Natural Limits to the Expansion of Subtropical Rainforest at Mt Nebo, Queensland

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Abstract

Small patches of rainforest are numerous in subtropical Queensland. Their expansion into adjacent eucalypt forests is limited by fires and other factors. This study was completed in 1980 within a compact site of 200 ha in conserved forest at Mt Nebo, Queensland. It describes the separate contributions of many natural site factors to the stability of the boundaries between these forest types. The survey area included areas of eucalypt forest with a grassy understorey and adjoining ecotonal areas. These, in turn, merged into patches of old-growth complex notophyll vine forest (CNVF). Three separate datasets were recorded from 160 plots, clustered around 32 grid points: (i) canopy species; (ii) woody species in the understorey stratum; and (iii) site characteristics, as indicators of the potential for localised progression from eucalypt to CNVF at canopy level. CSIRO Division of Computing Research in Brisbane processed the data, using methods developed to define initial stages of recovery from clearing inside old-growth CNVF at nearby Mt Glorious. Apart from recent fires, the long-term expansion of CNVF across an ecological gradient at Mt Nebo was limited at various stages by factors such as the orientation, aspect and shape of slopes, soil derivation, the type and thickness of litter cover, soil moisture levels, and the presence and persistence of the exotic shrub lantana (*Lantana camara*). The compact survey area was free of some confounding influences seen in broader regional studies (e.g. variations in elevation, soil derivation, temperature and rainfall, and incomplete records of fire, grazing and clearing). In this study the ranges of separate sets of observations of canopy and understorey trees, and natural site characteristics within each plot, were unusually broad, allowing definition of how natural site factors combine to allow, and limit, succession from eucalypt forest to mature subtropical CNVF in the absence of fire.

Keywords: rainforest, complex notophyll vine forest, eucalypt forest, canopy trees, understorey, history of wildfires, environmental gradients, vegetation succession, exotic *Lantana camara*

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Introduction

The irregular incidence of damaging wildfires can overshadow the influence of the many other natural factors which combine to limit the expansion of small patches of subtropical rainforests in Australia. Localised site factors vary in quality and importance, and may, in favourable conditions, enable the expansion of rainforest into the band (ecotone) which links them to nearby mature forests dominated by eucalypts (*Eucalyptus* spp.), with a flammable understorey of tufted grasses and dry litter. The changing species composition of the understorey tree stratum foreshadows future replacements of species within the associated canopy tree stratum. Over time, the forest structure itself will provide additional factors which can result in a shift of the ecotone linking eucalypt forests and old-growth complex notophyll vine forest (CNVF).

Historical records, based on years of personal observation and forestry experience in regional areas, provide insights into how site factors, including the incidence of wildfires, have influenced the location of rainforest boundaries in South East Queensland (Tommerup, 1934; Blake, 1941; Webb, 1956; Lahey, 1960; Ridley & Gardner, 1961; Florence, 1965). More recent reports of species groupings and locations in the broad area of the former Brisbane Forest Park (which is now included in the D'Aguilar National Park) include information directly relevant to the smaller Mt Nebo sections of the park (Young, 1982; Noble, 1982).

Several more recent regional studies of Australian rainforest communities have described their distribution and attributes in relation to site factors, such as the incidence of fire and other damage, soils, nutrient levels, climate and altitude (e.g. Russell-Smith et al., 2004; Laidlaw et al., 2011; Laidlaw et al., 2015; Hines et al., 2020). Their conclusions rely on treatments of field data appropriate for particular regions and purposes, but the results of such studies are not always easy to compare directly, even though some similar conclusions may be drawn. Young & McDonald (1987) observed that "given the usual constraints of time and money, it may be that the most meaningful studies of practical value for rainforest conservation are at local and local-regional scales, where plant-to-plant and plant-to-environment relationships can be accurately defined and described using site-specific, quantitative data".

In this study, using records from a compact, intensively sampled site, separate ecological gradients were defined for groups of trees and shrubs in canopy and understorey strata, as well as site characteristics and factors expected to influence the location of the ecotone between eucalypt forest and rainforest (CNVF). Locations of discontinuities between the successional status of existing canopy groups and the understorey species that may replace them were also used to predict where, and why, significant changes to boundaries of canopy associations may be expected in the continuing absence of fire.

