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Dynamics and Regeneration of Central North Island Podocarp Forests: A Synthesis of Current Knowledge and Future Research Directions

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Abstract **Review Article**

Podocarp-broadleaved forest of Central North Island is characterised by long-lasting, tall-growing conifers of Podocarpeacea plants above a layer of shade-tolerant, broadleaved tree cover, and the mechanisms of how they regenerate have been a topic of contention for over half a century. One consistent observation, that is, a low number of podocarp juveniles and poles beneath seemingly intact, mature podocar stands unlike Truth is the broadleaved tree species have a continuous, age-distribution of a population, it has been the driving force for many decades of studying the trees in Central North Island. The main objective of this review is the integration of findings from studies carried out at the Purepora, Whirinaki, and Tihaki sites plus the stand age-structure analyses in Tongariro National Park with results of the current pest management and species recovery monitoring to identify and assess the possible causes of podocarp regeneration patterns in the region. Most importantly, the conclusions drawn here show that recruitment in this forest type happens not only after disturbance but also on cycles rather than being a never-ending process, as is the case of other forests, with podocarp reproduction being mainly a function of mast seeding and seed disperser bird activities, senescence of the overlayer gradually, wind disturbance, and long-lived canopy trees, which act as a kind of "nurse tree", giving facilitation, so that podocar seedlings can thrive. And, the data presented do not support two previous hypotheses: one that the succession process was linear until, in the end, the last trees were just podocarps, and the other that recent climate change has been a major cause of the failed regeneration due to a cooling in the thirteenth century. Also addressed here is an investigation into the ways selective logging in the last century and, more recently, the impact of invasive mammals as grazers have transformed this system of regeneration; it is Also an evaluation of the conservation measures that at the moment have kept the whole system going. The report finally outlines areas where the current dataset is limited and what further studies might be helpful. These include a lack of long-term remasurement of past experimental plots, limited information on the combined effects of browsing pressure of different levels and facilitation by nurse-trees and remaining uncertainties about the impacts of climate change on masting and disturbance regimes and a call for corresponding priorities in future research. It ends on an explanatory note, identifying specific research areas and data limitations - e. g. lack of remeasurement of historical study plots over time, insufficient knowledge of nurse-tree and browsing pressure combined effects, and questions about the effects of climate change upon mast cycles and disturbance pattern - and proposes directions for future research as a result.

Keywords: Podocarp-broadleaved forest, Regeneration dynamics, Masting, Seed dispersal, Nurse-tree pathway, Central North Island.

1. INTRODUCTION

Podocarp" broadleaved forest historically covered approximately 2. 9 million hectares of New Zealand's lowlands and hill country (New Zealand Plant Conservation Network, n. d.; Norton *et al.,*1988). The volcanic plateau surrounding Lake Taup in the Central North Island which includes the Pureora and Whirinaki forests, Tihoi and the Mamaku Plateau, these forests display some of their best features. Rimu (Dacrydium cupressinum) which is a type of podocarp tree and mata (Prumnopitys taxifolia), miro (Prumnopitys ferruginea), kahikatea (Dacrycarpus dacrydioides), and ttara

(Podocarpus totara) as the emergent (i. e. taller) trees, rise above a canopy of mostly tawa (Beilschmiedia tawa). Higher up where the temperature is cooler there are more kmahi (Weinmannia racemosa) trees. This is as Beveridge (1973) Norton *et al.,* (1988), Smale *et al.,* (n. d.).

Figure 1: Location map of the Central North Island, New Zealand, showing key podocarp forest study sites: Pureora Forest, Whirinaki Forest, Tihoi, Tongariro National Park, and the Mamaku Plateau

A central issue in plant ecology in New Zealand, called "its most lively local controversy" by one pioneer (Beveridge, 1973), is why so many podocarp saplings and poles are missing from underneath a mature podocarp canopy whereas the associate broadleaves often present continuously structured multi-aged populations that suggest ongoing reproduction (Lusk & Ogden, 1992). To understand this occurrence and to clarify if it is a long-term cycle in a state of equilibrium or an actual decline has largely directed the studies of the region that are reviewed below (Lusk & Ogden, 1992; Norton *et al.,* 1988).

2. Forest Composition and Structure

On the flat land river beaches, you will find a whole patch of podocarps. If it happens to be poorly drained then kahikatea is going to be the main player. In general, it is the combination or rather the dominance of mata and ttara in the well-drained fertile ground or the terraces (Norton *et al.,*1988). When moving up the hill slopes, the broadleaved species gain more of the ground, in particular tawa which is the canopy associate of the north island podocarp-broadleaved forest. Other species include rimu, miro, and in some areas, mata and the northern rt (Beveridge, 1973; Smale *et al.,* n. d.). At Pureora, one of the forest types is the scattered podocarp forest and tawa. A hectareusually contains about twenty-three podocarp old trees whose canopies are covered with a heavy tawa and hardwood foliage. In general, this open type of forest tends to support more abundant podocarp seedlings and saplings regeneration than the denser stands of podocarp found elsewhere on the plateau (Beveridge, 1973).

At the height of elevations around the Mamaku Plateau, shade-tolerant broadleaved species regenerate quite continuously in the understorey while podocarps need the periodic openings of the canopy to grow beyond the sapling stage which is a feature found in many of the region's forests (Lusk & Ogden, 1992; Smale *et al.,* n. d.).

In the study of the whole country using satellite SAR and optical imagery as well other aerial sensors including LiDAR it was confirmed that podocarp-broadleaved forests remain still as a large but much decreased element of the indigenous forest cover of New Zealand (Affeld *et al.,*2018; Dymond *et al.,*2019). Pureora and Whirinaki plus Mamaku and Tihoi remnants in the South are among the biggest continuous areas of this forest type left in the North Island, which is why they also became targets not only for the classic ecological studies reviewed here but also for present pest-management and species-recovery

programmes (Department of Conservation, 2023; Innes *et al.,*2024).

