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Ranges of woody plant species and ferns on forested elevational gradients on Aotea-Great Barrier Island, New Zealand: the role of zones of permanent and temporary establishment

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Abstract: The arrangement of plant species along elevational gradients is prominent in the debate between individualistic versus community-unit concepts in plant ecology. We obtained elevational ranges (upper and lower elevation limits) for woody species and ferns on the three highest mountains on Aotea (Great Barrier Island), Aotearoa-New Zealand. These data allowed potential species composition to be obtained for any elevation and were analysed using regression, ordination, and classification. Both woody plants and ferns demonstrated linear declines in richness with increasing elevation. The three mountains were distinct in ordination space, and their differences increased with elevation and were most marked in the fern flora. Site classifications indicated a change in composition at c. 300 m for woody plants on Hiramakimata. The elevational distribution patterns of individual species differed considerably between mountains. In particular, the higher-elevation flora of the highest peak (Hiramakimata) was largely absent from the other two summits, despite these being within the elevational ranges of most of the missing species. This pattern supports Steenis's (1972) hypothesis that species will be absent from, or ephemeral on, mountains not sufficiently high to intersect their zone of permanent establishment. A second observed pattern was that widespread forest species at lower elevations often did not extend to their potential upper limits on Hiramakimata. These two patterns are clear for both woody plant species and ferns. Combining Steenis's hypothesis with inferred redistribution of elevational vegetation during the Last Glacial and Holocene periods can explain these distributional patterns.

Keywords: altitude, climate change, elevation, Hiramakimata, Mount Hobson, mountain mass elevation effect, source-sink hypothesis, Steenis's hypothesis, refugia

Introduction

Species distribution patterns on mountains have been central to the concept of the plant community and influenced prominent themes in ecology and biogeography (Lomolino 2001). Although there are exceptions, declining plant species richness with increasing elevation is frequently observed in mountains where undisturbed forest extends from lowland to high elevations (Whittaker 1967; Peet 1981; Allen et al. 1991a). Elevation gradients in forest composition in New Zealand are well-studied (Mark & Sanderson 1962; Mark 1963; Wells & Mark 1966; Ogden 1971; Druitt et al. 1990; Allen et al. 1991b; Ogden et al. 1991). These studies, and other unpublished data (Ogden 1995; Fig. 2), demonstrate the monotonic (linear) decline in species richness with increasing elevation in forests in New Zealand. Most of this work, excepting Allen et al. (1991b), has been directed at demonstrating shifts in community composition and structure, rather than species range limits or differences between mountains. Moreover, none of these studies were north of 38° S where the forest composition is much richer than further south (Wardle 1963; McGlone 1985).

Within the northern latitudes, the vegetation of the Waitākere Ranges (maximum elevation 474 m) has been so modified by fire and timber extraction that any elevational zonation, if present, is no longer apparent (Esler 2006). The Hūnua Ranges (maximum elevation 688 m) have also been highly modified by logging and browsing mammals, but some zonation with elevation is apparent, and the elevational limits are given for a few selected species (Barton 1972). Burns and Leathwick (1996) reported that altitude was an important predictor of gradients in forest and scrub community composition at Waipoua (west Northland), noting that "... with increasing altitude, temperature decreases and rainfall, cloud and mist cover increase..." (p. 87-8). In the Hauraki Gulf region, Moore (1973) mentions "definite zonation" in the forest on Mount Moehau (892 m, Coromandel Range) but discussed only the flora of the upper zone. The elevation limits for some species have been described on Hauturu/Little Barrier Island (722 m, Hamilton & Atkinson 1961; Cameron & Young 2019). On Aotea-Great Barrier Island, the plant community elevational sequences on Hiramakimata (627 m, Ogden 2001) and Tataweka (526 m, Wright & Cameron

1985; Eadie & Broome 1990) have been described, but these studies provide little information on the elevational ranges of individual species. The vegetation of Ruahine (402 m) has not previously been described. It is worth noting that the peaks north of 38° S are all much lower in elevation than those further south; only Moehau has a treeline under current climates. Thus, the elevational gradients on these northern peaks may be less obvious over the shorter elevational ranges (of the northern mountains).

Although patterns of species richness and diversity with elevation are well documented (and not always linear) the causal mechanisms are poorly understood (Rahbek 1995; Leathwick et al. 1998). The uninterrupted slope of an idealised mountain can be considered a single environmental gradient, although many factors vary along it. The centres and boundaries of species distributions along such environmental gradients are usually scattered, rather than forming well-defined species groups (Whittaker 1975; Shipley & Keddy 1987). Relatively sudden transitions between different species assemblages (elevational zones) may occur, but these usually correspond with abrupt changes in environmental factors (e.g. cloud cover, geology, slope gradient, edaphic conditions, or a disturbance boundary). Cloud cover is particularly important as the increased humidity allows the growth of many epiphytic plants, especially bryophytes and ferns, giving a distinctive physiognomy to this cloud forest. Often, these environmental transitions are identified by the appearance, or disappearance, of a few dominant or distinctive species. However, Whittaker (1975) argued convincingly that species distributions along elevational gradients support Gleason's principle of species individuality, rather than the community unit concept, although the latter remains useful when describing continua (e.g. Drutt et al. 1990).

Species richness usually correlates with the decline in air temperature with elevation (i.e. the lapse rate) observed on mountains (Wardle 1991; Ogden & Powell 1979). Temperature is, however, a convenient simplification of a suite of climatic variables that have short- and long-term effects on vegetation, animal life, soil biota and geochemistry. 'Temperature' used in this sense is thus a proxy for many physiological processes, ecological interactions, and biotic and abiotic feedback loops. More than a century ago, the altitudinal temperature/diversity decline was broadly equated with the latitudinal equator-to-poles pattern (e.g. Merriam's Life Zones, Merriam 1894) and this analogy remains widely acknowledged (e.g. Huggett & Cheesman 2002), although the causal mechanisms are more complex than temperature alone (Rahbek 1995).

The observation that the upper elevational limit of vegetation communities is higher on large mountain ranges than on isolated peaks is termed the Massenerhebung effect (Grubb 1971). Steenis (1972) described a different "mountain mass elevation effect" on species' lower altitudinal limits, which he differentiated from the Massenerhebung effect. Steenis's (1972) mountain mass effect states that species often do not occur on mountains seemingly within their altitudinal range and suitable in other respects, judged from their distributions on other, larger, mountains. He stressed the tripartite nature of the altitudinal range of a species: a zone of permanent establishment and higher and lower zones where temporary establishment occurs at given points in space or time. Even if a mountain appears sufficiently elevated for a particular montane species, unless it intersects the "zone of permanent establishment", that species will not be present, except perhaps as occasional and essentially ephemeral individuals derived by long-distance dispersal from adjacent higher mountains (Fig. 1). This model is echoed in the "mass effect" of Shmida & Wilson (1985), "source-sink" distributions (Pulliam 1988) and the "transient species" of Grime (1998).