Methods

Survey Area

Field observations were conducted in an approximately 200 ha area of conserved subtropical forest adjoining Mt Nebo village. Two former small national parks and small parts of state forest reserves, which constituted the survey site, are now included in the 36,000 ha D'Aguilar National Park. The original walking tracks are still in use and can be used as reference points for locating grid points (Figures 1, 2 and 3).

The mean elevation within the survey site was 469 m (± 41 m). Average annual rainfall recorded in 1980 for the previous 27 years at the nearby Mt Nebo Post Office was 1466 mm. Local records have now been discontinued for many years and the nearest existing stations are not in comparable locations. Rainfall recordings from within forested areas may be complicated by dew and fog, which drip from the canopy to be available within the ground stratum (Specht & Turner, 2006). Timber trees, mostly eucalypts, had formerly been logged in small southern sections (then defined as 'Beauty Spots') of the survey area, but this had already been long discontinued. Routine controlled burning of separate compartments of the former state forest sections of the park were introduced about 11 years earlier, following which none of the survey area, the adjoining Mt Nebo village, or its only public access road, had been affected by wildfires. Previous fires had occurred in the survey area and elsewhere in the former 250 km^2 Brisbane Forest Park in 1936, 1939 and 1957 (Noble, 1982). The Brisbane District Forestry Office provided maps of fire-affected areas in and around the survey area, including where a major fire had burned almost half the site in 1968, but the limited available records of wildfire locations (1951–1968) overlap and were difficult to amalgamate for this study. Areas with no further record of fire between those years are indicated in Figure 2. The most widespread wildfire (1951) had badly affected the survey site and many other sections of local forests, as well as the western edges of the Mt Nebo village. Following the introduction of controlled burns of forests 11 years before this study, there were no further wildfires affecting the immediate local area.

Sampling Methods

Field observations were carried out over 22 days during a relatively dry period in spring 1979. A roughly rectangular set of 32 grid points was set out at 200 m intervals within the site. It was limited in shape by a public road adjoining the park boundary. Grid spacings of 200 m were chosen as the most suitable scale for determining site–species relationships, based on findings by Spenceley (1973). The survey pre-dated GPS technology, so grid points were located by direct measurement with the aid of maps, clinometer data, aerial photos showing key locations, records of permanent walking tracks, detailed forestry maps and direct measurement (Figures 2 and 3).

Each area of 50 m × 50 m enclosing the 32 grid points contained a cluster of five separated 12.5 m × 12.5 m plots, each set located randomly by compass points around the grid point (inset in Figure 3). Due to some steep slopes (range <2^0–18^0) and dense vegetation, grouped plots facilitated access to grid locations to position them and revisit the plots if needed. The total area of plots was 781 m^2, which was approximately 1.25% of the total survey area. The author had managed a family acreage property 1 km from the survey site and was familiar with the local flora. Unfamiliar species were identified with the aid of reference material or by submission of specimens to the Queensland Herbarium. Three separate lists were recorded for each of the 160 plots:

(a) Species and numbers of trees ≥20 cm GBH (girth at breast height) in the upper and lower canopy.
(b) Species and numbers of understorey trees (including shrubs) >1 m tall ("survival level"; Webb, 1956) and GBH <20 cm.
(c) Site characteristics.

Figure 1. General location of the survey area in the D'Aguilar National Park, Mt Nebo, Queensland.

