A COMPARATIVE STUDY OF THE EFFECTS OF INTRODUCED MAMMALS ON NOTHOFAGUS FOREST AT LAKE WAIKAREITI

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SUMMARY: Comparable sites were examined on Rahui Island, Lake Waikareiti, which is free of introduced mammals, and on the adjacent mainland, which is not. The forest understorey density in *Nothofagus fusca/N. menziesii* forest has been reduced on the mainland. In the mainland forest there are fewer plants of *Pseudopanax* and *Coprosma* spp. and more plants of *Dracophyllum pyramidale* and *Dicksonia lanata*. Regeneration of *Nothofagus menziesii, Phyllocladus glaucus*, and *Quintinia acutifolia* is greater in the mainland forest and regeneration of *Podocarpus* spp. and *N. fusca* is occurring. The vegetation cover below 6 in. is less on the mainland but there is no difference in litter and topsoil depths. Changes in the mainland forest composition are attributed to the effects of the mammals.

INTRODUCTION

Introduced mammals, principally red deer and opossums, have dispersed throughout almost the entire forest and mountain land in New Zealand. As a result, forests free of such mammals are rare and confined to a few islands. This paper compares the forest on Rahui Island, Urewera National Park, with forest on the nearby mainland.

Lake Waikareiti (2,900 ft.) is three miles north-east from the Waikaremoana Lake House. It contains five islands. The largest, Rahui, covers almost 50 acres and is separated by 200 to 1,000 yards of deep water from the lake shore and is 200 yards from the nearest island, Motungarara.

People long associated with the area have no knowledge of introduced mammals on Rahui Island, nor was any evidence of them seen by us during the study. The possibility that deer once inhabited Rahui is remote, as steep sides and deep water make landing difficult. Past Maori occupation is not evident.

On the mainland fresh deer and opossum droppings are abundant. Red deer were well established around Lake Waikaremoana in the 1920s (Forbes 1924) from six liberations between 1899 and 1918 (Logan and Harris 1967). Opossums were liberated around Lake Waikaremoana on five occasions between 1898 and 1925 (Pracy 1962), and wild pigs have probably been present throughout the Urewera since 1840 (Wodzicki 1950). Wild cattle were once numerous in the Waikaremoana area (Cockayne 1926).