Species-level abundance-elevation curves are frequently characterised by relatively sharp declines in abundance near their upper limits but long tails within lower zones (Whittaker 1956; Drutt et al. 1990). Zones of both temporary and permanent establishment will change with changing climate (Ogden 1989), and the population tails presumably facilitate this process. We focus on the population tails because they facilitate changes in composition along elevational sequences; zones of both temporary and permanent establishment will change with changing climate (Ogden 1989). During cold climate phases, such as the Last Glacial (25–12 000 BP) the downwards migration of a species was facilitated by an elongated lower tail and lower refugia. During warm climatic phases (e.g. the Holocene, 10 000 BP to present), the upper zone of temporary establishment is more important in determining a species distribution. Uphill migration of species may eliminate species in small areas of former alpine or montane zones. This dynamic is evident if we consider the low-statured sub-alpine vegetation that covered much of New Zealand during the Last Glacial Maximum, which was subsequently replaced by forest except on the highest mountains (McGlone 1988).

Using vegetation surveys from three mountains on Aotea, we assess whether or not these mountains conform to Steenis's (1972) concept of zones of permanent and temporary establishment on mountains of varying height. Almost the whole of Aotea was forest covered before the arrival of the

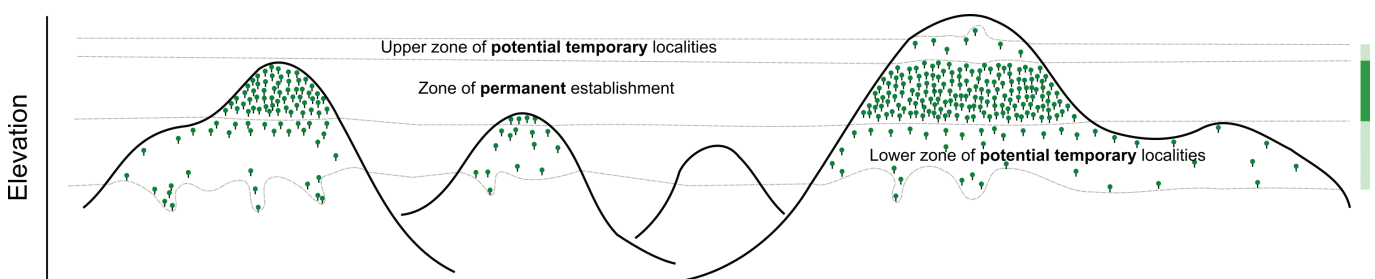


Figure 1. The source and sink zones for a montane species. The density of the tree icons is proportional to their abundance. Note the small central mountain, lacking the species. The straight line for upper limits is thought to be determined mainly by climatic factors (temperature) while the more variable or gradual lower limits are determined by increased competition with other species in higher diversity forest at lower elevations (Ogden 1989). Redrawn from Steenis (1972).

first humans in New Zealand c. AD 1280 (Wilmschurst et al. 2008). The three mountains carry continuous forest ranging in upper canopy height from c. 30 m at the lowest elevation, to c. 8 m at the highest. Hiraikimata seemed suitable for testing Steenis's hypothesis because its summit vegetation (Moore 1973; Ogden 2001) differed from other less elevated peaks on Aotea. We aimed to quantify the elevation ranges of plant species on Hiraikimata and two smaller isolated mountains on the same island. We describe the elevational patterns and test Steenis's hypothesis that species will be absent from mountains not sufficiently high to intersect their zone of permanent establishment.

Methods

Study area

Aotea is c. 285 km² in area and is located c. 90 km east of the North Island of New Zealand on the outer edge of the Hauraki Gulf. It has a mild maritime climate with mean daily maximum temperatures ranging from 12°C in July to 22°C in February, and minima from 7°C to 14°C. Mean monthly precipitation ranges from c. 70 mm in February to c. 112 mm in July (Chapter 7 in GBIET 2010). The three highest mountains on Aotea are Hiraikimata (Mt. Hobson, 627 m), Tataweka (526 m) and Ruahine (Mt. Isaacs, 402 m) (Fig. 2). These mountains differ geologically, being respectively predominantly rhyolite, greywacke, and andesite (Moore 2004). Hiraikimata is situated in the island's centre, while Ruahine and Tataweka mark the southern and northern extremities, respectively. Hiraikimata is surrounded by five subsidiary peaks greater than 400 m in elevation. Except for nearby Mt Heale (510 m), these were not visited in this survey and are not included in the area greater than 400 m a.s.l. in Table 1.

The Holocene vegetation history of Aotea has been the subject of several palynological and stratigraphic studies (Horrocks et al. 2000; Deng et al. 2004; Ogden et al. 2006). The contemporary vegetation of Aotea has been described by Ogden (2001) and the dynamics of forest vegetation change following

fire by Perry et al. (2010) and Taylor (2017). Disturbance by Māori and European fires, logging, and introduced mammalian herbivory and predation have occurred on the three mountains we surveyed, and their vegetation cover partially reflects this (Ogden et al. 2006). The summit vegetation of Hiraikimata comprises a low mossy cloud forest inhabiting a cool, often wet and cloudy, environment similar to that on Hauturu (Little Barrier Island), but not represented on the other, lower, Aotea summits.

Field methods

On each mountain, six sea-level to mountain-top traverses were undertaken in January 2002 (Table 1). The steep, often rocky, nature of the terrain made it challenging to work off-track and control for aspect, so the traverse lines followed established walking tracks on different aspects on Hiraikimata and Tataweka. On Ruahine, where no suitable public track was present, traverses were made from the north-west and east (see Appendix S1 in Supplementary Materials for a description of the survey lines). Species occurrences were recorded on upwards

Table 1. Study locations and relative sample sizes of the three mountains surveyed. The area above 400 m was estimated by gridding area > 400 m a.s.l. on NZTopo50-AY34.