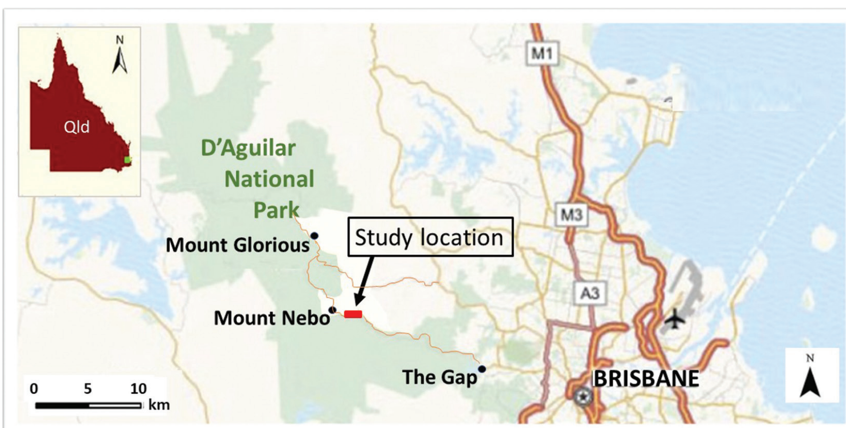


Figure 2. Close-up of the Mt Nebo district where the survey was conducted, showing landmarks, contours, permanent roads and tracks, and limited information about previous fires.

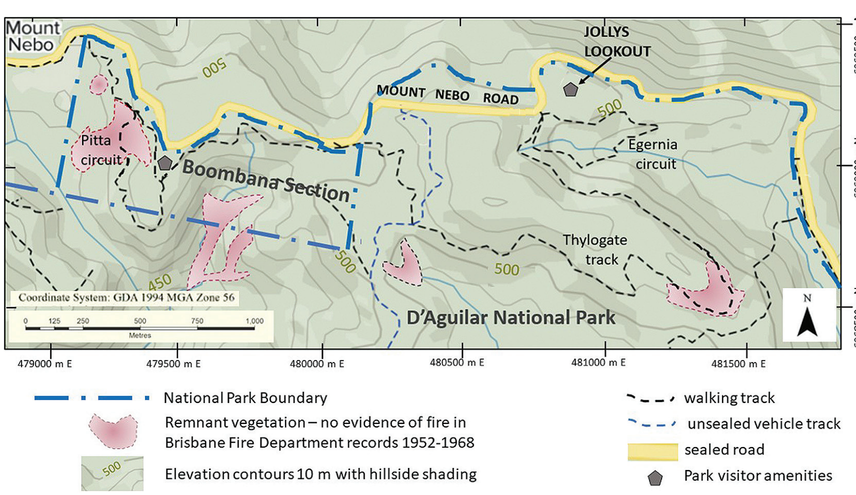
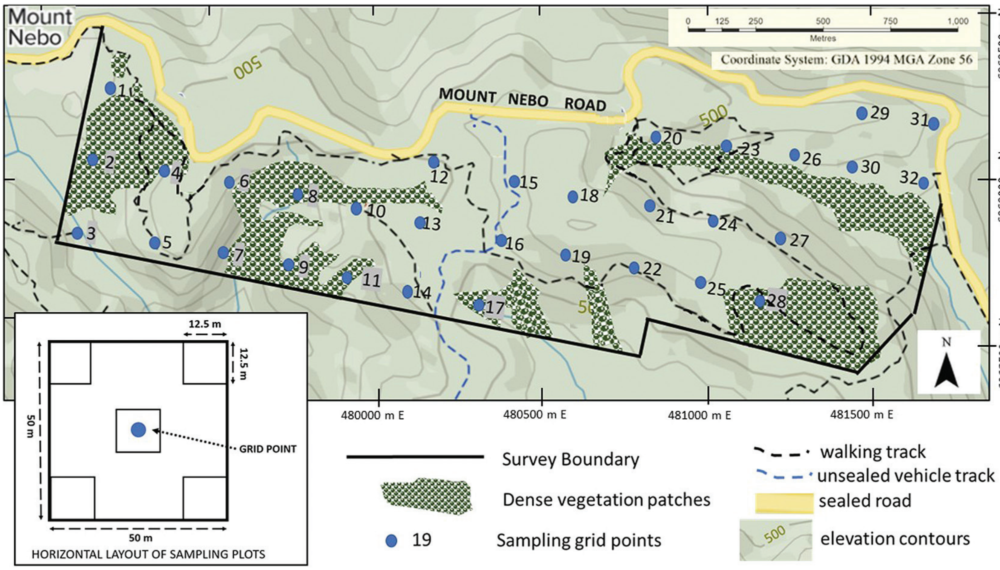


Figure 3. Location of boundaries of survey area, grid points, layout of clustered plots, and approximate areas of denser vegetation, extracted from aerial photos.