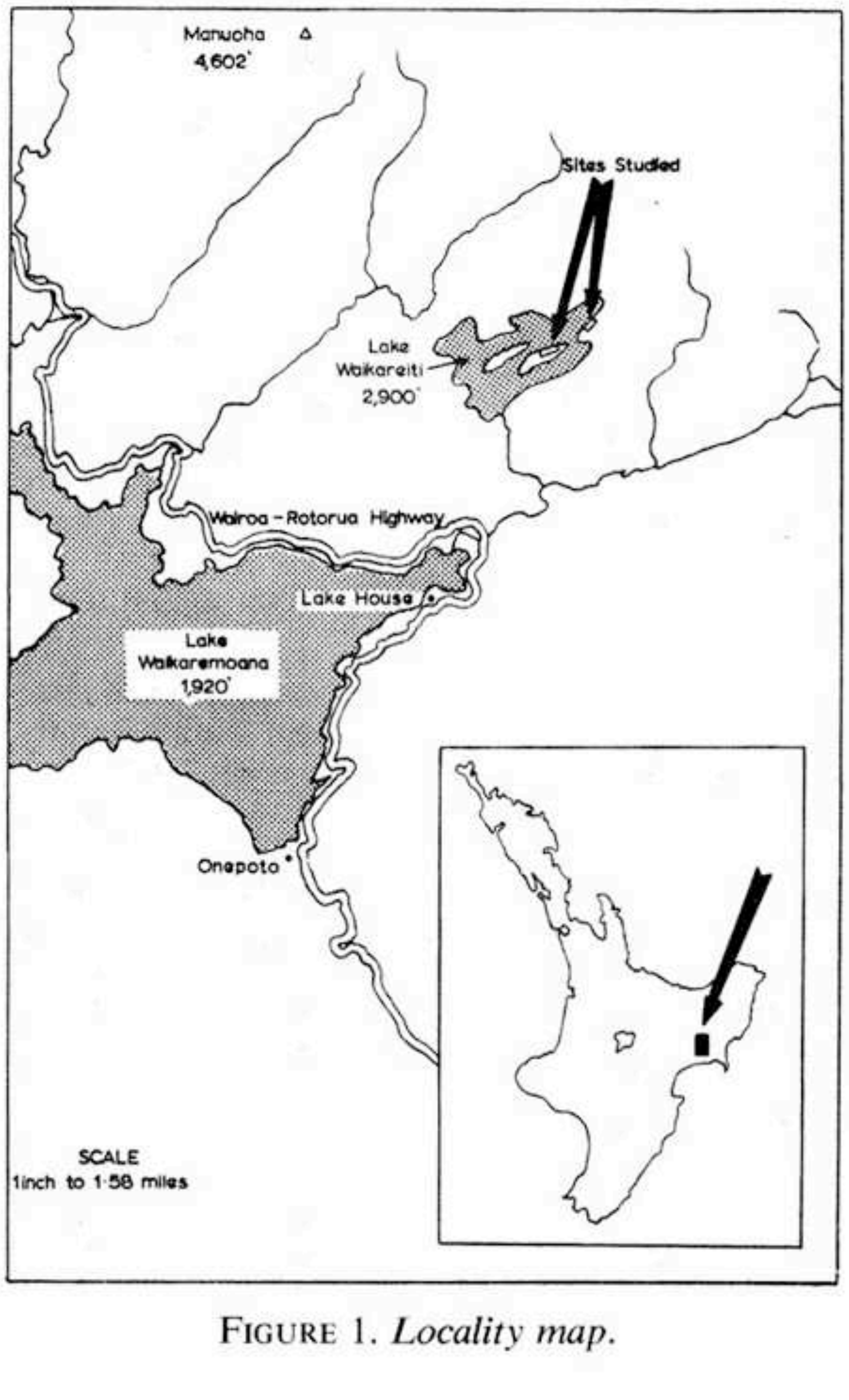

FIGURE 1. *Locality map.*

The forest on Rahui Island and within a similar altitudinal range on the mainland is a mixture of *Nothofagus menziesii*, *N. fusca*, and *Podocarpus* spp. A detailed description of forest composition for the sites studied is given in the results.

The soils at Lake Waikareiti are derived from a series of volcanic deposits, the most recent being Kaharoa ash (A.D. 1020 ±70 years) lying in its 6 in. to 12 in. isopach range (Vucetich and Pullar 1964).

Annual rainfall is approximately 100 in. No other climatic data exist for Lake Waikareiti. The nearest meteorological station is seven miles away at Onepoto (2,110 ft.).

METHODS

Two sites of similar physiography were chosen, one on Rahui Island and one on the mainland. The vegetation was sampled by the point-centred quarter technique (Cottam and Curtis 1956). This gives plant density estimates from distances measured from a random sampling point to the nearest plant in each quarter around the point. The vegetation was recorded in five classes:

1. Fern and monocotyledon species, 6 in. high and over.
2. Woody plants, 6 in. to 18 in. high.
3. Woody plants, 18 in. to 5 ft. high.
4. Woody plants, above 5 ft. in height which were up to 4 in. diameter at 4 ft. 6 in. above ground level.
5. Trees, 4 in. diameter and larger at 4 ft. 6 in. above ground level.

Forty sampling points were located at each site, at one chain intervals, along eight parallel transects established with a random origin and lying at right angles to the lake shore. At every point four measurements were made to the nearest plants within each vegetation class. These measurements were recorded to an accuracy of 0.1 ft. between 0 ft. and 10 ft.; beyond 10 ft. the accuracy was to 0.5 ft. In addition, diameter in 0.1 in. intervals was recorded for all trees sampled. Four operators sampled at both sites to reduce observer bias.

Comparisons of the species composition between sites were made using the numbers sampled, and the significance of differences were tested with probability tables for binomial samples (Mainland *et al.* 1956).

Relative estimates taken from a plant population by randomly placed point-centred quarter samples are reliable only when the plant population is randomly dispersed. For any plotless technique in which a constant number of plants is sampled at each point, departures from randomness by individual species may be tested by comparing the observed and expected number of sampling points containing 0, 1, 2, . . . n plants of a species (Bray 1962). For the point-centred quarter technique the expected number of points containing 0, 1, 2, 3, and 4 plants of a species is obtained from the 4th power binomial expansion with p (probability of occurrence) equal to the species' relative density. For each site the observed and expected number of a species occurring at sampling points were compared in a 2×5 contingency table.