	Tataweka	Hiraikimata	Ruahine
Latitude	36°04 25 S	36°11 20 S	36°20 10 S
Longitude	175°22 35 E	175°24 50 E	175°30 50 E
Elevation (m)	526	627	402
Area > 400m a.s.l. (ha)	157	109	2
Number of traverse lines	2	2	3
Combined traverse length (km)	8	7	5
Number of traverses	6	6	6

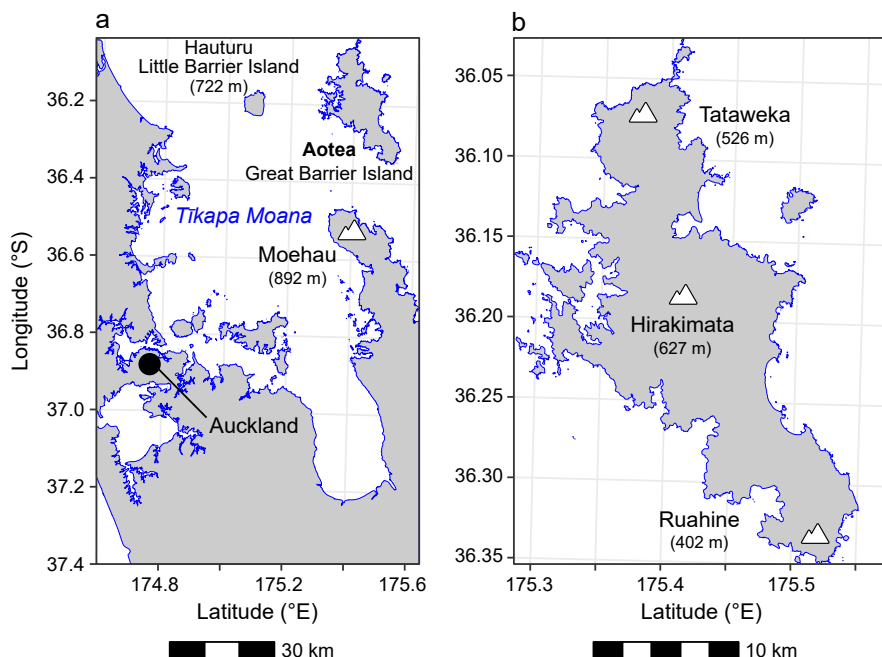


Figure 2. Map of the study sites (b) and regional context (a). On Aotea-Great Barrier Island, data were collected from Hiraikimata, Tataweka and Ruahine.

and reverse traverses, constituting two data sets. On Hauturu species have similar (or higher) upper boundaries on ridges compared to valleys (Fig. 22 in Hamilton & Atkinson 1961; Cameron & Young 2019), justifying ridges as the preferred transect line. Randomisation of lines was impractical, but we replicated lines on different aspects and repeat sampled each line twice (Ruahine) or three times (Hirakimata, Tataweka) (Table 1 and Appendix S1). Species nomenclature follows Ngā Tipu Aotearoa – New Zealand Plants (<https://nzflora.landcareresearch.co.nz/>).

On each upwards traverse, sampling points were separated by 25 m elevation so that horizontal distance between samples varied with steepness. At each sample point, the presence of all woody species (trees, shrubs, and climbers, whether epiphytic or on the ground), and ferns (including fern allies) within a radius of c. 5 m was recorded. Due to their generally small size and restriction to specific microsites, ferns were possibly under-represented in the samples, so their ranges may be less accurate than for woody plants. Sample elevation was recorded with a handheld barometric altimeter. Repeat records at the same point on different days indicated a maximum error of ± 10 m. The elevation that a species was first observed at was recorded (this was often between sampling points) on both uphill (lower limit) and downhill (upper limit) traverses. These limiting elevations constitute the species' range, and attention was concentrated on defining them as accurately as possible. Repeat traverses focused on checking the obtained ranges and sampling between prior stops. The slight daily variation in the barometric height for any point meant that replicate observations did not sample exactly the same location, giving greater confidence in the richness measure for that elevational sample. Additional observations were made close to all transects, mainly to look for species occasionally present at lower elevations than recorded on the traverses themselves.

It is possible that species not recorded on the traverses, may have been present elsewhere on the mountain. However, searches elsewhere suggested that such outliers were infrequent and unlikely to have affected the patterns obtained. For example, kauri (*Agathis australis*), although restricted to Hirakimata in the data set, occurs as a few individual trees on some of the eastern spurs of Tataweka and rarely in forest close to Ruahine. These sites were not near any of the transect lines and were not visited. Consequently, precise elevations were not obtained and kauri was not included in the Tataweka or Ruahine data sets. However, as the history of its exploitation demonstrates, kauri has mainly been restricted to Hirakimata and the surrounding areas for at least several hundred years (Kirk 1869).

Statistical analysis

We assumed that if a species was present at two different elevational locations, it could potentially be present in the interval between them—that is, elevation was not a limiting factor between recorded locations (this mirrors the assumptions of Shipley & Keddy 1987). The data were, therefore, the species potentially present at any elevation, even when not necessarily recorded at it. These species' elevational ranges were used to construct virtual site-species matrices for woody species and ferns. The virtual sites were 50 m elevational intervals (ten sites on Hirakimata, eight on Tataweka, and six on Ruahine). A 50 m sample interval, rather than the 25 ± 10 m used in the field, was chosen to allow for records between field points and possible errors in elevation measurement. For woody plant species, these data constituted a matrix of 113 species \times 24

sites, and for fern species, a matrix of 54 species \times 24 sites.

Although most traverses commenced close to sea level, the lower 150 m of each mountain were excluded from the analyses; often, they were steep cliffs or were visibly disturbed by human activity or exotic browsing animals. The forest cover of the excluded coastal zone is distinguished from that above by the presence of some species not common elsewhere and the dominance of *Metrosideros excelsa* (Ogden 2001; Cameron & Young 2019). From 150 m above mean sea level, the sites comprised 50 m elevational intervals e.g. 150 m (150–199 m), 200 m (200–249 m) etc. The uppermost sites for Hirakimata, Tataweka, and Ruahine, respectively, were 600 m (600–627 m), 500 m (500–526 m), and 400 m (400–402 m). The elevational range was small for the upper interval on Ruahine; consequently, we searched c. 1 ha there. Species with unresolved identification and those found once only on any mountain were excluded from the analyses because their ranges could not be established. These species are included in the data list (see Data Availability section for download link). Eleven species (9%) were eliminated from the woody plant list, and the same number (17%) from the ferns; four of the fern species eliminated were from the upper forest (>400 m) on Hirakimata. *Beilschmiedia tawa* and *B. tawaroa* show intergradation in leaf morphology and were not consistently distinguished and were amalgamated as *B. tawa*.

We tested the null hypothesis that woody species were distributed randomly across the mountains, assuming that species were distributed as a function of mountain area, which is proportional to elevation. For the multinomial distribution we had $p_1 = 6 / 15$, $p_2 = 5 / 15$, $p_3 = 4 / 15$ (reflecting heights of Hirakimata, Tataweka, and Ruahine, respectively). We used a multinomial distribution to estimate the probabilities of three objects (observations of the same species) to three classes (the mountains) and hence the null probability of a species occurring across all the mountain combinations. From these values we calculate the expected number of species occurring in each combination of the three mountains. To describe the patterns of species composition on the mountains three types of analysis were carried out: (1) species richness for woody species and ferns was regressed against elevation for each mountain using a Poisson generalised linear model (GLM), (2) the site \times species data were analysed using hierarchical classification, and (3) ordinated using non-metric multi-dimensional scaling (nMDS). Ordination and classification were required to establish the nature of the compositional continua and identify any breaks in species composition. We evaluated differences in locations between mountains using PERMANOVA (Anderson 2001) and tested differences in scatter (multivariate homogeneity of variance; Anderson 2006) on the dissimilarity matrices. Classification and ordination analyses used the Bray-Curtis dissimilarity; analyses were conducted in R v 4.1.0 (R Core Team 2021) using the *vegan* v 2.5-7 library (Oksanen et al. 2020).