Characteristics of the sites were recorded in the following formats:

Presence/Absence

Recent soil disturbance, observed evidence of fire: 0–11 years and older (separately for canopy and understorey trees, as described in the final paragraph below), stony ground >10%, soil moisture above mean level, tufted grasses, ferns (not epiphytic), climbing palms, scrambling vines. buttressed trees, layered canopy with emergent vines.

Numeric

Slope (^{0}), altitude (m), projective foliage cover (%), lantana (vertical leafy branches only), soil pH ($\log_{10}$ value).

Multistate

(5 classes, 25 subclasses of characteristics)

(i) Litter depth: a. ash/bare; b. eucalypt litter <2 cm; c. 2–5 cm; d. >5 cm; e. soft CNVF >5 cm.

(ii) Aspect (^{0}): 0–89, 90–179, 180–269, 270–359, flat (top-slope).

(iii) Surface rock derivation: Granodiorite, hornfels, andesite, recrystallised andesite, altered sediments/conglomerates.

(iv) Slope position: Flat/top, convex, concave, evenly sloping, gully.

(v) Canopy dominants/co-dominants: Eucalypts, eucalypts/brush box (*Lophostemon confertus*), previous group plus CNVF spp., brush box/CNVF, CNVF.

The site factors (a)–(c) listed above were considered most likely to affect the natural progress of succession from understorey to canopy species composition in the absence of fire. While all such factors were included in analytical procedures used during Stages 2 and 3 of the investigation, only those items correlated at high levels with understorey species along an ecological gradient are shown in Stage 4 of the five Stages of the results.

As well as the short period for which official maps of widespread forest fires were available, the maps were also not at a suitably fine scale to be related to the location of the small survey plots. On-site records, included in (c) above, were of persistent evidence of locations of multiple fires over an indeterminate (longer) period than the most recent 11 years, and included trunk damage (e.g. hollowed trunks, charcoal, and recovery by coppicing and suckering rather than by establishment from seed). Figure 2 includes an estimation of wider areas where fire evidence was not as closely observed during the survey.

Data Treatment

A team of statisticians at the CSIRO Division of Computing Research (Brisbane) had recently used and adapted traditional methods of analysing patterns in forest vegetation and regeneration, enabled by collaborations with plant taxonomists and other expert botanists. Earlier versions of this suite of methods allowed interpretation of subtropical rainforest patterns elsewhere in the region (e.g. Hopkins (1975) in Lamington National Park) and in old-growth CNVF at Mt Glorious, 10 km from Mt Nebo (Williams et al., 1969; Webb et al., 1972; Dale & Williams, 1978).

The group generously transferred information from punched cards (prior to the availability of programs for direct input from large spreadsheets as noted in Table 1). The data were processed using a CYBER 76 computing system and programs from the in-house CSIRO TAXON suite (Dale et al., 1979–1980), to provide all analytical results included in this paper.

The first three stages of analysis described species associations in (1) the canopy and (2) understorey, and (3) associations between the many site factors. Each set of results was then separately ordinated to determine parallel ecological gradients. Stage 4 related the successional associations in the understorey stratum to site factors along an ecological cline, to determine the major factors contributing to the expectation of longer-term change to canopy speciation in the absence of fire. Stage 5 sought to identify areas where there were substantial localised differences between the composition of canopy and understorey strata, and to provide explanations of such patterns.

Table 1. Summary of computing processes used for data analysis in Stages 1–5 of Methods, as documented in Dale et al. (1979–1980) and other authors noted below.

