limited occurrences on the main island, Raoul, and some adjacent islets (Sykes et al. 2000), where it formed "lofty trees" with "thick patches" of seedlings (Oliver 1910, but see Sykes et al. 2000, p. 101). Stevenson (1978) suggested that Maori actually took karaka in the reverse direction, from the New Zealand mainland to Raoul Island. If Maori brought karaka seeds across water as oral history describes, then its probable origin was Northland, New Zealand, or nearby islands (Molloy 1990), but a wider Pacific origin is improbable, as it is not water-dispersed (Oliver 1910; JAC pers. obs.).

When the ancestors of the Moriori people journeyed from New Zealand to the Chatham Islands about 400–800 years ago (King 2000) in the canoe Rangimata, they carried karaka seed to the north coast of Rekohu or Wharekauri, local names for Chatham Island (Shand 1896). This translocation is supported by the discrepancy between Rangimata (Shand 1904) and later traditions (Dieffenbach 1840) about the availability of timbers suitable for canoe-building. Once on the island karaka could be readily dispersed by parea, the large local woodpigeon, *Hemiphaga chathamensis* (Powlesland et al. 1997). Dieffenbach (1840) recorded that karaka formed "the largest part of the forest", with trees growing to 3 feet in diameter, to eventually dominate the vegetation around the large, central lagoon and the northern portion of the island, but is currently not a component of the less disturbed southern plateau vegetation (GLR pers. obs.), although it does occur in coastal gullies (Powlesland et al. 1997). Preliminary genetic evidence suggests that Chatham and Kermadec karaka are identical to mainland material (Wagstaff & Dawson 2000).

Thus, karaka's natural distribution is probably restricted to the coastal districts of northern North Island (Molloy 1990; Leach & Stowe 2005), and it was dispersed from there by Polynesian voyagers to the Kermadec and Chatham Islands, as was originally concluded by Molloy (1990) from tree ecology, and is supported by recent detailed distribution studies (Stowe 2003; Leach & Stowe 2005). All other occurences represent human translocations and plantings or recent vertebrate dispersal. Therefore, in more southern areas of New Zealand karaka must be considered an invader into native forest, and may even be weedy there. Karaka's ability to become a weed has been demonstrated on the Hawai'ian islands of Kaua'i, Koke'e, O'ahu, and Moloka'i (Wagner et al. 1999). In 1929 it was spread by aircraft over Kaua'i to aid reafforestation and now forms dense shade in shrubland and forest from 500 to 1500 m a.s.l., endangering rare plants (Harris 2002; Sawyer et al. 2003).

Lowland forest remnants of the lower North Island, outside the natural range of karaka, were chosen for an extensive study of its invasiveness. Aims were to describe the invasion, both process and state, of karaka into native forest, to assess its effects on the vegetation, and to consider the future regeneration patterns of the forest. The approach was to use detailed measurements of dispersion and dispersal in parallel with studies of vegetation in paired plots, with and without karaka, sampled across the region.

METHODS

Site and plot selection

Fourteen sites were sampled within the lower North Island of New Zealand (Fig. 1; Table 1). All are lowland native forest remnants accessible to the public, mostly coastal, and fenced to exclude stock, though the Otoki Gorge karaka plot showed signs of recent grazing. Bushy Park, Otoki, Waiopehu, and Westoe are relatively undisturbed forest remnants averaging 12 km from the coast, the karaka at Westoe being descended from seed of two nearby trees which were planted in 1950 by the father of the current owner (J. Howard pers. comm.). Round Bush has been a landmark patch for coastal navigation since the 1840s, where karaka was noted as present in 1968 with seedlings occuring by the thousand (Esler & Greenwood 1968). Other sites are more disturbed, and some are near sites of former Maori kainga (villages), where karaka was probably planted (Molloy 1990; van Essen & Rapson 2005). The karaka plot at Lake Papaitonga, where a drought in 1973 led to extensive regeneration of karaka (Duguid 1990), was near the site of Te Reinga kainga with the non-karaka plot in nearby Manga-piko Gully (Adkin 1948, fig. 153). The sampled areas at Onaero and Okoki are both pa, with clearly preserved earthworks amongst the regenerating forest (Best 1975), the latter area having the largest known fruit in the Taranaki district (Jones & Simpson 1995, p. 108). The Akitio site is also a suitably defensible position, as pa, kainga, and karaka were found all along the North Island's lower east coast (Mitcalfe 1969).

At each of the 14 sites, areas for a karaka plot and a non-karaka plot were identified less than 200 m apart. These were as similar in environmental characteristics as possible, to facilitate comparisons between them. The karaka plot was determined by the presence of at least one mature karaka tree, and the non-karaka plot by the absence, as far as possible, of mature karaka trees. Within each area, one 20 × 20 m plot was placed as randomly as possible, considering the small size of some sites.

Also studied was a small (0.2 ha) revegetation project, Greenwood's Bush, established in 1954 on the margin of Palmerston North (Greenwood 2004). At this site in 1962, about 50 fruits of karaka were planted directly into the growing bush; many of these grew and are now producing seedlings.

The karaka invasion process

At each of the 14 sites, karaka dispersal was estimated from an assumed parent tree. A 50 m transect was laid from the mature karaka tree nearest the edge of the karaka plot, or of the karaka grove (if extending outside the plot), and angled randomly away from the plot. At 2 m intervals a 0.8 × 0.8 m quadrat was placed on either side of the transect line. Numbers of karaka seedlings within the pair of quadrats were recorded in the height classes 0–50 cm and 51–199 cm.

At Round Bush, where the karaka stand was well developed within the karaka plot, the dispersion of karaka was mapped by taking co-ordinates and diameter at breast height (DBH, 1.3 m above ground) of every individual of every woody species over 2 m tall. The plot was divided into 16 subplots, 5 × 5 m, within which all seedlings (<2 m tall) of all woody species were identified and counted.

In Greenwood's Bush, all stems of karaka ≥ 1 cm DBH were measured in February 2005.