Absolute density estimates (stems per acre) for all vegetation classes are obtained from

$$\sum_{i=1}^{n}\sum_{j=1}^{4} Y_{ij}^{2}$$

(sum of the distances squared) and n, the number of sample points, as follows:

$$\text{Density } \lambda = \frac{16\ n\ 43560}{\pi \sum_{i=1}^{n}\sum_{j=1}^{4} Y_{ij}^{2}}$$

As $\frac{1}{2}\pi\lambda \sum_{i=1}^{n}\sum_{j=1}^{4} Y_{ij}^{2}$ is distributed independently as χ^2 with 8n degrees of freedom (after Kendall and Moran 1963), the 95% confidence limits for λ are obtained for large samples by using the normal approximation to χ^2 as follows

$$95\% \text{ confidence limits for } \lambda = \frac{(16n \pm 15.68\sqrt{n})\ 43560}{\pi \sum_{i=1}^{n}\sum_{j=1}^{4} Y_{ij}^{2}}$$

The precision of λ is known only for random populations.

Student's *t* test is used to determine the significance of the difference of the species' mean diameter between sites.

The ground cover below 6 in. was sampled at each sampling point by 40 point quadrats at 4 in. intervals arranged in a cruciform pattern over the sampling point. The cover was recorded in three classes; vegetation, litter, and exposed rock and soil. The recorded cover values for each plot were transformed into arc sines as they were not random samples. The mean totals for Rahui Island and the mainland were compared as percentage binomial samples.

Two soil pits were dug at each of the 80 sample points. The depth of litter and topsoil was measured from the surface down to a distinct upper limit of Kaharoa ash. The significance of mean depth differences was ascertained by using Student's *t* test.

At each sample point the slope was measured with an abney level. The slopes at both sites were similar and ranged between 5° and 45°.

RESULTS

Table 1 compares the numbers of trees of each species sampled and their mean diameter at each site. The observed occurrence and the random expectation of the numbers of trees at sample points did not differ significantly ($p < 0.1$) for any species. Both sites contained similar numbers of *Podocarpus** and *Nothofagus* spp., *Ixerba brexioides*, *Quintinia acutifolia* and *Dracophyllum pyramidale*. On Rahui Island *Weinmannia racemosa* is more abundant and *Phyllocladus glaucus* is less abundant than on the mainland site. There were also larger trees of *Nothofagus fusca* on Rahui Island, but on the mainland *Podocarpus hallii* and *Ixerba brexioides* were larger.

The differences in understorey composition are presented in Figures 1 and 2. Within each vegetation class on the mainland there were fewer plants of animal-preferred species and more plants of less-preferred species. For example, the highly preferred *Pseudopanax*[1] and large leaved *Coprosma*[2] spp. together constitute 52%, 45%, and 14% of the first, second, and third woody plant classes respectively on Rahui Island (Fig. 3) but on the mainland only traces of these genera were found in each class. The differences in plant numbers of small-leaved *Coprosma*[3] spp. are statistically significant in the 6 in. to 18 in. woody class and the 18 in. to 5 ft. woody class ($p < .05$, $p < .05$, respectively) but low numbers were still present on the mainland.

The less-preferred species, *Phyllocladus glaucus* and *Dracophyllum pyramidale* were very prominent on the mainland, where *Nothofagus menziesii* and *Quintinia acutifolia* also occurred in higher numbers in all woody classes. There were more *Nothofagus fusca* and *Podocarpus* spp. on the mainland in the 6 in. to 18 in. woody class.