<table>
<tr><th>Stages of analysis</th><th>Methods and purposes</th><th>Where shown in Tables and Figures</th><th>Method of input and data processing</th></tr>
<tr><td>1. Canopy trees – coenocline (successional gradient)</td><td>ISA (Hill et al., 1975); CANMAR (Lance & Williams, 1967; MULCLAS with flexible classification (Lance & Williams, 1966); GROUPER; Ordination by GOWER (principal coordinates analysis) (PCA; Gower, 1967).</td><td>Table 2, Figures 4–5</td><td rowspan="5">As available and appropriate in 1980 to the data and purpose of analysis, Stages 1–5.

Data was input for processing by a CYBER 76 computing system, using punch cards. This was prior to availability of spreadsheet programs suitable for large data matrices, such as Lotus 1-2-3, EXCEL, SPSS, R, and in-house suites of methods.</td></tr>
<tr><td>2. Understorey trees – coenocline (ecological gradient)</td><td>CENPERC3 (classification; based on Shannon diversity; Williams, 1973); CANMAR; GROUPER. Followed by GOWER.</td><td>Table 3, Figures 6–7</td></tr>
<tr><td>3. Site factors (environmental gradient)</td><td>CANMAR; MULCLAS with flexible sorting; GROUPER. Followed by GOWER (with centring adjustment).</td><td>Figures 8–9</td></tr>
<tr><td>4. Relation of understorey regeneration and site factors in ecological sequence</td><td>Results from 2 and 3 by GOWER followed by CANONGO (Williams & Lance, 1968; Williams, 1976) and principal coordinate analysis (PCA; Gower, 1967; Gittins, 2012) followed by GOWECOR (first 20 Spearman correlations).</td><td>Figures 10–11</td></tr>
<tr><td>5. Identification of areas of greatest potential change to canopy composition</td><td>Comparison of separate MULCLAS classifications of 160 survey plots using canopy and understorey data, from Stages 1 and 2.</td><td>Based on results from Stages 2 and 4; summary included in text.</td></tr>
</table>

The classifications (dendrograms) from Stages 1–3 were truncated at various levels (6, 7, 12, 25) depending on the scale required to provide and relate separate sets of results from each stage of analysis (1–5) most clearly and effectively, as explained in results. Summaries of the methods and results described above are given in Hegarty (1981) and Clifford & Stephenson (1975).

Results

A total of 141 species of trees was identified in canopy and understorey strata during the survey.

Stage 1: Canopy Trees

Classification

The least abundant canopy tree species, and a further four of unknown taxonomic identity, were excluded from analysis, leaving 94 species. Records from each set of five plots surrounding the 32 grid points were combined for this initial stage of classification because records of canopy-size trees rooted within single plots did not indicate the extent of the canopy cover over individual plots, which extended unevenly across the 50 m × 50 m area surrounding the grid point. Although the classification defined 15 species-groups, as used in subsequent stages of these results, the fusions were truncated at the 10-group level to simplify the constituents of groups involved at each stage, and their subsequent arrangement as an ecological sequence when superimposed on the results of ordination (Figure 4).

Indicator ('leading') species groups were determined by ISA at the simplified 6-group level (4 main groups plus 2 intermediate 'neutral' groups) (Table 2). The results are confined to the indicator ('leading') species (Table 2).

Figure 4. Classification into 10 groups of the combined canopy tree data from clusters of plots associated with 32 grid points (=160 plots), abstracted from the original 15-group fusions.