Karaka invasion effects

At each of the 28 plots, altitude, and grid reference, aspect, and slope along the line of maximum slope of the perimeters of the plot were recorded (Table 1). A visual assessment was made of cover of ground flora (≤ 50 cm high), bare soil, litter, rock, and water (totalling 100%). Canopy openness was assessed as the amount of visible sky from 1.5 m above the ground (Table 1). All vascular plant species present, as shoots for herbaceous species, and as rooted individuals for woody species, were identified, and percent cover estimated (as a horizontally projected monolayer). Species were categorised as native or exotic, with karaka in the former class. The number and DBH of all karaka individuals over 2 m tall were recorded, as was diameter for all other trees ≥ 10 cm DBH rooted within each plot. A single-stem DBH value was calculated for all multi-stemmed trees.

To estimate future regeneration of karaka and other woody species within each plot, 10 (20 in the Round Bush karaka plot) 0.8 × 0.8 m quadrats were randomly positioned, and seedlings ≤ 50 cm high and 51–199 cm were counted and identified for all woody species plus *Rhopalostylis sapida* Wendl. et Drude and *Cordyline australis* (Forst.f.) Endl., two tree-like monocots.

Analysis

For the Round Bush karaka plot, with detailed dispersion data, tree distributions in space were graphed for karaka trees and for trees of all other species. Isolines, representing dispersion waves, were imposed in response to values for tree basal area (on a natural log scale) in Systat (1996). We assumed that size of stem matches age and, hence, date of establishment;

Table 1 Site locations and characteristics of the 14 areas sampled and plot characters for karaka and non-karaka plots. In vic., in vicinity; K, karaka plot; NK, non-karaka plot. The balance of ground cover (totalling 100%) is rock and/or water.

Site	Planted?	Size (ha)	Latitude and longitude	Altitude (m)	Distance to coast (km)	Plot	Aspect (°)	Slope (°)	Canopy openness (%)	Ground cover (%)		
										Plant	Litter	Bare Ground
Akitio	no	1	40°35'27.5"S 176°25'54.5"E	20	1	K	326	26	15	30	50	15
						NK	300	28	60	85	0	10
Bledisloe Park	no	5	40°27'47.7"S 175°37'4.2"E	20	36	K	205	30	20	5	74	15
						NK	218	26	30	5	70	25
Bushy Park	in vic.	110	39°47'50.5"S 174°55'26.6'E	100	9	K	41	10	15	15	85	0
						NK	71	11	35	20	80	0
Lake Papaitonga	in vic.	122	40°38'39.8"S 175°13'32.4"E	10	5	K	320	2	15	2	98	0
						NK	70	10	30	15	60	20
Muritai Park	maybe	2000	41°18'17.5"S 174°53'44.4"E	20	0.5	K	305	36	20	20	66	2
						NK	305	35	15	10	88	2
Okoki Pa	yes	17	38°59'17.3'S 174°25'33.9"E	120	1.5	K	118	2	40	10	74	2
						NK	71	2	20	3	91	2
Onaero Bay	yes	12	38°59'51.8"S 174°22'0.5"E	15	0.3	K	4	30	15	20	75	5
						NK	21	35	20	20	69	10
Otari-Wilton's	no	90	41°16'8.3"S 174°45'2.8"E	120	2	K	141	7	20	10	80	10
						NK	141	10	20	15	80	5
Otoki Gorge	no	20	39°34'47.3"S 174°27'19.9"E	80	6.5	K	218	36	50	10	74	15
						NK	308	24	20	40	55	5
Overton's Bush	maybe	1	41°17'56.9"S 174°49'49.9"E	10	0.1	K	65	40	40	15	80	5
						NK	76	23	20	15	80	3
Porirua	no	156	41°8'12.2"S 174°49'36.3"E	60	4	K	110	35	30	20	50	28
						NK	110	39	15	15	74	10
Round Bush	no	51	40°26'39.5"S 175°17'5.7"E	15	6	K	240	2	35	40	44	1
						NK	90	2	20	45	65	0
Waiopehu	no	15	40°37'35.0"S 175°20'34.2"E	60	13.5	K	210	1	20	15	85	0
						NK	330	1	25	15	80	5
Westoe	in vic.	5	40°6'41.3"S 175°26'17.6"E	60	22	K	284	2	20	45	55	0
						NK	240	2	25	5	80	5

Table 2 Descriptors of karaka invasion at the sampled sites for both karaka and non-karaka plots (20 × 20 m). Seedling averages are of 10 quadrats (0.8 × 0.8 m) per plot, except for the Round Bush karaka plot (20 quadrats). Two replicate plots for the Onaero karaka site were averaged (as no plot lacked karaka), and were excluded from grand averages. Averages in bold type differ significantly ($P < 0.05$, d.f. = 12) between plot types, by pairwise t-test for sites.