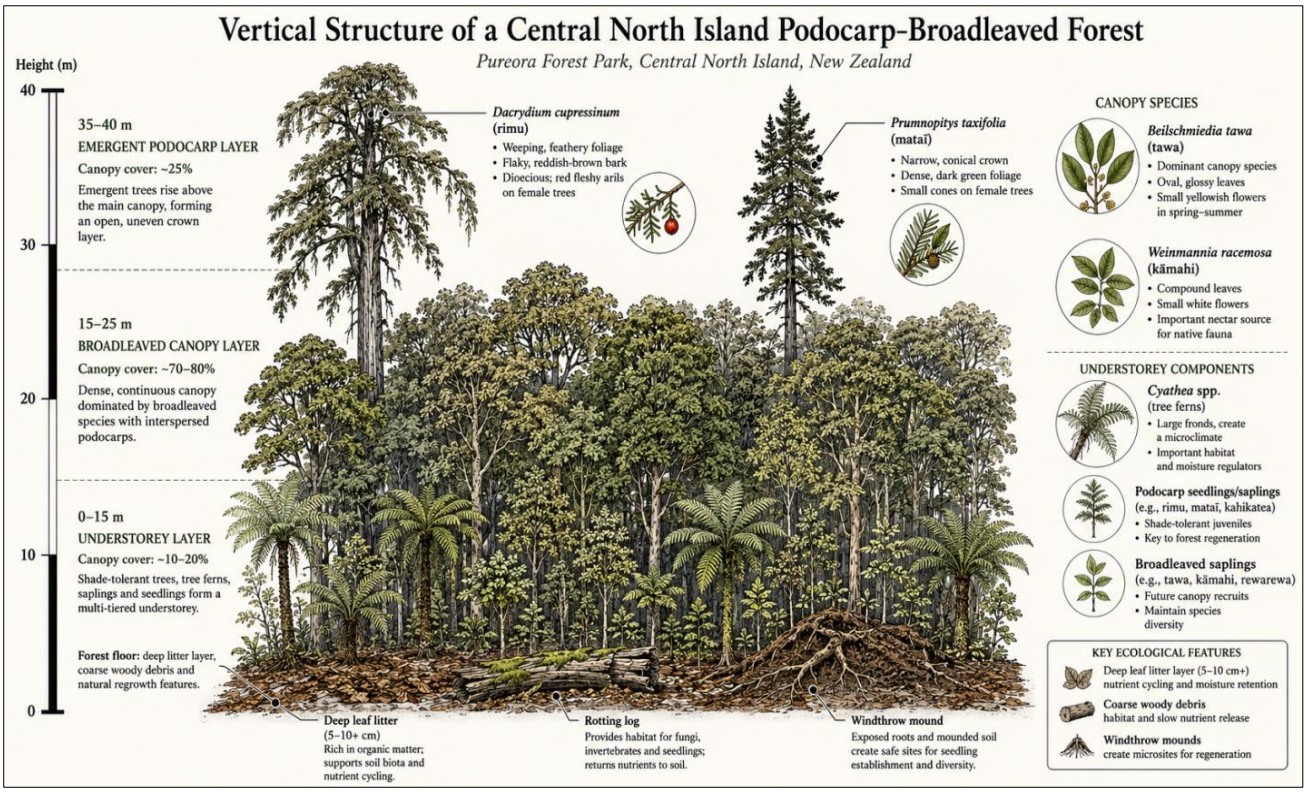

Figure 2: Vertical structure of Central North Island podocarp-broadleaved forest (Pureora). Emergent podocarps (rimu, mataī) above tawa/kāmahi canopy and fern/seedling understorey

3. Seed Production, Masting, and Dispersal

As Podocarp regeneration derives from reproduction, the five combined Pureora species rimu mata miro kahikatea, and ttara display widely different reproductive stratgies (Norton *et al.,*1988). Female cones are initiated during autumn, and in miro, mata, and rimu the time interval between pollination and fertilization extends to two growing seasons, while ttara and kahikatea complete fertilization within one season (Norton *et al.,*1988). Periodicity of seed production demonstrates strongly contrasting trends among species, with kahikatea being the most exaggerated masticator, exhibiting occasionally spectacular seedfalls (thousands of sound seed per m2) in good years separated by 2-3 years of toothless seed production (Norton *et al.,*1988).

Mata has proven Mostly unreliable at Pureora, never producing a good seed year during the 20 year study period, despite the expectation of 2-3 year intervals, largely because of insect attack to developing ovules (Beveridge, 1973; Norton *et al.,*1988). A prolonged reproductive cycle is characteristic, as from cone initiation to seedrain lasts 2-3 years (3 growing seasons). Very concentrated seed crops, making mast years, seem to result from an interaction of seed production 2-years before, and the Temperatures in the year of seedrain, and masting against 2 regions, North island central and South Westland, does not always find the same records of seedrain (Norton *et al.,*1988). The reasons of masting in rimu continue to be discussed: predation satiation cannot be proved by data, Though reproductive efficiencies from long lasting male and female effort in a dioecious tree, have been proposed as an explanation (Norton et al.

1988). Seed dispersal in these species is Mainly ornithochorous (Norton *et al.,*1988). The main dispersers of seed for the central North Island woodlands are the t and bellbird, with the New Zealand pigeon, the kerer, playing little role in the dispersal of rimu in this region, compared to further north and west (Beveridge, 1973; Norton *et al.,*1988). Miro is practically entirely reliant on kerer to spread its seed to suitable sites for several years (Norton *et al.,*1988). Wind is only capable of dispersing seed over the short range, as for most the rimu seed falls within10m of the parent and only infrequently more than40mfrom it; this further emphasizes the importance of bird secondary dispersal for colonising distant gaps and secondary vegetation (Norton *et al.,*1988). The seed is also readily consumed by rats, wt and finches, with up to 80% of a rimu crop, in the tree crown, being destroyed in some years, but this consumption does not seem to be having a major effect on overall seed production (Norton *et al.,*1988).

4. Seedling Establishment and Early Growth

Along the forest and in which they occur, podocarp seedling recruitment has been identified as being influenced by substrate and light, but not shade tolerance (Beveridge, 1973; Lusk & ogden, 1992; Norton *et al.,*1988). When it comes to Pureora, sulphur is unlikely to be an issue to seedbeds as they readily germinate under the broad range of microsite conditions present, but seedling emergence is highly sifted, as the germination response (Mainly to miro) is induced by where an opening occurs in the canopy (for example, due to logging). And, tu ite seeds of all species establish at the presence of, or beneath, large tawa, supported by the relatively large reserves of food in the seed (Beveridge, 1973). Small podocarp seedling gent due to seedling emergence is most constrained by abundant leaf litter from treefern (Cyathea spp.) and broadleaved species, but is much improved by ground scarification that removes buffering vegetation or promotes the emergence of mineral soil (Beveridge, 1973; Norton *et al.,*1988). This same pattern of association has been repeatedly described in several central North Island and Westland studies, which have documented the formation of potocarp-dominated forests in areas with high microsites rotting logs stumps windthrow mounds, and root plates with increased light and no thick layer of organic material that has been found to inhibit small-seeded species in particular (Beveridge, 1973; Lusk & Ogden, 1992; Norton *et al.,*1988).