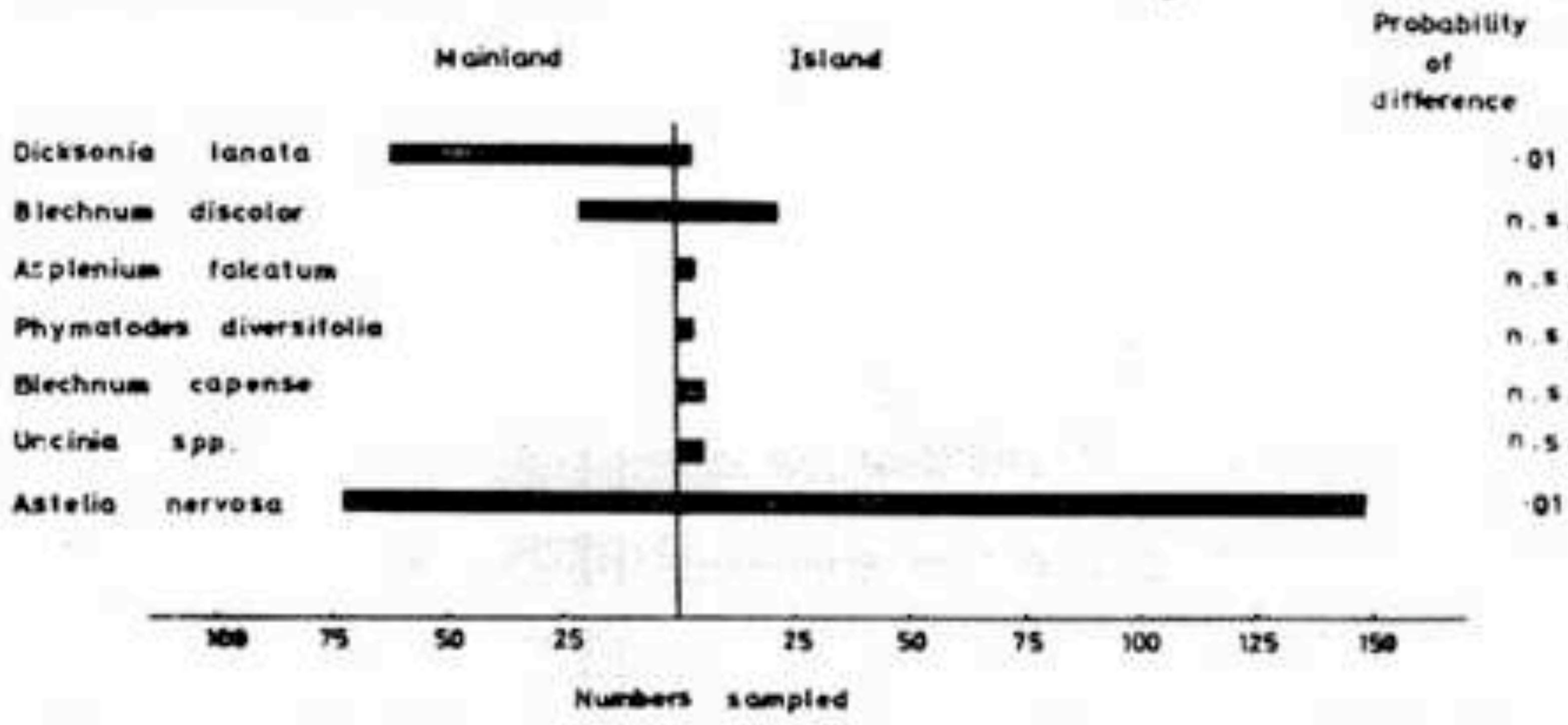

FIGURE 2. *Numbers of ferns and monocotyledons sampled at the Rahui Island and mainland sites. (When a plant was a clump of stipes or tillers and appeared to have originated from one individual it was classed as one plant.)*

TABLE 1. *Numbers sampled and mean diameters of tree species on Rahui Island and the mainland sites.*

	Numbers sampled		p. of	Mean diam. in.		p. of
	Island	Mainland	difference	Island	Mainland	difference
Phyllocladus glaucus	5	15	.05	7.64	11.04	n.s.
Dracophyllum pyramidale	4	4	n.s.	4.35	4.75	n.s.
Quintinia acutifolia	9	9	n.s.	6.32	5.94	n.s.
Nothofagus menziesii	15	18	n.s.	13.01	11.15	n.s.
Podocarpus hallii	10	3	n.s.	22.11	39.90	.05
Podocarpus spicatus and *P. ferrugineus*	1	3	n.s.	14.50	12.80	n.s.
Nothofagus fusca	23	29	n.s.	24.47	17.88	.01
Weinmannia racemosa	50	23	0.1	8.68	8.34	n.s.
Ixerba brexioides	43	54	n.s.	7.99	9.24	.01

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[1] Pseudopanax spp. include *P. arboreum*, *P. simplex*, and one *P. anomalum*.