	Karaka trees						Non-karaka trees		Seedlings			Species richness		
	Number of trees	Mean DBH (cm)	Number of trees >10cm DBH	Mean dbh of trees >10cm DBH	Basal area (m^2/ ha)	Cover (%)	Number	Mean DBH (cm)	Number of species per plot	Total density (m^{-2})	Karaka density (m^{-2})	Total	Trees (>10cm DBH)	Exotic species
Karaka plots														
Onaero Bay	29.5	16.0	17.5	27.6	1.07	62.5	22.5	16.6	4.5	2.3	1.0	31.5	6.0	6
Akitio	6	8.5	2	11.4	0.05	10	11	22.3	4	5.3	3.9	39	7	13
Bledisloe Park	18	5.2	4	10.6	0.05	25	24	23.7	6	8.3	5.9	27	5	2
Bushy Park	45	2.9	2	32.1	0.19	50	37	29.0	6	38.3	26.7	30	8	1
Lake Papaitonga	3	39.9	3	39.9	0.49	50	30	29.2	7	4.7	1.1	23	8	0
Muritai Park	12	15.1	12	15.1	0.24	50	34	18.8	4	10.9	7.7	40	12	11
Okoki Pa	5	38.6	5	38.6	0.69	20	36	24.4	6	6.4	0.2	33	6	6
Otari-Wilton's	5	29.0	5	5.0	0.54	35	78	17.8	9	11.8	6.1	26	6	0
Otoki Gorge	13	21.2	12	22.2	0.82	40	14	25.5	6	4.2	0.5	52	11	2
Overton's Bush	58	8.0	12	30.9	1.44	75	24	19.7	2	12.8	11.9	21	7	3
Porirua	10	18.0	9	18.9	0.31	25	39	16.4	8	24.7	19.7	32	10	2
Round Bush	187	2.8	9	18.5	0.35	55	17	35.8	14	19.1	10.9	19	4	0
Waiopehu	30	7.8	11	16.3	0.27	30	16	28.6	6	12.5	9.1	24	7	0
Westoe	16	19.9	12	25.1	0.68	75	12	50.2	8	43.1	42.5	11	5	0
Average	**31.4**	**16.7**	**7.5**	**21.9**	**0.46**	**41.5**	**28.6**	26.3	6.6	**15.6**	**11.2**	29.0	**7.4**	3.1
Non-karaka plots														
Akitio	0	0.0	0	0.0	0.00	0.5	23	18.9	3	7.3	0.0	33	7	8
Bledisloe Park	1	2.0	0	0.0	0.00	1	24	25.4	9	1.9	0.5	22	3	2
Bushy Park	2	6.5	0	0.0	0.01	0.5	17	37.3	5	9.5	0.9	31	4	1
Lake Papaitonga	0	0.0	0	0.0	0.00	0.5	30	21.8	4	8.9	0.2	36	8	0
Muritai Park	0	0.0	0	0.0	0.00	5	10	20.2	8	1.6	0.3	35	8	1
Okoki Pa	0	0.0	0	0.0	0.00	0	74	19.7	6	8.4	0.0	28	6	1
Otari-Wilton's	0	0.0	0	0.0	0.00	0.5	35	24.3	8	10.0	0.2	24	5	0
Otoki Gorge	6	15.9	5	17.3	0.13	15	33	20.8	8	3.8	0.0	33	10	1
Overton's Bush	1	0.5	0	0.0	0.00	0.5	48	23.4	4	0.6	0.0	16	5	0
Porirua	0	0.0	0	0.0	0.00	0.5	46	18.2	8	6.8	0.2	32	9	1
Round Bush	0	0.0	0	0.0	0.00	0	35	26.4	6	13.3	0.0	23	5	0
Waiopehu	0	0.0	0	0.0	0.00	0.5	20	25.7	4	2.8	0.0	29	6	0
Westoe	0	0.0	0	0.0	0.00	0.5	27	41.0	2	3.3	0.5	18	6	1
Average	**0.7**	**1.9**	**0.4**	**1.3**	**0.01**	**1.9**	**32.5**	24.9	5.8	**6.0**	**0.2**	27.7	**6.3**	1.2

attempts to age karaka stems failed due to their copious parenchymatous rays and probably non-seasonal growth, growth rings being undetectable even on disks (Patel 1973; P. R. van Essen pers. comm.). Over the graph of karaka dispersion 100 random points were sampled for their isoline categories, and the same points were similarly sampled on the graph of non-karaka tree species. These categories were correlated (pairwise Pearson coefficient) to examine the coincidence of zones of karaka and non-karaka trees with similar basal areas. For the seedling quadrats, karaka and non-karaka woody seedling numbers were graphed.

Using data from karaka plots, karaka dispersal was plotted as distance from the parent karaka tree or grove against density of karaka seedlings in two height classes.

Differences between karaka and non-karaka plots in a range of environmental and summary variates calculated from the vegetation and tree demography data were tested by paired sample *t*-tests using Systat 6.0 (Systat 1996). Due to the dominance of karaka in the whole of the vegetation at Onaero Bay (60–65% cover; Table 1), the karaka and non-karaka plots at this site were treated as replicates; they are reported in summary tables but were otherwise excluded from the analysis.

Vegetation data for karaka and non-karaka plots (excluding Onaero), linearly related to each other, were analysed by Principal Component Analysis using Canoco (ter Braak & Smilauer 2002), looking at the distribution of plots in ordination space, and comparing these with the species' plot.

To examine the effect of karaka invasion on vegetation, the distances between the paired plots of each site (excluding Onaero) in four dimensional PCA ordination space were calculated, using presence/absence data as these were uninfluenced by the quantity of karaka present, and so avoided circularity. These distances, measuring vegetational dissimilarity between a karaka plot and its uninvaded non-karaka plot, were correlated (pairwise Pearson's correlation) with the difference in percent cover of karaka between the plots of each site, as well as a range of other measures of karaka invasion. Similar correlations were conducted against PCAs using the vegetation cover data (with a range of transformations), including and excluding karaka.

To identify which portions of the vegetation were responding to karaka invasion, changes in cover and diversity between karaka and non-karaka plots were calculated for each of the habit classes, tree, shrub, liane, fern, and herb (monocot or dicot), and correlated with differences in karaka variates between plots.

Seedling regeneration patterns were examined for a number of parameters reflecting abundance and diversity, using correlations with karaka invasion measures.

RESULTS

Site representativeness

Although occasional plants do occur further from the coast (D. Havell & P. R. van Essen pers. comms), all our sites were located at low altitudes, within 25 km of the coast, and were a mixture of naturally arising populations, such as Bledisloe, and populations established by humans, such as Okoki Pa (Table 1). No measurable populations were located in other areas. Sites were well dispersed amongst karaka habitat in the lower North Island, the only major gap being the lower east coast, where karaka is now largely present as isolated trees in pasture and so could not be sampled.

Plots from within a site paired up closely in PCA ordination space, based on their environmental descriptors, except for Lake Papaitonga, Round Bush, and Otoki Gorge (data not presented), where plots differed in aspect, slope, or litter cover. There were no significant differences between the karaka and non-karaka plots in canopy openness, and the various categories of ground cover (data not presented).

The karaka invasion process

Considering the karaka plots as examples of the karaka invasion process, the cover of karaka trees ranged from 10 to 75% (Table 2). Some plots had just a few large karaka tree present (e.g., Lake Papaitonga and Otari-Wilton's), while others had a large number of stems of varying size, including at least one large tree (e.g., Bushy Park or Round Bush). Karaka seedling density within karaka plots also varied, from <1 to >40 m^{-2} (Table 2).

The transects of karaka seedling density away from parent trees showed that just over half of the karaka seedlings under 50 cm in height were found within 6 m of the parent tree (Fig. 2). Between 8 and14 m from the parent, numbers of seedlings halved, then declined to <1 seedling m^{-2} over the last 25 m of most transects. Seedlings in the 51–199 cm height category (0.12 m^{-2}) were evenly spread over the length of the transects.