In Tongariro National Park, a detailed seedling establishment survey concluded that the extent of seedling establishment on highly microsited pads was negatively related to seed size: towards 70% of seedling establishment of the small-seeded kmahi occurred on highly microsited pads and establishment on highly microsited pads also was important, but comparatively less dominant, for larger-seeded nia and mata (Lusk & Ogden, 1992). Growth from seed to sapling is usually slow, often over many years showing zero positive change in height, Mostly under a closed canopy a unique feature being attributed to terminal shoot dieback overshadow seedling death (Beveridge 1973, Norton *et al.,*1988). Growth rates increase rapidly once seedlings are released from persistent overstorey shade either from natural senescence or windthrow, or by logging (Herbert 1980 Norton *et al.,* 1988). Studies from NZ examining seedling performance and environmental filtering of evergreen temperate rainforests has demonstrated that seedlings of conifers (including podocarps) exhibit specific abiosic preferences to that of their angiosperm associates with light, substrate and browse effects accounting for seedling survival (Schlesselmann *et al.,*2025). This evidence lends additional support to the need for microsite specific conditions for podocarp regeneration as shown from studies at Tongariro and Pureora almost four decades earlier (Beveridge, 1973; Lusk & Ogden, 1992).

5. Age Structure and the Nurse-Tree Pathway

Granulometric determinations have completely redefined the woody forest history of podocarp advents (Lusk &Ogden, 1992; Norton *et al.,*1988). Research within Tongariro National Park, based upon total-stand age records from chronosequences within clear-felled plots, has indicated that all three studied podocarp species rimu, miro, and mata, demonstrated pronounced, juxtaposed age groups in stark contrast to broadleaved associates (kmahi and Nestegis cunninghamii), which displayed unbroken all-sized populations indicative of continuous recruitment (Lusk & Ogden, 1992).

Crucially, this break represented not a single 'catastrophic' disturbance (Lusk & Ogden, 1992). Determination of the ages of growth releases and scars on cross-sections of stems revealed that many the podocarp age classes originated over a long period of gradual overstorey dieback, approximately 120 years ago, with two well defined peaks of denudation, rather than one single exogenous disturbance like fire or major storm event (Lusk & Ogden, 1992). The thing of long term progressive dieback within a predominantly even aged parent stand, rather than because of a single catastrophe, has been observed in Westland remu stands and others in central North Island as well (Norton *et al.,* 1988), suggesting a common aspect of podocarp population dynamics in the vicinity. A last important aspect is that of where podocarp regeneration actually becomes established (Lusk & Ogden, 1992). Few podocarp seedlings and saplings in the Tongariro study established in canopy gaps. Instead, podocarp species mainly established away from their own parent trees and show a positive association with large, aging kmahi "nurse" trees as do other central North Island podocarp broadleaved forests (Beveridge, 1973; Lusk & Ogden, 1992). Spatial analysis demonstrated that miro saplings were highly clumped at radii similar to the size of gaps generated by aging kmahi (Lusk & Ogden, 1992). This nurse-tree pathway has been explained by the relatively light, thinning crowns of kmahi, Elaeocarpus dentatus, and Nestegis which senesce slowly, producing an improving gradation of light instead of the sudden pulse of light characteristic of a canopy gap (Beveridge, 1973; Lusk & Ogden, 1992).

At Pureora, Beveridge (1973) characterized the nurse-tree corridor as a clearly-defined succession series: a sudden wind-throw, presumably of a big, overly-old podocarp tree, opens a gap in the canopy; tree ferns invade rapidly and for some time their litter is so thick and impenetrable to light that no regeneration at all is occurring. In this way, kmahi first gets hold of tree-fern stems and grows on them in a sort of symbiotic way, and eventually the ferns are totally suppressed and the tree ferns are totally replaced by the kmahi trees, through competition and suppression of the ferns; as the kmahi tree gets taller and stronger it becomes the ideal perch for the kerer birds which, in their defecation, drop podocarp seeds beneath it; Next,

podocarp saplings develop quite a bit slowly beneath the older kmahi tree; when finally the kmahi tree's cover becomes so thin that the podocarp seeds can germinate and start growing freely, a group or a "cohort" of new podocarp saplings is born. The whole rotation from the original windfall to the new pole podocarp generation was reckoned approximately two to three centuries in Pureora a duration which also helps to clarify that why podocarp poles (10-30 cm dbh), are typically so few, scattered over great areas of otherwise apparently healthy central North Island podocarp forest. (Beveridge, 1973; Norton *et al.,*1988).