[2] Large-leaved *Coprosma* spp. include *C. australis*, *C. lucida*, *C. tenuifolia*.

[3] Small-leaved *Coprosma* spp. include *C. foetidissima*, and *C. arborea*.

* Plant nomenclature follows Allan (1960) except for *Astelia nervosa* (after Moore, 1966), and *Pseudopanax species* (after Philipson, 1965).

In the fern and monocotyledon class on the mainland there were more plants of *Dicksonia lanata* and fewer *Astelia nervosa* plants. Four species sampled at Rahui Island were not sampled on the mainland.

There appeared a tendency for the common understorey species at both sites to be non-randomly distributed. On Rahui Island *Pseudopanax arboreum* in the 18 in. to 5 ft. woody class and *Dracophyllum pyramidale* in the 5 ft. to 4 in. diameter woody class show differences ($p < 0.1$, $p < .01$, respectively) from random occurrence. Similarly, on the mainland *Phyllocladus glaucus* in the 18 in. to 5 ft. woody class, and *Dicksonia lanata* are non-random ($p < .01$, $p < .01$, respectively). *Astelia nervosa* is non-random at both the Rahui Island and mainland sites ($p < .01$, $p < .05$, respectively). The differences are all binomial which suggests aggregation; that is, more sample points have either none or four plants of these species than what would be expected if they were randomly dispersed.