These analyses do not test the hypothesis that species elevational distributions are different on mountains of different heights; instead, they provide a quantitative description of the vegetation (not previously published for two of the three mountains). Steenis's hypothesis is addressed directly by looking at the elevational limits of the suite of species occurring across all three mountains and comparing them between Hirakimata and the other two sites (Figs 7, 8).

Results

Distribution of species across mountains

The multinomial analysis (Table 2) indicated more woody species than expected on Hirakimata compared to a null distribution, and more species than expected were shared across all three mountains ($\chi^2 = 93.8$, $df = 6$, $p < 0.01$). These patterns were similar for ferns (Table 2).

Changes in species richness with elevation

On average for the three mountains, woody plants have a higher linear decrease in species richness with increasing elevation than ferns (2.7–3.2 species lost per 50 m elevation gained in woody plants, 0.8–2.6 in ferns; Fig 3a and b). The linear decline in both groups (with no mid-domain effect) presumably reflects the elevation trends in temperature and humidity over the relatively small elevational range covered (Kessler et al. 2011). Based on the regression model, there were slightly more woody species than expected at c. 400 m and fewer than expected on the summit of Tataweka (500 m; Fig. 3a). Fern richness decreases with elevation overall, and

Tataweka was less speciose at all elevations. The differences between the mountains (Fig. 4) are relatively small at the lowest elevation but increase with elevation. Over comparable elevational ranges, Tataweka and Ruahine are more alike at all elevations than either is to Hirakimata. Beta-diversity values (mean Sorensen’s score) at Hirakimata, Tataweka and Ruahine were 0.318, 0.273 and 0.168 for woody species and 0.366, 0.366 and 0.193 for ferns, respectively.

Multivariate analysis of community structure

Where structure and species composition were undisturbed, the forest < 300 m on all mountains equates to the oceanic temperate forest described by McGlone et al. (2016): dominant trees include *Didymocheton spectabilis*, *Vitex lucens*, *Beilschmiedia* spp. and the often-emergent conifers *Dacrydium cupressinum* and *Podocarpus totara*. Palms (*Rhopalostylis sapida*), tree ferns, lianas and epiphytes are abundant.

Sites from the different mountains on Aotea tend to be clustered together, especially for ferns (Fig 5b). Classification of the woody plant data separates sites above 300 m (predominantly the upper cloud forest assemblage) on

Table 2. Observed and expected (based on a multinomial distribution) number of woody species on each mountain, mountain pairs and all three mountains with total $S = 108$ and for ferns ($S = 53$). + indicates observed number > expected; - indicates observed no. < expected. The % contribution to the X^2 value is $(O-E)^2 / E$ for each category, rescaled to sum to 100. Hirakimata = H; Ruahine = R; Tataweka = T.

		H	R	T	R & T	H & R	H & T	H, R & T
	Expected prop.	0.064	0.019	0.037	0.16	0.213	0.293	0.213
Woody species	Observed no.	23 +	4	6	15	6 -	8 -	46 +
	Expected no.	7	2	4	17	23	32	23
	% contribution to χ^2	39.9	2.0	1.1	0.30	13.4	18.9	24.5
Ferns and allies	Observed no.	12 +	1	0	3 -	8 -	10 -	19 +
	Expected no.	4	1	2	8	11	16	11
	% contribution to χ^2	61.4	0.0	5.5	10.0	2.7	5.6	14.8

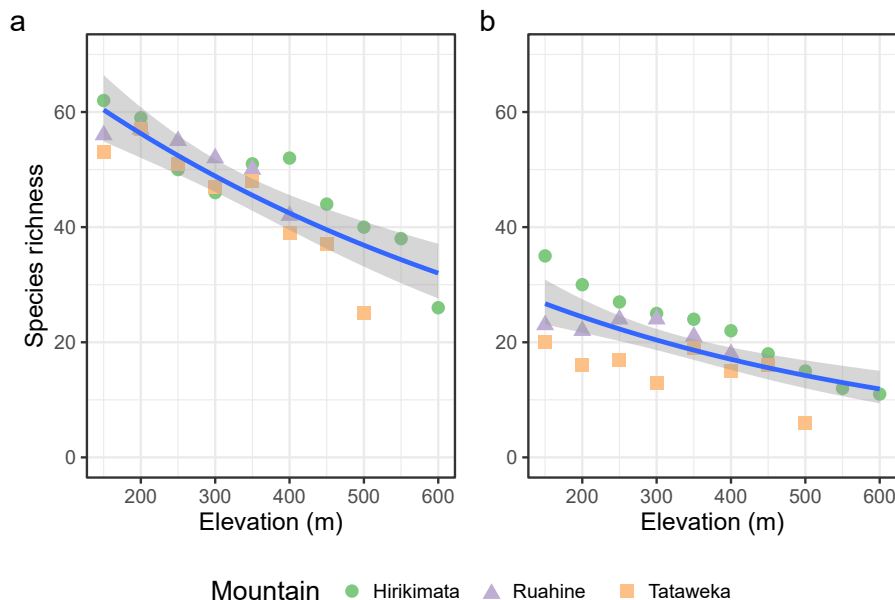


Figure 3. Poisson GLM of species richness v. elevation for woody species (a) and ferns (b). Here we show a single regression for all mountains. See Appendix S3 for model coefficients for Poisson regressions for each mountain individually. The grey zone represents the 95% confidence interval.