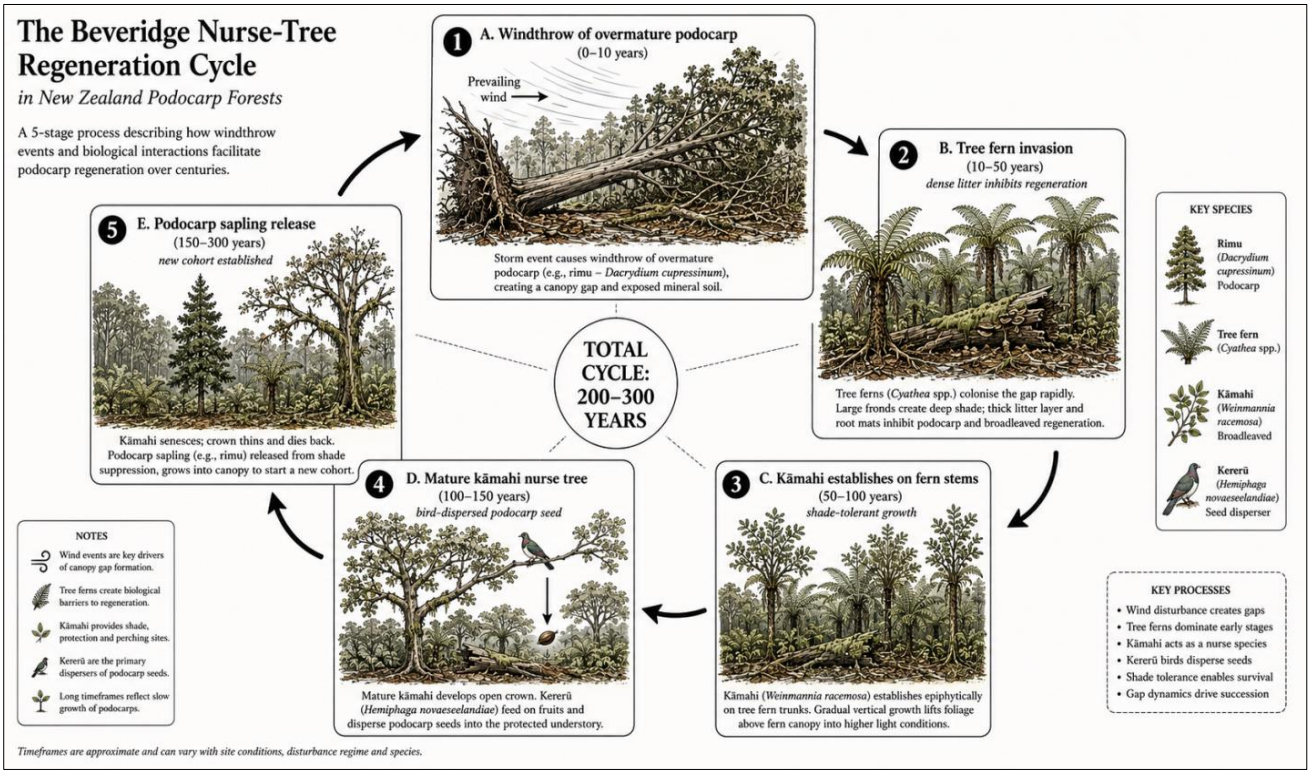

Figure 3: The Beveridge nurse-tree regeneration cycle in New Zealand podocarp forests (after Beveridge, 1973): windthrow (0–10 yrs) → tree fern invasion (10–50 yrs) → kāmahi establishment (50–100 yrs) → mature nurse tree with kererū seed dispersal (100–150 yrs) → podocarp sapling release (150–300 yrs). Total cycle: 200–300 years

6. Growth Phases and Longevity

Trees were stumps from an experiment of harvesting at Tihoi (within a densely packed mixed forest with Podocarps planted in Taup pumice soils between Pureora and Titiraupenga) showed that one individual rimu tree often goes from three to four stages which are connected directly to the developmental stage and not the calendar age (Herbert, 1980; Norton *et al.,*1988). A first phase which we call "pole" that has a very slow-growth phase usually lasting 60 - 80 years from seed growing beneath a nurse canopy. This is eventually followed by a "rapid growth phase" that starts approximately when the tree reaches 16-cm diameter, this coincides with the pole penetrating and clearing the top of the nurse canopy, and lasts about 50 - 100 years at a very high rate of diameter increment (Herbert, 1980). After this, the tree enters a longer steady-growth phase which is the main bulk of the tree's lifetime growth and finally, many older trees undergo a period of very slow growth in the final decades before felling, or death (Herbert, 1980). The only reliable parameter of measuring tree age proved to be tree diameter which was not a consistent tree age parameter as very similar diameter trees at Tihoi covered several centuries in actual age which was a finding repeated in Tongariro and Westland studies alike (Herbert, 1980; Norton *et al.,*1988; Lusk and Ogden, 1992).

Data from Tihoi on Age-class distribution of sampled trees showed that majority of 61% of rimu were only 400 years old. Age-class data from Tihoi showed that 61% of sampled rimu were 400-500 years old, with the remainder split between 500-574 years (14%) and 200-400 years (25%), giving an overall age span of roughly 400 years within a stand that appears superficially even-aged (Herbert, 1980).

The mata wood sampled that originated from the same site where rimu wood was also sampled in general were older (up to 676 years) while the miro wood was uniformly younger, which fits well with In reality miro's lifespan is shorter compared to that of mata and rimu as well as Truth is miro is a later coloniser that usually grows beneath stands of mata and rimu (Herbert, 1980; Norton *et al.,*1988). Only two individuals of 195 aged rimu were found to be older than 700 years by comparison at Tihoi, Whirinaki and, Mahinapua State Forests which indicates that the practical upper limit of

the longevity time of rimu in these forests is probably 700 years. Most trees would probably fall from internal decay and windthrow and die well before attaining such an age (Norton *et al.,*1988).