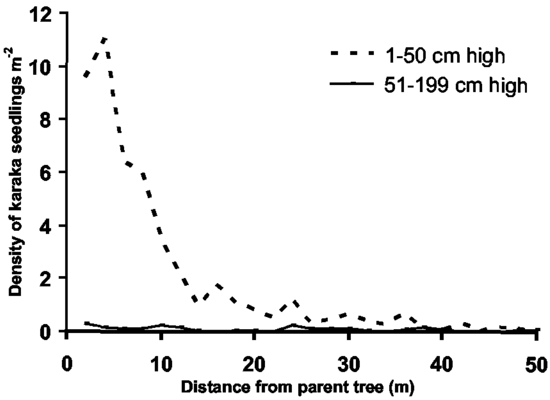


Fig. 2 Dispersal of karaka seedlings away from a parent tree, in two height cagetories, averaged over all 14 karaka plots.

At the Round Bush karaka plot, which was mapped in detail (Fig. 3A), *Dacrycarpus dacrydioides* (A.Rich.) Laubenfels forms most of the basal area, followed by *Laurelia novae-zelandiae* A.Cunn., both common trees in the bush remnant. However, karaka is the most common stem, with a reverse-J shaped demographic, so there is a high density of small stems and a few very large stems (Fig. 3B). The similar 0.2 ha plot from Greenwood's Bush contained 195 stems $\geq$1 cm DBH and 16 stems $\geq$20 cm DBH only 43 years after sowing (Fig. 3C). Seedling numbers exceeded 10 000, as a weeding party discovered in April 2005.

The detailed Round Bush map (Fig. 4A) demonstrates the pattern of spread of karaka within the area. Size-derived isolines of karaka dispersion show development of radial patches which appear around three points, apparently points of first invasion of karaka. High densities of karaka occur in areas of low basal area of other forest tree species (according to 100 random points sampling the plot isolines for karaka and non-karaka trees; karaka basal area = -0.22*(non-karaka basal area) + 3.5; $P = 0.001$). Seedling numbers in the 16 subplots into which the plot was divided show that karaka are 66% more common than all other species combined, and occur in a diagonal belt across the plot (Fig. 4B).

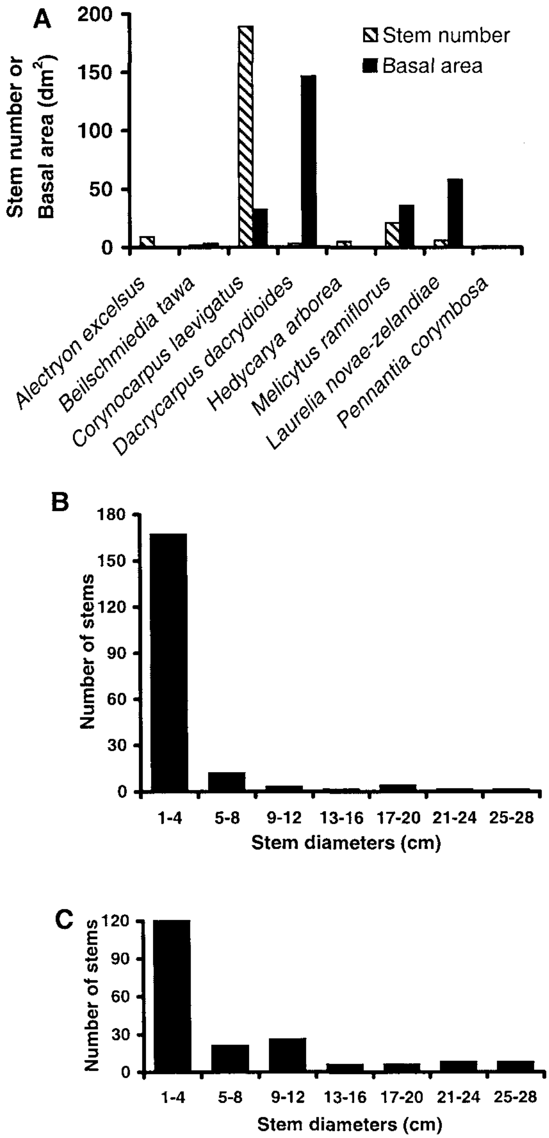


Fig. 3 Demography of woody plants in studied sites. **A**, Woody plant diversity of the dominant species by basal area (hatched) and stem number (open), for the karaka plot in Round Bush. Size (diameter at breast height) frequency distribution of karaka trees in **B**, the karaka plot of Round Bush, and **C**, Greenwood's Bush, a 0.2 ha stand, originating from 50 fruit planted in 1962.

Effects of karaka invasion

The expected differences occurred between the karaka and non-karaka plots; there were significantly more karaka, of larger diameters (both for total number and for stems $\geq$10 cm DBH), and with greater cover in the karaka plots (sample of 477 karaka, and 839 trees of other species $\geq$10 cm DBH; Table 2). Both the Onaero plots had many large karaka.

Karaka increased species richness by about 1 (i.e., karaka itself) in the karaka plots of the 13 sites,