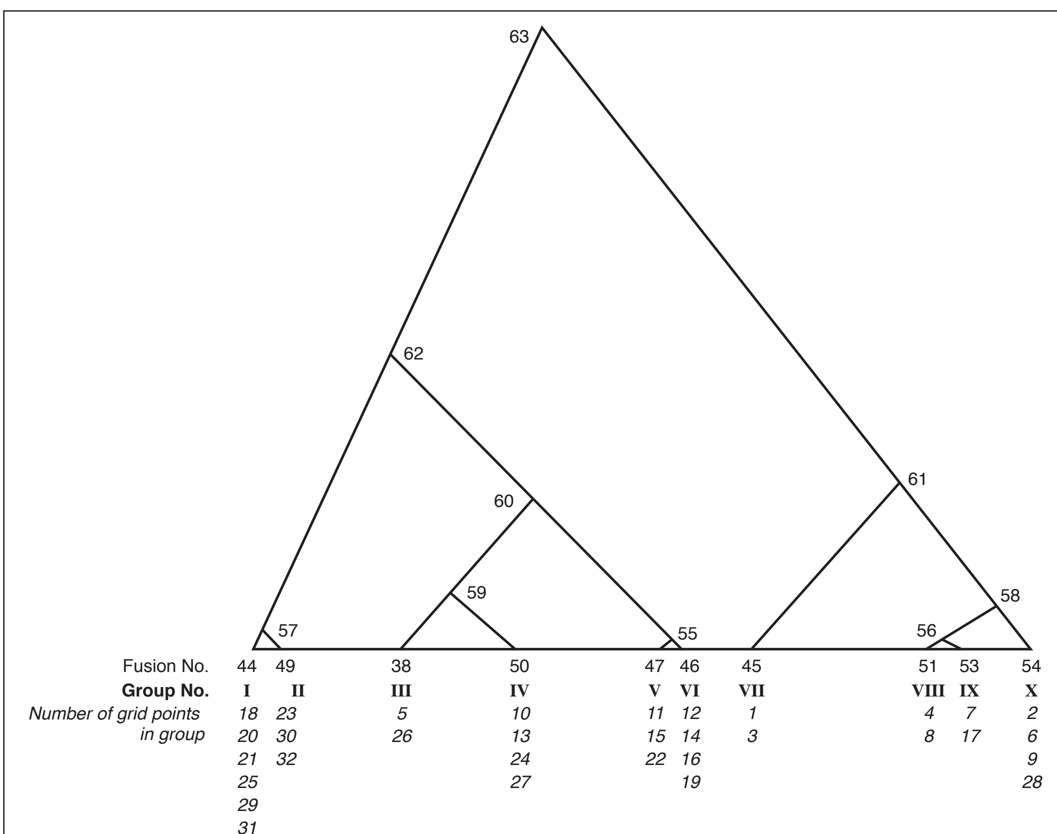


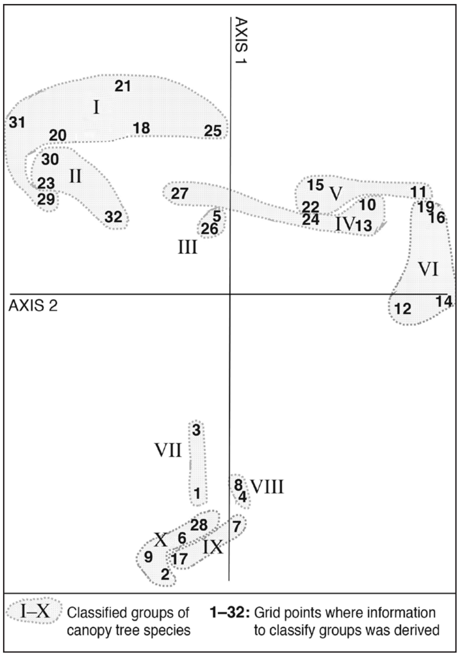
Table 2. Indicator ('leading') and associated canopy species within the Mt Nebo survey site (ISA; Hill et al., 1975).

Group	Leading and associated canopy species
Eucalypt forest:	
Group 1	*Eucalyptus tereticornis* associated with *Callistemon salignus* and *Allocasuarina torulosa*.
	Group 1 merges into Group 2 via intermediate species; *Alphitonia excelsa*, associated with *Eucalyptus acmenoides*, *E. siderophloia*, *Corymbia intermedia*, *E. microcorys*, *E. propinqua* and *Lophostemon confertus*.
Group 2	*Cryptocarya glaucescens*, *Synoum glandulosum*, *Polyscias elegans* and *Duboisia myoporoides*, with *Acacia disparrima*, *Eucalyptus saligna*, *Euroschinus falcatus*, *Guioa semiglauca* and *Trochocarpa laurina*.
Rainforest (vine forest) margins and later stages:	
Group 3	*Acacia maidenii*, *Eucalyptus propinqua*, *Streblus brunonianus* and 30 associated species of eucalypt forest and rainforest, including *Eucalypus acmenoides*, *E. siderophloia* and *E. microcorys*; most other members of the group were more characteristic of rainforest.
	Group 3 merges into Group 4 via 18 intermediate species mostly regarded as rainforest species, but with no *Eucalyptus* spp.; *Lophostemon confertus* and *Synoum glandulosum* (both found widely in the area and included in other groupings).
Group 4	*Cryptocarya macdonaldii*, *Alangium polyosmoides*, and 16 associated rainforest species including *Argyrodendron actinophyllum*, *Sloanea woollsii*, *Syzygium* spp., *Ficus watkinsiana* and remnant *Eucalyptus saligna*.