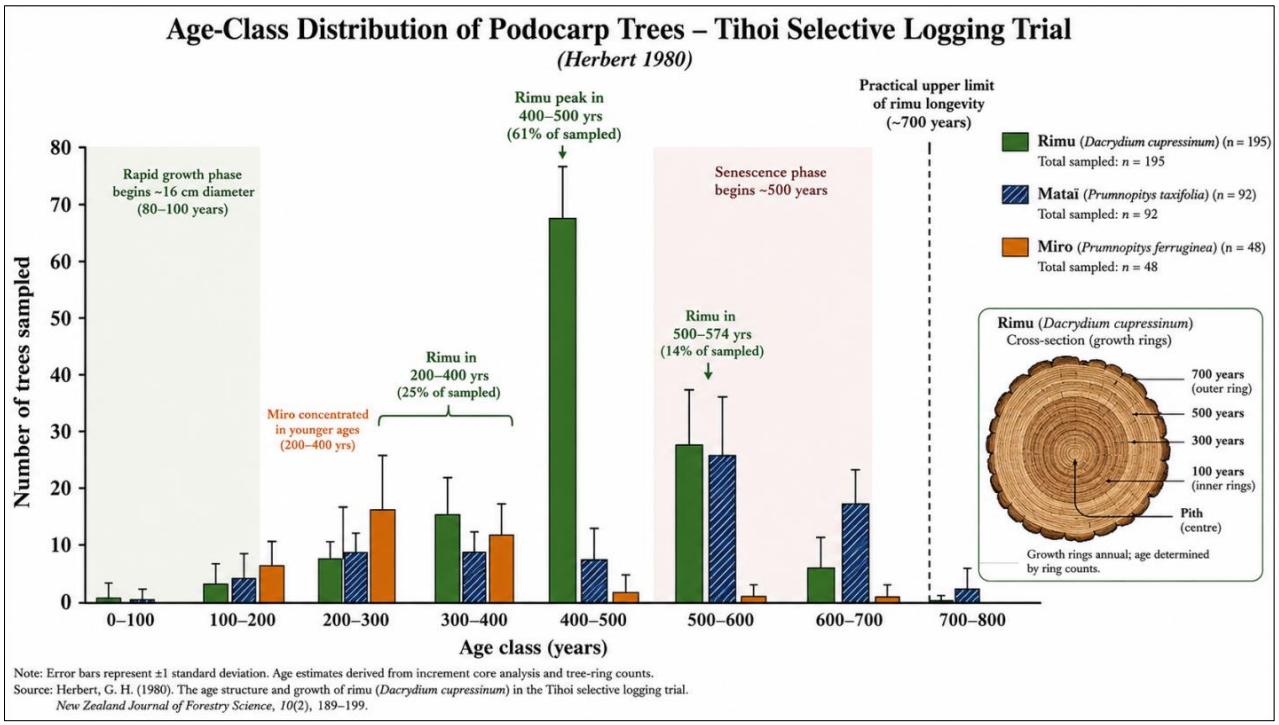

Figure 4: Age-class distribution at Tihoi (Herbert, 1980; Norton *et al.,* 1988): rimu peaks 400–500 years (61%); mataī older (≤676 yrs); miro younger

Larger and healthier-looking crowns of rimu at Tihoi are often found on older and taller trees than younger trees of the same size, which is quite likely the explanation since the larger growing space is slowly but surely secured by the older trees while the surroundings nurse canopy is getting old. Yet, crown conditions had shown little correlation with the ongoing growth rate thereby showing that the two different indicators for the vigour of a tree, namely its visual appearance and the actual amount of growth, can quite often be very different Actually (Herbert, 1980).

7. Selective Logging Trials and Stand-Level Impacts

The Tihoi trial also furnishes one of the clearest examples of quantitative data on the impacts of selective logging in dense stands of podocarps (Herbert, 1980). While the unlogged 12 ha control block garnered an estimated 1. 8 m 3 /ha/yr in gross in another three-year post-logging measurement period measured natural losses from windthrow and standing death averaged 2. 5 m 3 /ha/yr, which implied the stand had been maintained very close to, or in some cases already moving away from, a natural steady state (Herbert, 1980). In blocks where 30% and 55% of merchantable volume had been removed, net volume balances were 3. 4 m 3 /ha/yr and 7.

9 m 3 /ha/yr negative in net loss respectively victims of logging damage to root systems and wider opening of the canopy increasing exposure levels which drove windthrow and standing death to much higher levels in proportion, mostly among the non-merchantable"cull"trees, including the defective mata and rimu, whose deaths further widened the opening of the canopy and exposed the merchantable trees to higher wind forces (Herbert, 1980). The experience that even carefully imposed selective loggingtended to destabilise stand structure soon without any clear compensating growth response from residual trees directly shaped later trial design in Whirinaki Forest, and supported the general conclusion (in agreement with Beveridge's (1973) Pureora work) that central North Island podocarp forest management for sustained timber production can only be very limited:podocarp growth is slow at all stages in the life cycle (easily outstripped by competition from fast-growing broadleaves in early regeneration), the cost of removing competing ferns and broadleaves exceeds the returns, and even a second growing crop of merchantable rimu would take over 150 years to produce in ideal circumstances (Beveridge, 1973; Herbert, 1980; Norton *et al*.,1988). Later selective felling trials in Whirinaki also revealed the dominance of introduced browsers (deer and possums) at this site (greater than at Pureora), such that post-logging podocarp regeneration was rare and growth was further retarded from browsing. Alongside this, the early quantitative association established between logging disturbance and the magnitude of browsing pressure, outlined below (Norton *et al*).

8. Disturbance History: The Taupō Eruption and Regional Zonation

The c. 232 CE [abbreviated to 'c.] Taup eruption (dateee. g. 232 CE (10 years), commonly cited elsewhere in earlier forestry literature as c. 130-186 CE before the 'refinement' of the radiocarbon chronology) eradicated much of the central North Island through a monumental pyroclastic flow, and its effects on the landscape and vegetation were immense and enduring (Lowe & Pittari, 2021; Norton *et al.,*1988). This event was unearthed in 1983 at Pureora where drainage works brought to light an updomed plantation blanketed and preserved by a pumice flow and ash fall, where montane forest components of tawhero, rimu and tnekaha dominated, in stark contrast to the calliandra (mata and rimu) dominated forest that is present there today (Norton *et al.,*1988). A influential early hypothesis, generated from the work at west Taup, tested for evidence of pollencentric, ring-like recolonisation of the Taup pumice surfaces of the type created by the Taup eruption: I. e. that the heavy podocarp forest of the densest forest nearest the lake was the result of postdisturbance colonisation of the lake-side of the pumice plain, of that time generation, with the older puremata-rimu, and ultimately broadleaved dominant (northern rt-rimu-tawa) forest of the more distant areas (Norton *et al.,* 1988). Once again, the relationship between tree size and distance (time) from the centre was that large podocarps in the outer zone should be older than the smaller trees of the densest and apparently more recent inner zone, as well as existing dense podocarp stands being the first high forest on these sites (Norton *et al.,*1988). But, subsequent dendrochronological investigations have failed to support these hypotheses (Herbert, 1980; Lusk & Ogden, 1992; Norton *et al.,*1988). Studies of age structure at Tihoi and in Whirinaki Forest also demonstrated long periods of continued podocarp establishment of 350450 years and again there was little to no reliable relationship between age and diameter, even between trees in a single stand (Herbert, 1980; Norton *et al.,* 1988). More difficult to accept But, were the conclusions that because at Tihoi and Whirinaki Forest the oldest podocarp trees observed (7501000+ years, given site) are not old enough to have been the last to establish on the original post-eruption pumice surface, but are too old to have been the first generation established on the recently cooled, much-reduced, and ash bed cover connected to the period of intense Polynesian-driven burning (ca. 700800 years ago), the second hypothesis, that the pre-existing dense podocarp forest is the original colonising high forest is also not supported (Norton *et al.,*1988). In fact, evidence from both study areas would seem to support an alternative proposition which is that podocarp forest can be self-sustaining under appropriate climatic and topographic conditions and, that at least some direct replacement of podocarps by future generations of podocarps is possible, Mainly on sites like basins and inward-sloping valley floors with deep cold widely-spaced frost-free surfaces, like are in-filled with redeposited pumice, where the establishment of competing tawa is hampered (Norton *et al.,*1988).