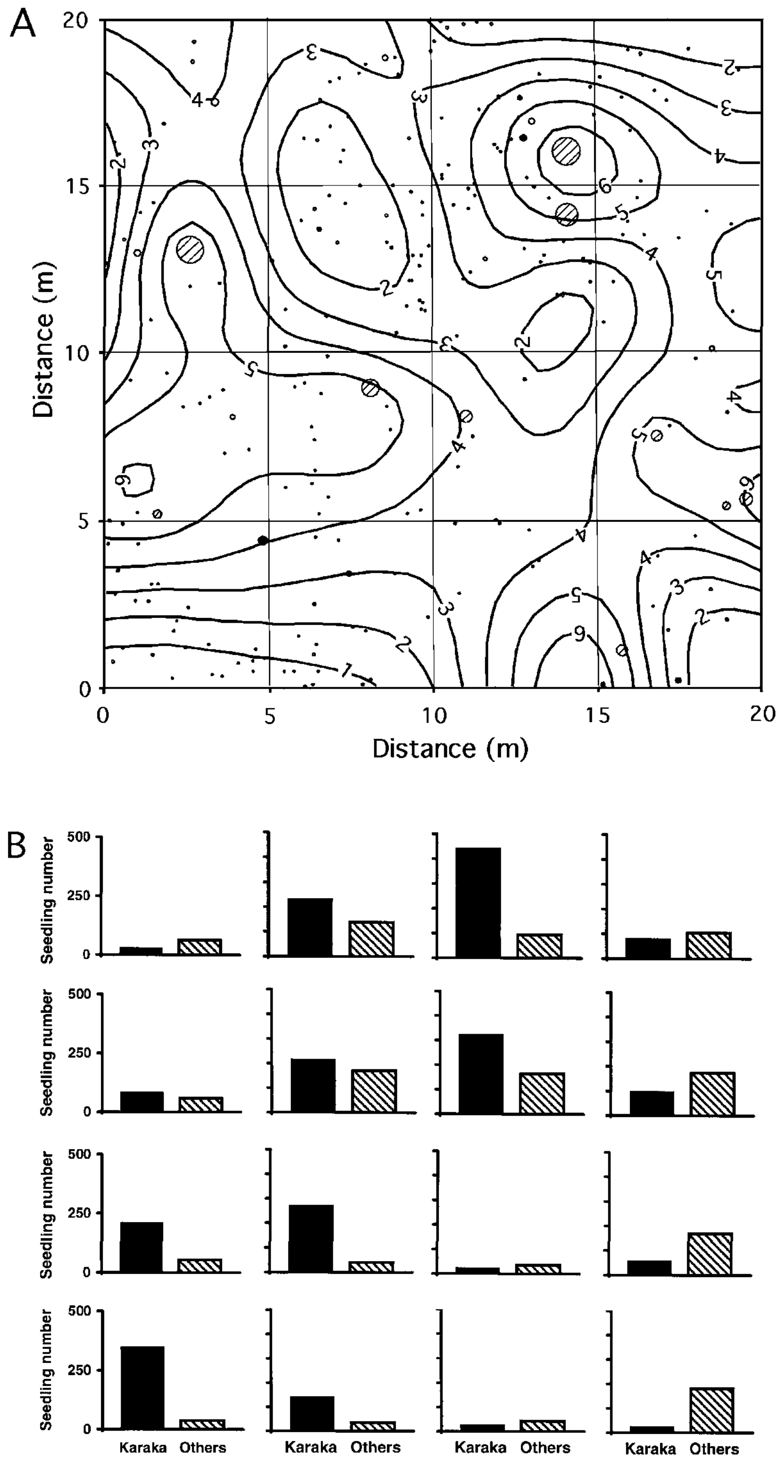


Fig. 4 Invasion pattern of karaka at the Round Bush karaka plot. **A**, karaka trees (solid symbols including dots) and other tree species (hatched symbols) in space, with size of symbol representing basal area. Isolines link areas of similar basal area of karaka. **B**, seedlings (<2 m high) of karaka (solid) and of other tree species (hatched) in each of the subplots in the same spatial arrangement as the grid in A.

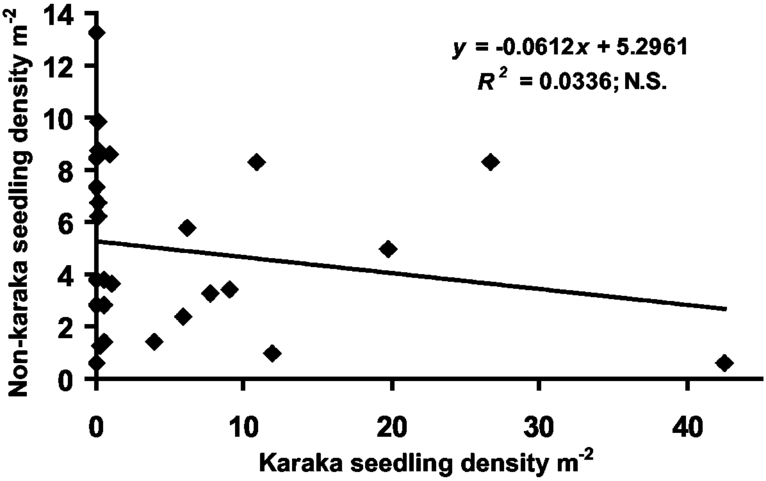


Fig. 5 Non-significant relationship between karaka and non-karaka seedling density in the 26 plots. Each value is the mean of 10 quadrats (20 for Round Bush karaka plot).

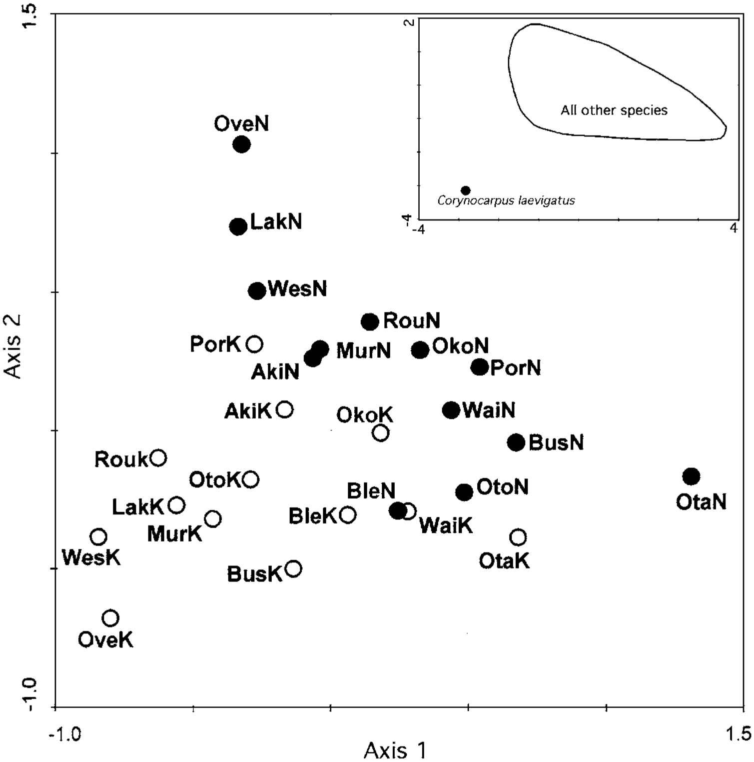


Fig. 6 Ordination by PCA of the plot cover data, with karaka (solid symbols) and non-karaka (open symbols) plots, and (inset) the ordination of the species, showing the distribution of karaka and of all other species. The first three letters are of the site name, followed by plot (N or K).

though the number of non-karaka trees was 12% greater in the non-karaka plots (Table 2). Karaka plots had non-significantly higher exotic species richness ($P = 0.055$; Table 2).