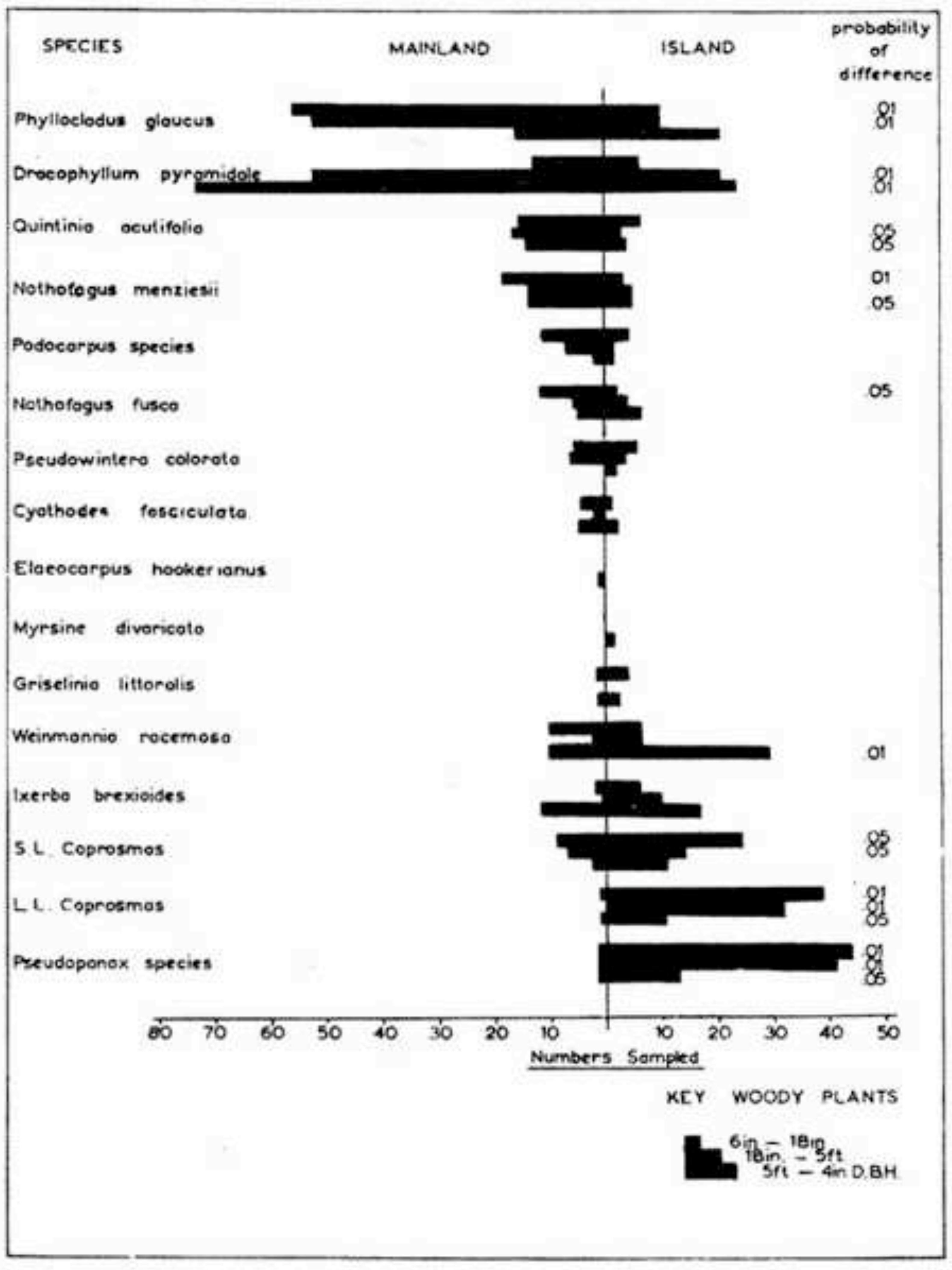

FIGURE 3. *Numbers of woody plants sampled at the Rahui Island and mainland sites.*

TABLE 2. *Vegetation class densities (plants per acre) compared for the Rahui Island and mainland sites.*

	Mainland	Island	p. of difference
Ferns and monocotyledons	1622	3916	.001
Woody plants, 6 in. to 18 in.	641	1431	.001
Woody plants, 18 in. to 5 ft.	595	1173	.001
Woody plants, 5 ft. to 4 in. diam.	751	650	.05
Trees, 4 in. diameter and over	373	372	n.s.

Table 2 (the estimates of λ for each vegetation class) indicates a difference of 58% in the fern and monocotyledon class, 57% in the 6 in. to 18 in. woody class, and 49% in the 18 in. to 5 ft. woody class. The greater number of woody plants 5 ft. to 4 in. diameter is because of higher numbers of *Dracophyllum pyramidale*.

The results of the 1600 point quadrats measured at each site (Table 3) show little difference in percentage cover values of vegetation, litter, exposed soil and rock, between the mainland and island sites.

The mean litter and topsoil depths from 160 soil pits were 6.62 in. for Rahui Island and 7.45 in. for the mainland. The difference was not statistically significant.

TABLE 3. *Soil cover percentages for the Rahui Island and mainland sites.*

	Mainland	Island	p. of difference
Vegetation	9.0	14.0	n.s.
Litter	90.5	85.8	n.s.
Exposed rock and soil	0.5	0.2	n.s.

DISCUSSION AND CONCLUSIONS

The two sites are similar in environmental features, apart from the influence of introduced mammals, and in the composition and density of the tree species. The fewer *Weinmannia racemosa* on the mainland may have resulted from persistent opossum defoliation or, more likely, from a difference in sociological vegetation pattern. We assume that differences in understorey composition caused by unequal numbers of *Weinmannia racemosa* and

Phyllocladus glaucus trees are insignificant. We can also assume, in the absence of evidence, that any past intrinsic changes or unknown ecological differences have not caused the obvious major differences.

The dispersion of the common understorey species is significantly non-random in five instances, where there is evidence of aggregation. When the point-centred quarter technique is used to sample a population of plants in which certain common species are aggregated, the relative density of those species tends to be under-estimated. Because the effective mean area of a species with an aggregated distribution is reduced, there is a lower probability of a random sampling point falling near an individual of that species. Therefore the numbers of plants of *Pseudopanax* spp., *Dracophyllum pyramidale* and *Astelia nervosa* on the island, and *Phyllocladus glaucus* on the mainland, are under-estimated, whereas the numbers of plants of the remaining species are over-estimated.

We are unable to comment on the precision of the λ estimates without knowing the nature of the total dispersion. No inferences can be made from individual species dispersion; the dispersion of a composite population consisting of several non-random sub-populations is unrelated to the sub-populations' dispersions. Despite these dispersion effects the major differences are undeniable.