Continued improvements to the Taup eruption timeline (Lowe & Pittari, 2021) together with a study into the contemporary magmatic activity underneath the Taup Volcano (Mestel *et al*.,2025) are providing the basis for a deeper insight into the disturbance history that underpins the development of the forests as well. Even so, the actual effects of such disturbances on the dynamics of the forests are still the focus of active debate.

9. Cyclical and Gap-Phase Regeneration Models

Of the considerable body of work synthesised in the extensive review of rimu ecology (Norton *et al.,*1988) the prevailing conclusion is that most remnant populations of central North Island and Westland podocarp were established by a fundamentally cyclical disturbance process, rather than continued replacement within a closed canopy (Lusk & Ogden, 1992; Norton *et al.,*1988). In forest ecology, forest stand regeneration regimes range from catastrophic, with the establishment of an entire cohort in large-scale canopy gaps following rare, catastrophic disturbance, to gap-phase, from canopy openings in the wake of the death of one or a few canopy dominants, to continuous, incremental recruitment within the closed forest (N Norton *et al.,*1988). New Zealand's podocarps most often fall into the variable intermediate of the two end members; episodic but sometimes catastrophic phases of overstorey mortality, alternating with more gradual recruitment stages, rather than either an entirely continuous recruitment regime or a single stand-destroying event (Lusk & Ogden, 1992; Norton *et al.,*1988).

Modern interpretations of cyclical change with New Zealand forests have replaced these two previous competing hypotheses as explanations for the historically recorded lack of small podocarps under mature podocarp canopies (Norton *et al.,*1988). First, a (by the 1920s) proven "linear succession" hypothesis suggested that podocarps as an ancient, declining forest element would be gradually displaced by vigorous, shade-tolerant broadleaves (tawa in the North Island, k? mahi in the South Island), but this has gained limited support in the field, as there is a poor prevalence of complete podocarp-to-broadleaf state changes and podocarps tend to regenerate reliably after disturbance (Norton *et al.,*1988). Second, the popular "recent climatic change" hypothesis as proposed by Holloway (mid-twentieth century), responsible for the lack of regeneration being produced, attributes a cooler or drier environment from c. A. D. 1300, as restricting the regeneration of podocarps throughout broad regions of New Zealand (Norton *et al.,*1988).

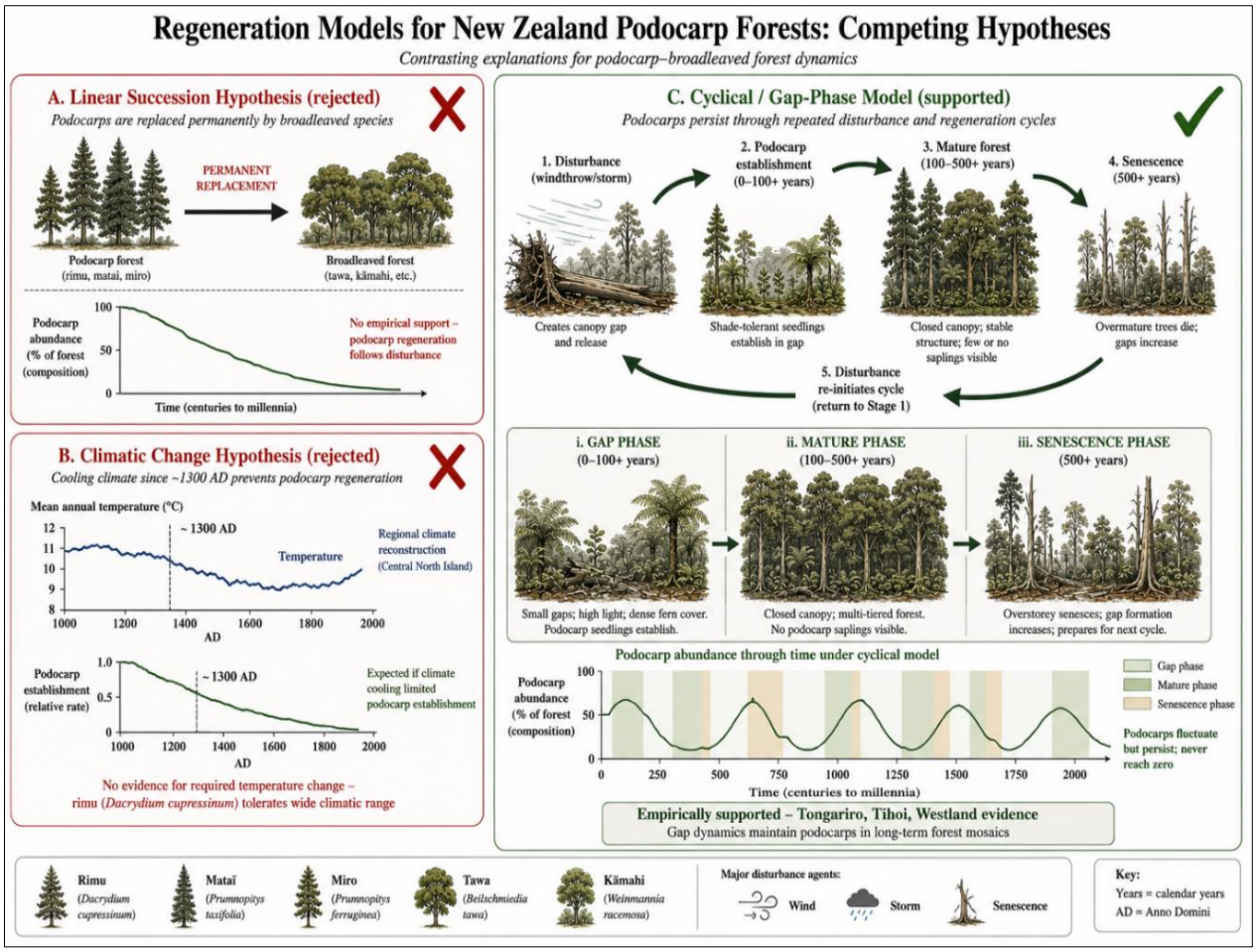

Figure 5: Regeneration models: linear succession (rejected), climatic change (rejected), cyclical/gap-phase (supported; Lusk & Ogden, 1992; Norton *et al*., 1988)