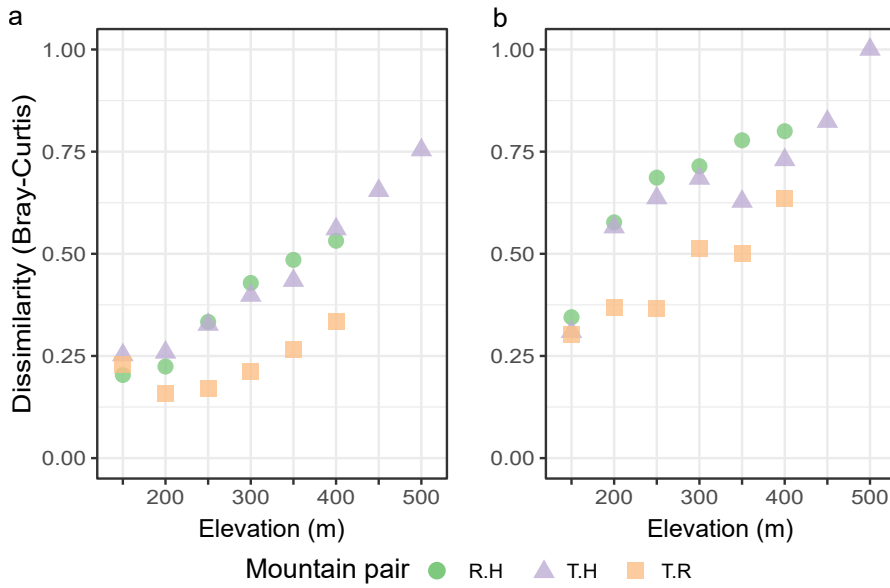


Figure 4. Pairwise dissimilarity (1 – similarity) between mountains for sites at the same elevation for (a) woody species and (b) ferns. Note the strongly increasing dissimilarity between the mountains with elevation. H = Hirakimata; R = Ruahine; T = Tataweka.

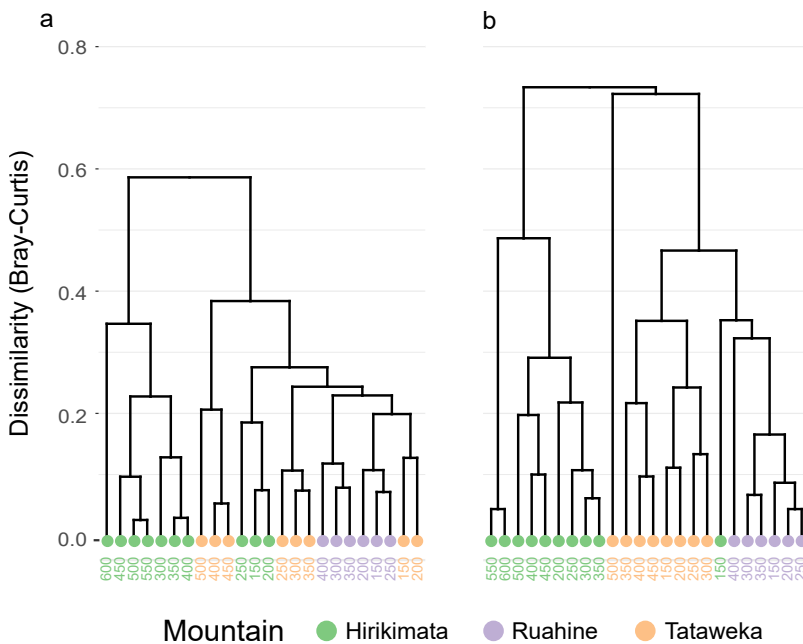


Figure 5. Hierarchical classification of (a) woody species and (b) ferns. Classification used the weighted average linkage method and the Bray-Curtis dissimilarity. Colours represent sites.

Hirakimata from the lower forest, and all Hirakimata sites from the other two mountains (Fig 5a). The cloud forest above 400 m is low in stature, with tree trunks often convoluted and branches covered in filmy ferns (Hymenophyllaceae), mosses, and large epiphytic monocots. It comprises a mix of conifers (*Agathis australis*, *Lepidothamnus intermedius*, *Halocarpus kirkii*, *Phyllocladus toatoa*) and broadleaf angiosperms (*Ixerba brexioides*, *Quintinia serrata*, *Metrosideros umbellata*) not found on the other mountains. There is a suggestion of a break at an elevation of c. 200 m on Tataweka, splitting off the coastal *Metrosideros excelsa* zone (Fig. 5a). Classification of the fern data (Fig 5b) differentiates the three mountains and identifies distinct upper groupings (or absences) on Hirakimata and Tataweka. See Appendix S4 in Supplementary Materials for the outcomes of tests of differences in dispersion and location for the multivariate analyses.

Distributions of species on Hirakimata compared to the other mountains

The twenty-three woody species recorded only on Hirakimata were mostly limited to sites at or above 400 m (Fig. 6). However, in many cases, their lower limits (tails) are below 400 m and so might have been expected on the two other mountains. Thirty-three species occurred in the lower elevation forest (> 150 m, < 500 m) at all three mountains. Twenty-eight of these extended to higher elevations on either Ruahine or Tataweka (or both) than on Hirakimata. These distributional patterns were clear for some of the lowland zone’s characteristic and dominant forest plant species (Fig. 7a). For example, the common tree species *Beilschmiedia tarairi*, *Vitex lucens*, *Didymocheton spectabilis*, *Metrosideros robusta*, *Meliccytus ramiflorus* and *Brachylottis repanda*, and the palm *Rhopalostylis sapida*, all extended more than 150 m higher on Ruahine and/or Tataweka than on Hirakimata.