The assumption that the composition of understorey on the mainland was once similar to that on the island is a basic premise of this paper. There is no evidence that it was otherwise. What changes have occurred can only be a direct and indirect result of the effects of mammals. The near-elimination of *Pseudopanax* spp., and large-leaved *Coprosma* spp. has been previously observed as a direct result of browsing pressure (Holloway 1950). Since *Dracophyllum pyramidale* and *Phyllocladus glaucus* are lightly browsed, they have been able to increase their numbers. Other moderately favoured species have made smaller changes depending on their browse resistance and their reaction to changes in the micro-environment. The amount of light in the understorey has undoubtedly increased with reduction in density of the broad-leaved *Pseudopanax* and *Coprosma* spp. The increased *Nothofagus* regeneration is probably a response to these light changes.

The *Nothofagus* and *Podocarpus* spp., *Quintinia acutifolia, Ixerba brexioides, Weinmannia racemosa,* and *Phyllocladus glaucus* are potential canopy species which ensure the perpetuity of the forest. The present mainland understorey composition suggests that the future forest will have more *N. menziesii, Q. acutifolia,* and *P. glaucus* and less *I. brexioides* and *W. racemosa. N. menziesii, Q. acutifolia,* and *P. galucus* have increased, despite the presence of browsing animals, to a density greater than in the forest on Rahui Island.

It is unlikely that the vegetation on the mainland is static or in equilibrium with its use by browsing mammals. In the past, the composition will have altered with their changing population levels. It appears that there has been insufficient time for less preferred species to completely fill the niche created by the elimination of highly preferred species. Further changes in animal feeding patterns, of which some evidence is now apparent, are likely to complicate future trends in understorey composition. Thus, in presenting a static comparison, the observations in this study have preliminary value for more detailed work which may be done in the future.

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APPENDIX

Derivation of the density estimator, λ (after Kendall and Moran 1963).

Consider a random number of points in a plane so that the number occurring in any region of area A is a Poisson variate with a mean area λA. λ may then be called the density of the points. Let P be any sample point and r_1 the distance to the nearest point. Then the distribution of r_1 is:

$$2\pi\lambda r_1 \, e^{-\pi\lambda r_1^2} \, dr_1 \quad \ldots\ldots \quad \ldots\ldots \quad (1)$$

so that $2\pi\lambda r_1^2$ is distributed as χ^2 with two degrees of freedom.

This result may be used to provide a means of estimating the density of the points in a plane by choosing random sample points and measuring to the nearest point. In the point-centred quarter method, a random point P is chosen together with two perpendicular axes fixed in advance. The distances Y_1, Y_2, Y_3, and Y_4, from P to the nearest point in each of four quadrants about P are measured from above $\frac{1}{2}\sum_{i=j}^{n}\sum_{j=1}^{4} Y_{ij}^2$ is distributed independently as χ^2 with 8n degrees of freedom. Hence $\frac{1}{16}\pi\sum_{j=1}^{4} Y_j^2$ is an unbiassed estimator of λ^{-1} with variance $\frac{1}{4}\lambda^{-}$.

Therefore:

$$\lambda = \frac{16n}{\pi\sum_{i=1}^{n}\sum_{j=1}^{4} Y_{ij}^2} \text{ per unit area.}$$

and furthermore 95% confidence limits for λ are $2\chi_1^2/\pi\sum_{i=1}^{n}\sum_{j=1}^{4} Y_{ij}^2$, and $2\chi_2^2/\pi\sum_{i=1}^{n}\sum_{j=1}^{4} Y_{ij}^2$ where χ_1^2 is the value of χ^2 at the 2.5% probability level. Approximately 95% confidence limits for samples with greater than 100 degrees of freedom are:

$$16n \pm 15.68\sqrt{n}/\pi\sum_{i=1}^{n}\sum_{j=1}^{4} Y_{ij}^2.$$

Most previous authors (Cottam and Curtis 1956, and others) used the mean of the four distances squared as an estimator of λ^{-1}. From (1) the mean of $(\frac{1}{4}\sum_{j=1}^{4} Y_j)^2$ is $\lambda^{-\frac{1}{2}}$ and its variance is $\frac{1}{4}\pi^{-1}(4-\pi)\lambda^{-1}$. When $(\frac{1}{-}\sum_{i=1}^{n}\frac{1}{4}\sum_{j=1}^{4} Y_{ij})^2$ is used to provide an estimate of λ the efficiency of the procedure relative to using $\sum_{i=1}^{n}\sum_{j=1}^{4} Y_{ij}^2$ is therefore $(4(4-\pi))^{-1} = 0.9149$.

If the points in the plane under consideration do not lie at random then these methods will give biassed results.