Once again, this hypothesis has been greatly refuted due to the inability to substantiate past temperature rises quantitatively, the scale of any temperature change being insignificant relative to the extant latitudinal and altitudinal climatic range of rimu, plus the great uncertainty of the agediameter relationships used in their own ageing studies (Norton *et al.,*1988). The other, gap-phase or 'mosaic' model most clearly developed by Ogden and as supported by the disturbance-history evidence obtained from Tongariro, Tihoi and Westland alike (Lusk & Ogden, 1992; Norton *et al.,*1988) describes disturbance as the primary driver of forest replacement at different spatial scales from the felling of an individual tree through to general storm damage. The resulting mosaic of variable-aged stands would then be a normal, rather than an abnormal, structural feature of a podocarp forest (Norton *et al.,*1988). As a result in this structure, absence of podocarp saplings beneath stands of mature trees does not necessarily imply that forest is in decline but only that regeneration is not expected to be present beneath a relatively unbroken canopy. Regional winds appear the most likely primary proximate disturbance agent, as would be necessary to account for the marker growth rings which have been observed in Tongariro cross-sections (Lusk & Ogden, 1992). On top of that senescent shallow-rooted podocarps are renowned for their fragility and proneness to storm-topping, a fact that fits readily with the estimates of wind's role in the ecosystem (Norton *et al.,*1988).

10. Introduced Mammals and the Modern Regeneration Bottleneck

If we add to these historical influences the more recent and ever-increasing impact from introduced browsing mammals Mostly Brushtail possums (Trichosurus vulpecula) and Red Deer (Cervus elaphus) (Fraser, n. d. ; Norton *et al.,*1988) then Clearly the traditional podocarp regeneration pathway, following Beveridge's (1973) cyclical nurse-tree model, is now being expressed in a context of near-absence of these pressures (Beveridge, 1973). This assertion is supported by trials of selective logging at Whirinaki in the early 1970s, which found far more substantial impacts on the vegetation from browsing animals, with regeneration of podocarps scarcely evident and growth slow from the mid-1970s due to browsing pressure. Today, the widespread and severe impacts from both deer and possum browsing in the surrounding areas forecast a scenario in which the protection of the pre-emergent stage of the traditional pathway should be achieved through long-term possum and deer control (including

aerial 1080 drops), to see the growth of kmahi and other prime nurse species (Innes *et al.,*2024; Department of Conservation, 2023). National-scale recent monitoring has established introduced copredator mammals continue to pose a threat across most New Zealand's native forest, exerting Browsing pressure on tree regeneration, seedling survival and composition at the scale of hundreds or thousands of hectares (Hawcroft *et al.,* 2024; Jo *et al.,*2024). Examples of long-term predator control in farmland-adjacent New Zealand North Island sites elsewhere can show predictable biodiversity improvements outside the confines of formally protected areas (Glen *et al.,*2019) indicating that the predator-control approach established across the Pureora and Whirinaki stands is not geographically isolated but is following nationally established practice. The combined impacts of possums, deer and rodents on podocarp seedling and sapling survival though the nurse-tree path way have yet to be fully demonstrated, although evidence from several current programmes suggests insight might be gained from ongoing collection of data on recovery trends (Department of Conservation, 2023; Innes *et al.,*2024; Peltzer *et al.,*2019).

National-level programmes like the Predator Free 2050 have been developed in an attempt to control the problem, and yet such large-scale and far-reaching goals of being predator free over the different landforms in New Zealand are not without problems. These are, for instance, the various interactions and balance of the ecosystems, different methods of pest control, and also the governance system, to name a few. (Goldson *et al.,*2015; Peltzer *et al.,*2019; Samaniego *et al.,*2024) Experts have pointed out too that these kinds of very big and long-term initiatives - like the so-called "moonshots" - come with both risks and rewards, no matter if they result in actual eradication or not, and continued control of prey at a level that is not yet eradicted could also bring about ecological wins. (Palmer & McLauchlan, 2023) Forest restoration, biodiversity monitoring and pest control efforts must go hand in hand to protect and ensure podocarp-broadleaved forests get their share of the future (Bellingham *et al.,*2020; MacLeod *et al.,* 2024).

11. Conservation Response and Management Outcomes

The conservation result that has been achieved most obviously since there has been a steady implementation of regional pest control is that the North Island kkako (Callaeas wilsoni), a bird that is closely related to the health of a particular type of forest and which is classified as a threatened species, has been restored. Surveys conducted in Waipapa South block, northern Pureora recorded 124 kkako pairs in 2023 compared to 87 pairs in 2015 (around 4% annual increase). Together the larger Waipapa area and northern Pureora pest-control blocks are thought to have approximately 672 pairs (Department of Conservation, 2023; Innes *et al.,*2024).

Figure 6: North Island kōkako (*Callaeas wilsoni*) in Pureora—recovery (124 pairs, 2023) reflects pest management success

At the national level, it seems the kkako population has grown from about 458 pairs in the year 2000 to approximately 2,327 pairs in 2023. Though, really several sites individually saw a decline highlights Truth is their recovery has not been secured and it is still dependent on continuous, properly funded, control measures. Innes *et al.,* (2024) Whirinaki Forest, a neighbour of ours, once a site of fierce protests against logging during the 1970s, now shows a similar pattern. The area started becoming a home for reintroduced kkako birds in 2009 and Later also supplied population for translocations to sites such as Ark in the Park in the Waitkere Ranges (Innes *et al.,* 2024).

The restoration of the populations of kkako and other forest birds is mostly attributed to persistent, predator control measures, In particular aimed at rat and possum populations that reduce the predation risk for

nesting birds and thereby facilitate the recovery of their own populations (Fea *et al.,*2020; Innes *et al.,*2024). Pest control Though doesn't only help birds, there are also signs that the communities of land snails (Barker 2016) and forest vegetation in general (Hawcroft *et al.,*2024; Jo *et al.,*2024) are responding positively. The protection of certain understory species like those palatable to animals, including the nurse trees necessary for podocarp seedlings development is an important and yet not visible result of long-term pest management in central North Island Forests (Fraser, nd; Norton *et al.,*1988).

12. Current Gaps in Knowledge

Long-term validation of dendrochronological models.