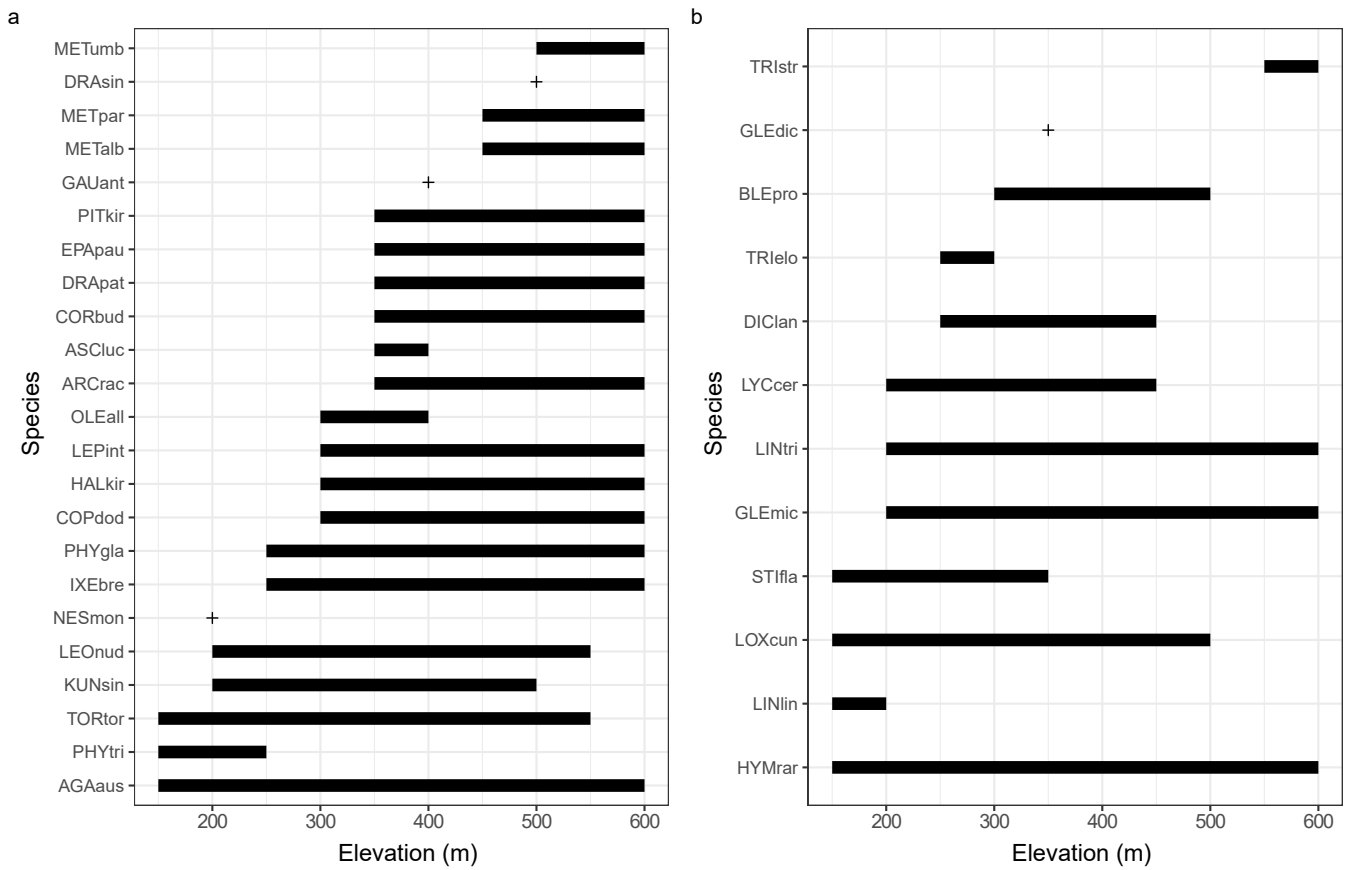


Figure 6. Elevational range of (a) woody and (b) fern species found only on Hirakimata. The + symbol denotes a species occurring at only one elevation. See data availability for download link for species list and species abbreviations (first three letters of genus-species).

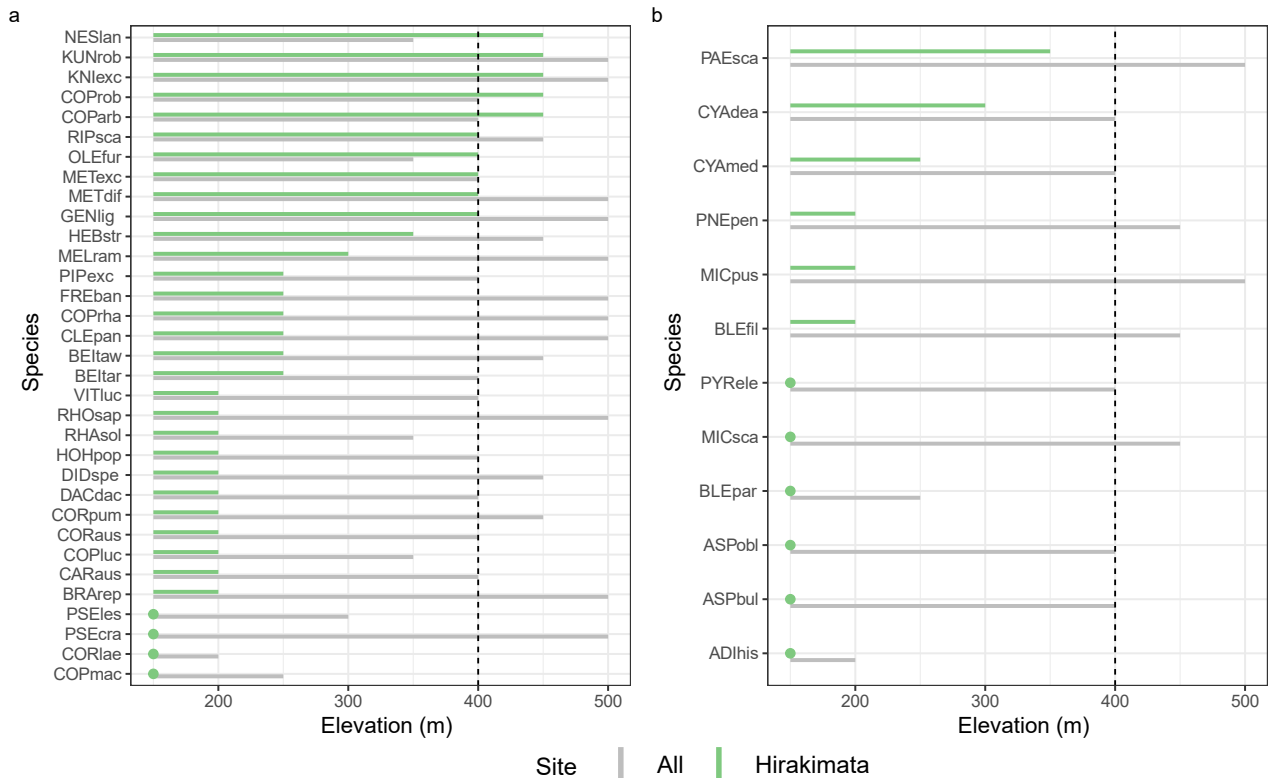


Figure 7. Elevational range of lowland (a) woody and (b) fern species found on all three mountains. Green lines show species elevational range on Hirakimata and grey lines Tataweka and Ruahine combined. Lowland species had to occur at either 150 m or 200 m across all sites and not above 500 m. The circles denote species occurring at only one elevation. Species are sorted by elevation on Hirakimata. See data availability for download link for species list and species abbreviations (first three letters of genus-species).

The ferns show similar patterns to the woody species: of the twelve species found only on Hiraikimata, eight extended above 400 m (Fig 6b); however, all except one (*Trichomanes strictum*) occurred below this elevation and hence might have been expected on the other mountains. Of the 12 lowland fern species found on all three mountains, all were recorded at higher elevations on Ruahine or Tawateka (Fig 7b).

Summary of results

There are similar linear declines in species richness with increasing elevation on all three mountains; the absolute rate of loss is lower for ferns than trees (although the proportional changes are similar between the groups). The classifications indicate a transition c. 300 m on Hiraikimata (upper limit of Oceanic Temperate Forest) and the distinctness of the fern flora on Hiraikimata; ordinations confirm the continuity of species composition. A group of predominantly upper elevation woody species on Hiraikimata does not occur on the other two mountains, despite the species' lower elevational tails being within the elevational ranges of the other mountains in almost all cases. Furthermore, a group of widespread lower elevational species do not extend to their potential upper limits on Hiraikimata. These patterns can also be discerned in the ferns.