Ordination

A 15-stage ecological sequence of canopy species-groups was derived, then truncated at the 10-group level as for the classification, and the results were overlaid with the locations of the 10 previously classified groups (Figure 5).

Figure 5. Ordination of 10 canopy species groups from 32 × 5 clustered plots.



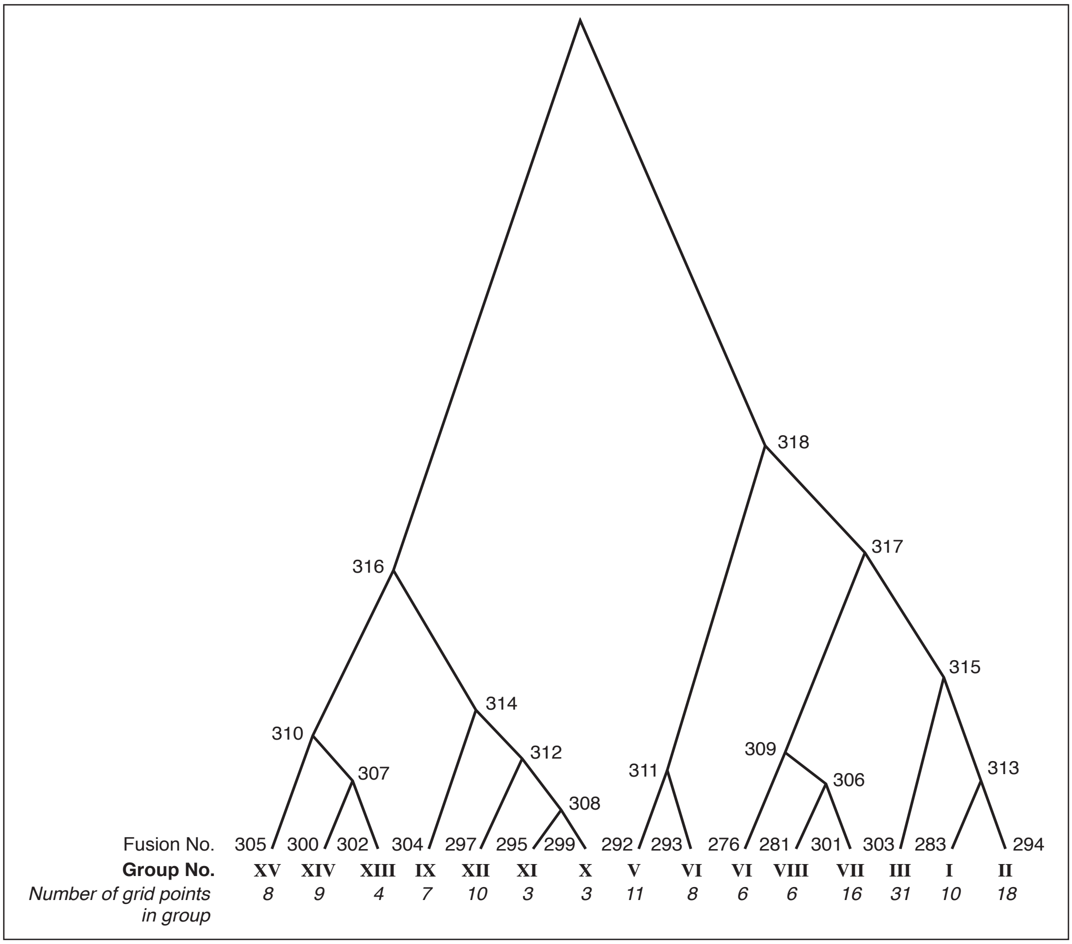
Stage 2: Understorey Trees

Classification

Records for 40 species of which ≤4 individuals were found were not included in further analyses (Figure 6). Data for the remaining 101 species were transformed using $\log_2(n+1)$ to reduce the influence of extreme values while preserving the relationship of intermediate values (Clifford & Stephenson, 1975). The analysis used CENPERC, followed by other procedures (Table 1).

In the final fusion, Groups I–VIII (from the eucalypt forest and ecotone: 116 plots) fused with the remaining groups IX–XV (vine forest stages; 44 plots) at a high level. The earlier of the ecotonal groups (IV–V, 19 plots) had chained to the remainder of groups I–VIII only at the second-highest level.

Figure 6. Classification of understorey tree groups from 160 plots showing fusions above the 15-group level.



As all 101 species from 160 plots were used in the classification, only those individual species that were found to be most closely related to particular site factors during succession are included in the results in Stage 5, below. Understorey species diversity increased steadily between Group I (19 species) and Groups IX–XI (78 species), and then decreased to 68 species in Groups XII–XV.

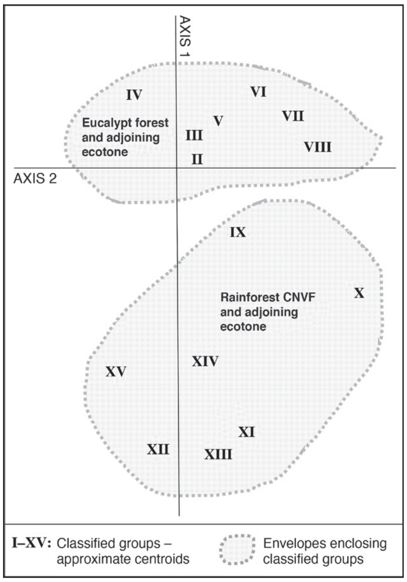
Ordination

Ordination of the understorey tree dataset followed, using GOWER with a centring adjustment (Table 1). The large number (160) of plots in the ordination resulted in overlapping groups of varying size which were difficult to superimpose on the ordination result for Axes 1 and 2. The approximate central points of each classified group could be linked in a continuous line surrounding the intersection of Axes 1 and 2 (Figure 7).