The core disturbance-history work underpinning current regeneration models (Tongariro, Tihoi, Whirinaki, Mamaku) was conducted between the 1970s and early 1990s (Beveridge, 1973; Herbert, 1980; Lusk & Ogden, 1992; Norton *et al*., 1988; Smale *et al*., n.d.). Given multi-century podocarp generation times, remeasurement of the same or comparable stands is needed to test whether the regeneration pulses identified decades ago are translating into genuine cohort replacement (Norton *et al*., 1988; Richardson *et al*., 2024).

Interaction between nurse-tree facilitation and browsing pressure.

Beveridge's (1973) Pureora nurse-tree cycle was described under conditions of low possum and deer impact; the extent to which sustained browsing disrupts this specific pathway for example, by removing kāmahi or *Elaeocarpus* regeneration before it can mature into a nurse canopy has not been directly tested experimentally (Fraser, n.d.; Norton *et al*., 1988).

Resolution of the eruption-chronology and post-eruption succession debate.

Ongoing disagreement over the precise dating and interpretation of the Taupō eruption sequence (Lowe & Pittari, 2021; Mestel *et al*., 2025) has direct implications for how forest ecologists interpret regional age-class patterns and the pace of post-eruption recolonisation (Norton *et al*., 1988).

Cumulative, multi-species pest impacts on regeneration, not just on birds.

Much of the quantitative pest-impact literature focuses on kōkako or other threatened fauna (Department of Conservation, 2023; Fea *et al*., 2020; Innes *et al*., 2024); less is known about the combined, current effect of possums, deer, and rodents specifically on podocarp seedling and sapling survivorship through the nurse-tree pathway (Fraser, n.d.; Jo *et al*., 2024; Norton *et al.,* 1988).

Climate-change interactions with masting and disturbance regimes.

Given the established sensitivity of rimu and kahikatea masting to interannual temperature variation (Norton *et al.,* 1988), and the reliance of the whole regeneration cycle on episodic wind disturbance (Lusk & Ogden, 1992; Norton *et al*., 1988), there is limited published research on how altered storm frequency, temperature, or rainfall patterns under climate change might shift the timing or reliability of both seed production and disturbance-driven establishment windows (Schlesselmann *et al*., 2025).

13. Future Research Directions

1. **Long-term permanent plot and dendrochronological remeasurement**, revisiting Tongariro, Tihoi, Whirinaki, and Mamaku Plateau sites to test whether documented regeneration pulses are producing lasting cohort replacement (Beveridge, 1973; Herbert, 1980; Lusk & Ogden, 1992; Norton *et al*., 1988; Richardson *et al*., 2024; Smale *et al*., n.d.).
2. **Factorial nurse-tree/browsing experiments**, manipulating both browsing pressure and the presence of broadleaved nurse trees to directly test how introduced mammals interact with the kāmahi/tawa nurse-tree regeneration pathway (Beveridge, 1973; Fraser, n.d.; Jo *et al*., 2024; Norton *et al*., 1988).
3. **Refined, high-resolution chronosequence dating of Taupō eruption deposits and buried forest material**, integrated with dendroecological studies of surviving old-growth stands to resolve ongoing debates about post-eruption forest succession (Lowe & Pittari, 2021; Mestel *et al*., 2025; Norton *et al*., 1988).
4. **Comprehensive, podocarp-focused (not only avifauna-focused) monitoring of multi-species pest-control outcomes**, tracking seedling and sapling survivorship alongside bird population responses (Bellingham et al., 2020; Department of Conservation, 2023; Innes *et al*., 2024; Jo *et al*., 2024).
5. **Masting and disturbance-regime modelling under climate change scenarios**, building on the established rimu/kahikatea seedfall periodicity datasets from Pureora and Westland (Norton *et al*., 1988) to project how future climate variability may affect regeneration windows (Schlesselmann *et al*., 2025).
6. **Landscape-scale genetic and dispersal connectivity studies**, given the reliance of these species on bird dispersal (tūī, bellbird, kererū) across an increasingly fragmented forest landscape (Innes *et al*., 2024; Norton *et al*., 1988), drawing on emerging methods for assessing adaptive potential in threatened New Zealand tree species (Balkwill *et al.,* 2025; Richardson *et al*., 2024).

14. CONCLUSION

The body of dendrochronological and silvicultural evidence synthesised here from existing body of studies, ranging from the initial fieldwork at

Pureora, interval-logging experiments at Tihoi, rigorous examination of stand age-structure at Tongariro, to a more comprehensive review of rimu ecology strongly corroborates a highly variable, cyclical interpretation of podocarp regeneration such that; at all three study sites, podocarp age structures comprise numerous age-discontinuities due to prolonged sequences of incremental overstorey mortality, But not through an isolated trunk and stand mortality, and regeneration regularly occurs in the proximal vicinity of increased microsites and incremental light change related to senescent broadleaved nurse trees, rather than from canopy openings. Such observations are not consistent with two previously-advanced hypotheses of podocarp decline in competition with broadleaved trees namely sustained podocarp decline relative to broadleaved competitors, and a climatic shift ca. 1300 AD across New Zealand curtailing regeneration: the latter's original quantitative evidence has not withstood further investigation. As a result podocarp recruitment across the region can most accurately be described as episodic and disturbance-dependent rather than continuous or declining, functioning within the temporal confines set by the multi-century lifespan of the seedling and nurse-stage species that facilitate regeneration.

Anthropogenic influences are dynamic modifiers of this native system, but one (twentieth-century selective logging) has a documented shortterm destabilising effect upon stand structure and demographics that might interact with introduced mammal browsing impacts on native nurse-tree regeneration that has yet to have an ecologically meaningful intervention experimentally segregated. Given the multi-decadal and multi-century longevity of the studies derived from the system of episodic stability and the timescales pertinent to seedling-emergent and nurse-stage dynamics, contemporary evidence is not yet sufficient to indicate whether the episodic recruitment pulses identified in the 1970s through 1990s constitute the perpetuated success of the continuing nurse-tree regeneration pathway (whether for a stable long-term baseline or a heavily disturbed environment). It is felt that further permanent-plot remeasurement and the implementation of pest-management programmes aimed at nurse-vegetation species rather than avian indicator taxa alone are the most direct pathways toward resolving this question and for ensuring the longevity of this forest type within its intrinsic and specific mode of natural existence.

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