Discussion

Individualistic species ranges and community boundaries

Overall, the species' ranges show an individualistic rather than community-unit arrangement along all three elevational sequences, although classification of the woody plant data indicates a shift in community composition c. 300 m on Hiraikimata. This elevation coincides approximately with a change in slope and an old fire boundary. High species richness at c. 400 m on Hiraikimata suggests a zone of overlap between the upper (cloud) and lower (oceanic temperate) forest assemblages. This elevation was often observed to be coincident with the approximate elevation of the cloud base.

Elevational zonation on Hauturu shows similar continuity in composition to that on Hiraikimata (Hamilton & Atkinson 1961; Cameron & Young 2019). On Hauturu, there is a transition from coastal forest under the strong influence of salt-laden air, and dominated by *Metrosideros excelsa*, to mainly *Kunzea robusta* forest, at c. 150 m. A further transitional zone occurs between 400 and 500 m, where the *Metrosideros robusta* / *Beilschmiedia tawaroa* / *Vitex lucens* assemblage shifts to *Ixerba brexioides* / *Beilschmiedia tawaroa* forest above. This community, in turn, becomes *Quintinia serrata* / *Ixerba brexioides* / *Metrosideros umbellata* forest above c. 600 m. All these transitions are gradual rather than abrupt. The upper (cloud) forest zone (> 600 m) is similar to the same zone, on Hiraikimata, but we refer to forest above 400 m as cloud forest. A similar threefold division of the vegetation into an upper mossy forest above 600 m, a wide and varied middle zone (collectively, *tawa Beilschmiedia tawa* / podocarp forest) and a narrow coastal strip (below 100 m) dominated by *Metrosideros excelsa* has been described for the Hūnua Ranges by Barton (1972). Unfortunately, no quantitative data on cloud cover duration are available from any of these mountains, but casual observations on Aotea (Hiraikimata is visible from most points on the island) indicate that when cloud is present, its base is usually between 400 and 500 m.

Steenis's hypothesis and the cloud forest

Steenis's hypothesis predicts that montane species will be absent from mountains that are not high enough to intersect their elevational zone of permanent establishment. Thus, it is a hypothesis about relative distributions on different mountains rather than elevational vegetation sequences *per se*. Many factors, which likely vary between mountains, are involved in the latter (Lomolino 2001), so comparisons of species patterns between mountains must consider many possible causal influences.

Mountains need a certain elevation to "capture" clouds and form a cloud condensation belt. The cloud forest on Hiraikimata constitutes the zone of permanent presence for several plant species. These species are not found on the other two mountains, although their lower elevational tails are within the elevational ranges of those mountains. These lower tails (< 400 m) may represent individuals in the zone of temporary establishment. The other two mountains may be too far from Hiraikimata for this sub-optimal elevation range to be colonised, even ephemerally, by some cloud forest species. However, the distribution of wind-dispersed species such as *Metrosideros umbellata* and *Quintinia serrata* is unlikely to be limited by dispersal so this explanation is only partial.

Thus, the species/elevation pattern we describe may be most parsimoniously explained by postulating cloud forest climatic conditions on Hiraikimata, but not (or rarely) on the other mountains. This may explain why high-elevation cloud forest species are missing on lower mountains lacking this habitat and, conversely, why low-elevation species can move higher on the lower mountains since the low-elevation climate goes higher. These two patterns are clear for the woody species and are reflected in the fern flora. The importance of soil and atmospheric water deficits in determining distributions for most New Zealand tree species was shown by Leathwick and Whitehead (2001). Moreover, extreme drought events, rather than long-term averages of atmospheric conditions, may be most important (Ogden 1976; Leathwick & Whitehead 2001), especially in cloud forest (Jane & Green 1986). Although atmospheric moisture and other causes (such as dispersal-limitation, soils and fire history) can be postulated, the absence of the cloud forest species on the lower mountains supports Steenis's (1972) hypothesis.

Disturbance and the elevational ranges of lowland forest species

The second important pattern – that widespread dominant lower elevation forest species often do not extend to their potential upper limits on Hiraikimata – suggests the possibility of competition with the higher elevation species, but again other factors are probably involved. Disturbance history, particularly fire, could explain the absence of expected lowland species on Hiraikimata. Areas within the elevational band (200–400 m) from which the lowland species are mainly absent were last burned during the kauri logging era about a century ago. Logging and fire would have largely eliminated dominant conifers and broadleaf trees, allowing widespread colonisation by *Kunzea robusta*, *Leptospermum scoparium* and other seral species (Perry et al. 2010). It would also have been accompanied by the loss of forest topsoils (Ogden et al. 2006). The early-successional vegetation and poor substrate may have inhibited colonisation by lowland angiosperm dominants, more so than downwards colonisation (or tail expansion) of the light-demanding montane conifers many

of which tolerate poor soil conditions (Enright & Ogden 1995). Although occasional juveniles of the montane conifers (e.g. *Agathis australis*, *Halocarpus kirkii*, *Lepidothamnus intermedius*) occur in this elevational range, seedlings or saplings of dominant lowland forest species (e.g. *Vitex lucens*, *Didymocheton spectabilis*, *Rhopalostylis sapida*) were absent. Thus, historical fires may have allowed some montane conifer species to establish, perhaps from surviving ‘tail’ individuals, in the seral post-fire communities, but inhibited the lowland angiosperms. Most of the latter require birds for dispersal (Thorsen et al. 2009), and the burned area on the eastern spur of Hirakimata is some distance from lowland forest seed sources. Combined with seed predation by rats, poor soil, and a harsh windy environment, limited uphill seed dispersal could have slowed succession to broad-leaved forest (Perry et al. 2015). However, dispersal limitation is unlikely to be the case on the western side of the mountain which was largely unburned and retains a good soil profile, but the upper limits of lowland forest species are likewise relatively depressed.

The effects of geology and soil fertility

The three mountains differ in their underlying geology; Hirakimata is rhyolitic, Ruahine andesitic and Tataweka sedimentary. Soil fertility would likely increase in that order, with Hirakimata having the lowest and Tataweka the highest fertility. Allen et al. (1991b) found greater species diversity on South Island New Zealand mountains with a gneiss substrate compared to granite. They attributed this to greater substrate instability and consequent disturbance on the former. Perry et al. (2010) demonstrated better quality soils in gullies rather than ridges on Aotea. On all three mountains, fertility might be expected to be less on ridges and to decline with increased leaching at higher elevations, but the presence of large colonies of burrowing seabirds on Hirakimata and probably formerly on the other mountains, implies nutrient addition rather than loss. Moreover, Yavitt’s (2000) analysis of litter and soil nutrient concentrations across different parent materials in the wet tropics, including andesite and limestone, showed there were no differences. This was attributed to weathering and soil mixing with erosion and disturbance, and implies that the influence of underlying geology on leached surface soils may be limited. It is plausible the same could be true on Aotea, strengthening comparisons among peaks. Many lowland species occur on nutrient-poor andesite (Ruahine) and sedimentary greywacke substrates (Tataweka), suggesting that many lowland species have a broad tolerance of substrate. However, if surface soils have been depleted by erosion after fire the rhyolitic substrate may have produced shallow infertile soil conditions unfavourable for the lowland angiosperms but tolerated by conifers due to their higher nutrient-use efficiency (Vitousek 1982; Enright & Ogden 1995). Ohlemüller & Wilson (2000, p. 264) reported that “richness of woody species was significantly lower in sedimentary-rock areas than those with metamorphic or volcanic rocks”, which is the pattern we also observed: Tataweka is sedimentary and has lower richness than the other two, volcanic peaks.