A total of 1897 seedlings <2 m tall (+21 seedlings at Onaero) of woody species was recorded in the 270 0.8 × 0.8 m seedling quadrats measured in the 26 plots, at an average density of 10.7 seedlings m^{-2}. All but 6 were of native species, and 1021 (54%; + 2 at Onaero) were karaka seedlings. Seedling densities for karaka, and therefore for all seedlings, were higher in the karaka plots (Table 2). The karaka plots

Fig. 7 Effect of greater karaka cover on the vegetation at each site, depicted as the difference in karaka cover between the karaka and non-karaka plots at each site, compared with the distance apart of the paired plots from each site in 4-dimensional ordination space (PCA of presence/absence data including karaka).

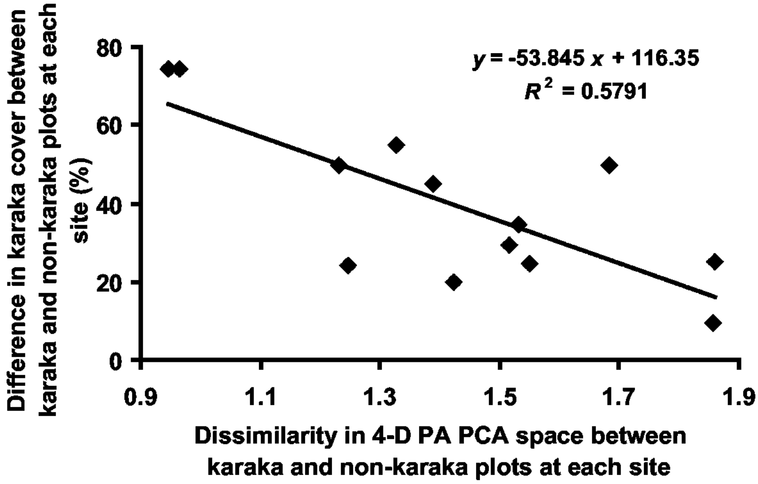
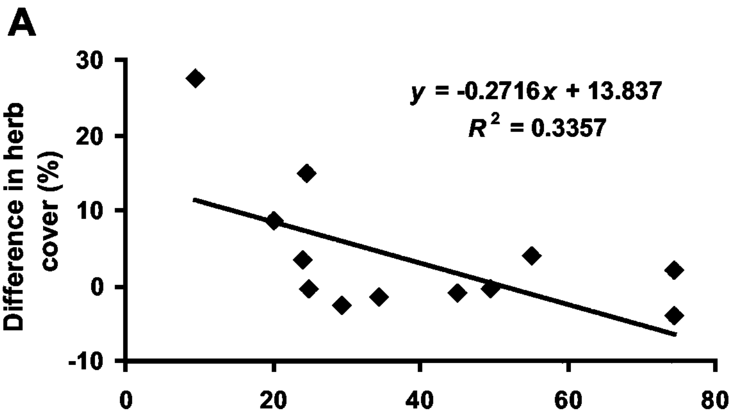
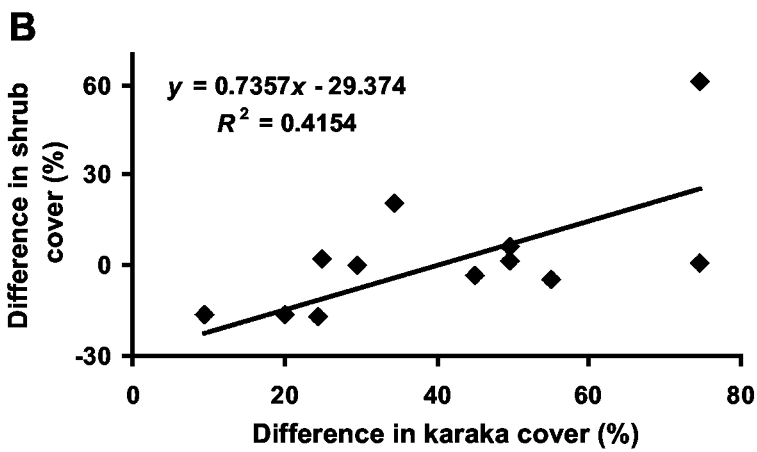


Fig. 8 Effects of differences in karaka cover between karaka and non-karaka plots at each site on **A**, herb cover, and **B**, shrub cover.





had 30% fewer seedlings of other woody species than the non-karaka plots, their density declining non-significantly ($P = 0.3$) as karaka seedling density increased (Fig. 5).

Ordination of the cover of vegetation of each plot (excluding the Onaero plots) showed a clear distinction between karaka and non-karaka plots in the first two dimensions, explaining 37% of the variation (Fig. 6). The species graph demonstrated that much of the pattern was due to the presence of karaka, which dominated one corner of the ordination space (Fig. 6 inset). Nevertheless, there is close proximity between most of the paired plots of each site, reflecting local differences in the flora.

The PCA of the presence/absence data explained 56% of the variation in data on the first four axes, and the distance between paired plots in that space was strongly negatively correlated with the difference in karaka cover between the plots (Fig. 7). This implies that when there is more karaka, the vegetation in the two plots of one site becomes more homogeneous. Other measures of the extent of karaka presence (such as basal area, or tree number) showed similar negative (though weak) relationships with some or all measures of vegetation dissimilarity tested, except for those with inherent circularity (such as species diversity measures and presence/absence dissimilarities; data not presented). Large differences in karaka cover between paired plots are correlated with lower differences in herbaceous species cover and greater shrub cover (Fig. 8), and a trend to higher exotic herb cover and lower native herb cover (data not presented).

DISCUSSION

In New Zealand, the potential of karaka to become a weed was indicated by Duguid (1985, 1990), Gabites (1993), Burrows (1996), Sawyer et al. (2003), and Greenwood (2004). However, the effects of karaka invasions have not previously been assessed quantitatively, which we here attempt.