Logging and farming

Although kauri logging did not occur on Tataweka and Ruahine, they suffered various disturbances as Europeans logged, mined and cleared scrub for farming. Grazing by goats (*Capra hircus*), pigs (*Sus scrofa*), and feral cattle (*Bos taurus*) has been extensive on Tataweka and has left a marked influence on the vegetation (Wright & Cameron 1985). Palatable ground

ferns have suffered considerable depletion (e.g. Fig 3b). The richness of woody species on the Tataweka summit area has clearly been reduced, but there is no evidence of the former presence of cloud forest species. At mid and lower elevations on Tataweka and Ruahine, areas briefly cleared for farming during the last century are dominated by *Kunzea robusta*. Goats and feral cattle have been eliminated, but past browsing will have decreased the abundance of palatable, and increased the abundance of unpalatable species, especially ground ferns. However, for most long-lived woody species grazing is unlikely to have influenced elevational ranges.

Past climates

While human disturbances, seed dispersal, soil fertility and related factors are proximal influences on species distributions, longer-term or distal factors also play a role. The influence of the climatic oscillations of the Pleistocene (broadly, glacial, and interglacial climates) on vegetation distributions have been thoroughly documented in North America, Europe and New Zealand (Davis 1976; McGlone 1985; Graham & Grimm 1990; Wood et al. 2017). With a shift to warmer (interglacial) times, a species might move to inhabit its upper zone of temporary establishment permanently, and Steenis’s (1972) entire within-species zonation system move upwards. During cooling phases, the zones presumably move downwards. During the upwards migration of a tree species, it invades a progressively smaller area with potentially fewer competitors, but reduced area implies increased extinction risk. In contrast, species moving downward must invade a larger area inhabited by a more diverse, taller closed forest. These differences imply different abiotic and biotic selection pressures (filters), seed dispersal mechanisms, and seedling survivorship (Ogden 1989). Canopy disturbance probably plays a role in both situations, but is more likely to be crucial in the downwards/cooling phase because canopy gaps are bigger in taller forest at lower elevations (Ogden et al. 1991). The asymmetry of the process, coupled with its repetition over repeated glacial/interglacial cycles, creates the “Pleistocene ratchet” described by McGlone et al. (2016). Stochastic local extinction of some species, when reduced to small population sizes, can account for their seemingly anomalous absences on some mountain summits.

The peaks on islands in the Hauraki Gulf and its surrounding area have species restricted to particular summits (Moore 1973), implying biogeographical pre-human effects. McGlone (1985) reviewed the Cenozoic legacy of plant species biogeography throughout New Zealand, and drew attention to the rich floristic region north of 39°S. In that region, Hirakimata and Hauturu (Little Barrier Island, 722 m a.s.l.) carry cloud forest with a composition similar to that which existed near sea-level much further north (Trig Road: 34°48 S. near Houhora) before 34 000 years BP (Ogden et al. 1993). Its species composition indicates a cooler and much wetter climate than that at present at similar elevations in the northern North Island (Ogden et al. 1993).

Seventy-five percent of the taxa represented as macrofossils at Trig Road occur in the cloud forest above 400 m on Hirakimata, suggesting that it is a relic of this once more geographically and elevationally widespread forest type. We speculate that this assemblage ascended individualistically onto cooler wetter peaks as the overall climate became drier. Today these summits (Te Moehau, Hauturu, and Hirakimata, now isolated from each other by sea-level rise) and other high points on the Waipoua plateau, Coromandel, Hūnua,

and Waitākere Ranges, carry remnants of that ancient contraction in their summit cloud forests. Glacial refugia for *Metrosideros* spp. have also been postulated for the Coromandel Peninsula and Barrier Islands areas by Gardner et al. (2004). Adjacent and slightly lower peaks do not now have a suitable combination of climatic and soil variables, so that, although their summits may be within the elevational range of some cloud forest species, most such species are absent. Occasional stochastic establishment from adjacent higher populations (i.e. sources) might occur, but a permanent presence cannot be established in effectively sink environments. Species relying on large infrequent disturbances for establishment, with wider ecological tolerances and great individual longevity (such as *Agathis australis* and *Libocedrus* spp., Ogden & Stewart 1995; Ogden et al. 2005), often have patchy idiosyncratic distributions (Clayton-Greene 1977, 1978). The absence of the cloud forest species, particularly the downhill tails of their elevational distributions, could have allowed the widespread angiosperm species of the oceanic temperate forest of lower elevations to ascend into the vacated zone.

In summary, we postulate that the cloud forest of Hirakimata is a relict species assemblage, formerly more widespread at lower elevations in the northern North Island of New Zealand. This once more widespread forest community has largely been eliminated by climatic changes (Holocene warming) from the lower peaks in the region (less than around 600 m elevation). The assemblage is not unique to Hirakimata and the vegetation at higher elevation on Hauturu is similar. Of note are *Metrosideros parkinsonii* and *Archeria racemosa*, which may represent relict distributions. However, a number of the high-elevation species occur on other peaks over 500 m across the Coromandel and Northland. Where these upper montane (primarily coniferous) species are absent, widespread species of the lower oceanic temperate forest (mostly broadleaved angiosperms) have ascended to higher elevations. This is the extension of Steenis's three-zone hypothesis into a Holocene biogeographical perspective.

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Data availability

Data used in analyses and species lists can be downloaded and cited as: Ogden, John; Perry, George (2022): Data accompanying Ogden & Perry, Ranges of woody plant species and ferns on Aotea-Great Barrier Island, New Zealand: the role of zones of permanent and temporary establishment. The University of Auckland. Dataset: <https://doi.org/10.17608/k6.auckland.16920979.v3>

Author contributions

JO conceived, planned, and executed the fieldwork (with acknowledged contributors). Both authors contributed to data analysis and the written results and discussion.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Sample locations.

Appendix S2. Ordination via non-metric multidimensional scaling of woody species and ferns.

Appendix S3. Generalised linear model Poisson regression models for elevation-species richness relationships for each mountain.

Appendix S4. Analyses of location and dispersion for site ordinations.

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