Karaka as a weed

Karaka possesses many characteristics that contribute to its weedy nature (following Williams & West 2000). It is a tree, as are more than 50% of problem weeds in New Zealand conservation areas (Timmins & Williams 1987) and most indigenous species which become major weeds in Victoria, Australia (Carr 2001); with light, spongy wood (Mueller 1864) and copious parenchymatous rays (Patel 1973), growth is vigorous (but see Mueller 1864). Karaka trees established from seed in a 1962 restoration planting in Palmerston North attained a height of 14 m in 42 years. The largest total stem diameter we recorded from this planting was 26.5 cm (Fig. 5), a growth rate of 0.68 cm/year, allowing 3 years to reach breast height (M. Greenwood pers. comm). The largest karaka tree at Westoe, planted in 1950, had a diameter of 36.5 cm, a growth rate of 0.70 cm/year. By unspecified means, Grant (1996, p. 69) dated a northern Hawke's Bay karaka of 55 cm diam. at 160 years, giving a growth rate of 0.34 cm/year, while Burstall & Sale (1984) dated the largest known mainland karaka (212 cm diam.) at >500 years (growth rate 0.43 cm/year). Stowe (2003) recorded a tree on Lady Alice Island, Hen and Chickens Islands, at 300 cm DBH, which may be older than 600 years.

Though the foliage and twigs of karaka do not contain the toxin karakin (Skey 1871), they do not appear to be palatable to native herbivorous insects, as little damage is ever seen to foliage above the cattle browse line (JAC pers. obs.); trees will persist in cattle pasture, though no seedlings are observed (Mitcalfe 1969; Stevenson 1978; GLR pers. obs.). Nor are leaves liable to disease (except Ashby 1977). A source of karaka's competitive ability is its large, thick leaves that create shade apparently too heavy for native tree seedlings (Duguid 1985; Ogle & West 1997), many of which are light-demanding (Ogden & Stewart 1995).

Flowers are small, inconspicuous, and probably insect-pollinated (A. W. Robertson pers. comm.) though they are investigated by native birds (I. Castro pers. comm.). The fruit is large, with fresh weights up to 13.2 g (cf. Williams 1982, 4.91 g), and dry kernel weights of 2.3 g (van Essen & Rapson 2005; cf. Moles & Drake 1999, 4.6 g). Production of fruit is prolific, though it varies greatly from tree to tree (Pigott 1927; Molloy 1990; GLR pers. obs.), perhaps due to gynodiocey (P. Garnock-Jones pers. comm. in Stowe 2003).

Karaka seeds show very high germination rates (>90%) provided they do not become desiccated (Simpson 1979; Bannister et al. 1996; Burrows 1996). Seedlings may attain a height of 40 cm within two months (T. Foster pers. comm.) and 1.2 m in 3 years (M. Greenwood pers. comm.). The seedlings rapidly establish large taproots (T. Foster pers. comm.), which probably enhance water uptake. This growth rate allows karaka germinants to emerge through such dense, robust, ground-covering weeds as *Tradescantia fluminensis* (pers. obs.) and wild ginger (*Hedychium gardnerianum*) (Williams et al. 2003), indicating that karaka can regenerate in their presence even though other native tree species would be excluded.

Thus, karaka has many characteristics which confer weediness and contribute to its aggressiveness in forest remnants.

The karaka invasion process

Our study sites varied in the extent of occupation of karaka. At Onaero Bay in Taranaki, karaka was a canopy dominant, and so abundant that a suitable non-karaka plot could not be located. Here large trees (max. diam. 81 cm; >160 years old) suggest that karaka has been present for the longest of any of our sites. The site surrounds a former pa, where karaka may have been deliberately planted for food. Karaka at Okoki were definitely planted as the trees were growing in a straight line adjacent to pa earthworks, though this contrasts with Molloy (1990) who noted that Maori normally planted karaka in circles. However, it is hard to envisage trees in many other sites being deliberately planted, as the small number of mature trees suggests a short period since initial invasion. The absence of older trees may be a consequence of trees senescing, or being managed for replacement as a tree crop (Leach & Stowe 2005), or being damaged by neighbouring activities, as well as reflecting a short time since invasion in many, especially non-cultural, sites.

Karaka is clearly bird-dispersed, with its fleshy mesocarp and red-orange exocarp, though it is well shaped to roll considerable distances and is even rather bouncy on hard surfaces. The flesh is strongly scented (Fountain & Couchman 1984), a vertebrate attractant (I. Castro pers. comm.). Fruits are consumed by the native wood pigeon, kereru (*Hemiphaga novaeseelandiae*; McEwen 1978), the only extant native forest bird with a gape sufficient to ingest whole karaka berries. Though not apparently a favoured part of the diet (McEwen 1978; Powlesland et al. 1997), kereru will gorge karaka before moving to the nearest sunny perch tree to digest their meal and defecate viable kernels (Wilkinson & Wilkinson 1952). Further, the increasing spread of karaka on islands around Auckland has been attributed to improved populations of kereru (Campbell & Atkinson 1999, 2002; Atkinson 2004). Thus, some seed could be dispersed distances of several kilometres via kereru. However, Grice (2004) pointed out that fruits which attract birds may also facilitate the invasion of other weedy bird-dispersed species.

Exotic pest animals do not significantly aid in karaka dispersal. Possum (*Trichosurus vulpecula*), an introduced forest pest, target fruiting trees, eating 84–98% of ripe fruit, but do not appear to ingest the kernels (Cowan 1990; JAC pers. obs.). Campbell & Atkinson (1999, 2002) compared forest regeneration on offshore islands with and without kiore (*Rattus exulans*), the rat brought to New Zealand by Maori, and found that karaka remained abundant in the presence of kiore, although there was some slight reduction in recruitment. Moles & Drake (1999) noted that less than 20% of karaka seed was removed after being placed on the forest floor in a possum-free reserve, indicating that predation of karaka seed is low even in the presence of rodents, although ship rats (*Rattus rattus*) are more likely than kiore to cache fruit (Williams et al. 2000).

However, the dispersal patterns away from the parent trees recorded in the present study indicate that most fruit falls directly beneath the canopy, with some seeds dispersing up to 40 m away from the parent tree (due perhaps to germination from rodent caches, or to gravitational dispersal). Seedlings 50–199 cm tall are relatively evenly dispersed away from the parent tree, suggesting recruitment is more successful further away from the parent. Perhaps even karaka finds survival difficult under karaka canopies.

As a consequence of relatively limited dispersal, the majority of karaka trees occur in concentric rings (cf. Molloy 1990) around parent trees as in the Round Bush karaka plot; seedling densities were highest in the subplots that contained mature karaka trees. New invasion rings spread outwards from the next generation as it reaches reproductive age, which can occur as early as five years (Pigott 1927; M. Greenwood pers. comm.) depending on habitat. At Round Bush the original parent trees still appear to be producing seed, suggesting that the rate of outward spread of karaka can only accelerate.

The invasion rate is further exemplified by the behaviour of karaka in a small patch of native bush planted 50 years ago, the first revegetation project in New Zealand with detailed records (Greenwood 2004). About 50 karaka seeds were planted in 1962, and today the grove has 16 karaka trees in the canopy with an average DBH of 24.1 cm.

Effects of karaka invasion

Karaka plots vary in the level of karaka invasion, with some plots having very few trees, all of small DBH, while Lake Papaitonga had 3 trees with an average DBH of 40 cm. The density of such stands makes the forest composition appear most unusual and is enough to draw management attention.

Many of the karaka plots have dense carpets of karaka seedlings, and this is reflected by total seedling abundances being significantly higher in karaka plots. However, the karaka plots also have lower numbers of seedlings of other woody species present than their paired non-karaka plots. As karaka and non-karaka plots had similar canopy composition (except for karaka and only 12% fewer non-karaka trees), the lack of seedlings of other species is not a reflection of availability of parent trees. Therefore, it seems likely that the reduction of non-karaka woody seedlings is due to relatively poor germination or survival underneath the karaka canopies, or to competitive displacement by karaka seedlings at high densities. The long-term effects of this apparent change in the regeneration of native woody species are unclear, but the diversity of native forest canopies may gradually decrease in the presence of karaka.

The presence of karaka seedlings in non-karaka plots is a concern, as the species is obviously expanding its range. Seeds may be dispersed widely in the landscape by kereru, and karaka is starting to be observed in novel habitats and regions (Gabites 1993, p. 97; D. Havell pers. comm.). Esler's (1962) species lists for Kitchener Park, near Feilding, Manawatu, document the arrival of karaka between 1928 and 1962. At nearby Kimbolton Reserve, Rangitikei, July 2004, eight karaka seedlings averaging 44 cm in height were found growing underneath a large perch tree (*Dacrydium cupressinum*); presumably they originated from seed dispersed by kereru, as the nearest parent tree was in a domestic garden 2.3 km away, as the kereru flies (GLR pers. obs.). Recently 27 seedlings were removed from Keeble's Bush, 1.8 km from the nearest source trees at Massey University (M. Greenwood pers. comm.)

Even in the short time since initial invasion of some plots in this study, karaka appears to be altering the forest composition. Though the effect of homogenisation of the vegetation at first appears counter-intuitive, it is clearly demonstrated by the greater vegetational similarity between karaka and non-karaka plots which differ more in karaka cover, compared with sites in which karaka cover is relatively low in both plots. This response also occurs for other comparisons of vegetational similarity. The cover of herbaceous species is lower in the karaka plots with higher karaka cover relative to paired non-karaka plots. It is possible that rare species in particular, which may vary erratically between plots, are especially vulnerable to the presence of karaka. Duguid (1985) commented on the loss of the forest floor herbs following karaka invasion at Lake Papaitonga. By contrast, plots with higher relative karaka cover tend to have higher cover of exotic species. Shrub cover is also greater at the sites with a higher relative karaka cover. Whether this trend towards vegetational homogenisation by changes in some plant groups will continue in the long term is unknown. It is possible that the real effect of karaka might only become obvious with successive cohorts, after a lag period (following Reichard & Hamilton 1997).

New Zealand's lowland and coastal forest has been greatly reduced and fragmented since the arrival of people. These small fragments typically have high levels of disturbance due to browsing or trampling by introduced mammals and, as many are in close proximity to human settlements, they have high numbers of exotic weeds and rubbish (Timmins & Williams 1987). Modified from their natural state, fragments tend to have very open understoreys and higher light levels (Batcheler 1989). Our study sites (excluding Muritai) were small fragments of forest, the largest being 156 ha, and four being less than 10 ha. Fragments apparently create ideal conditions for karaka to establish and grow, due to high levels of disturbance and high desirability as perch or roost sites. After a few generations we could expect karaka to become a prominent part of the canopy, or even dominant, in such areas.

Recommendations for future research and management

While these results indicate that karaka is a legitimate cause for concern in the southern North Island, the species' dynamics may be different in larger tracts of forest with lower levels of disturbance, and in populations in northern New Zealand. Within karaka's natural range, where it is apparently not invasive (GLR pers. obs; D. Havell pers. comm.), its population dynamics should be investigated, to confirm that it need not cause management concern.

The specific competitive abilities of karaka seedlings with respect to other forest trees should be investigated, in relation to light, water, space, nutrients, or a combination of these. It would be of use to clarify the role of animal dispersal in establishing new populations. Monitoring of the denser karaka populations studied here will show the long-term persistence and effects of this invasion. Finally, broad-scale monitoring, as initiated by Sawyer et al. (2003), is needed to investigate how fast karaka's range is expanding.

Karaka is native to New Zealand, though it is extremely unlikely to be native to the southern North Island or further south (Molloy 1990; Leach & Stowe 2005); based on its "weedy" habits, it would have already attained a substantial presence in forests there if it had been established for a long period. If karaka is allowed to spread unchecked in such regions there is a potential threat of loss of species diversity and, eventually, a change in the canopy composition. Removal of karaka seedlings from sites where there is no parent tree or history of presence should be seriously considered as routine forest management, especially in small reserves. The dominance of karaka in Greenwood's Bush is now causing concern, and management is directed towards removal; seedlings are first removed (there appears to be no seed bank) and seedling trees are then cut or poisoned. Similarly at Westoe, karaka are now being poisoned (J. Howard pers. comm.), and seedlings are also being removed from Keeble's Bush.

In contrast, many existing groves of karaka have cultural significance. As a tree that provided food for Maori it is taonga (treasure), creating an obligation for conservation in such areas. There, management should not proceed with the aim of elimination, but instead should consider reduction in the number of karaka present where the species is causing concern or where it interferes with other site preservation or conservation goals, while retaining the local gene pool, there being evidence that karaka on such sites derives from material deliberately selected and planted by local Maori (Jones & Simpson 1995; Platt 2003; van Essen & Rapson 2005). The use of karaka in restoration and re-vegetation projects, however, as advocated by Ogle & West (1997) and Sawyer et al. (2003), should be re-examined in light of this study and the observations of Greenwood (2004).

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