Stage 3: Classification and ordination of plots based on site factors

In the methods used (Table 1), MULCLAS with flexible sorting was “a suitable option for data in multiple states” (Williams, 1973). Groups I–II were clearly distinct from Groups III–XI, with Groups XII–XV forming a separate cluster. Groups IX–XII, the later stages of CNVF-type site characteristics, fused at the highest level. Again, the results were truncated at the 15-group level to facilitate comparison with the results of Stage 2 above and Stage 4 below (Figure 8).

Figure 7. Ordination of 15 classified groups from Figure 6 based on understorey tree data, showing sections of the ecological gradient as discrete groups.



Ordination

An ecological sequence of 15 groups was defined (Method: Table 1), using descriptors of site characteristics from 160 plots. Groups III–XII were very diverse. They had fused early in classification (Figure 9), but a clear ecological sequence was shown by the ordination, and they finally linked to the CNVF groups XIII–XV at a high level. Only 17 plots had evidence of recent fire or surface disturbance (due to maintenance activity), but evidence of past damage by fire alone was observed in canopy tree records for 122 plots and 109 understorey plots. No evidence of fire had been found in 18 plots, all in old-growth CNVF. Forestry maps showing fire locations between 1952 and 1968 for all wildfires had suggested that approximately 128 plots may have been affected.

Stage 4: Relation of Understorey Regeneration and Site Factors in an Ecological Sequence

Previous results in Stages 2 and 3 defined separate ecological sequences for both sets of data, which were then compared by GOWECOR, to show only the higher correlations with the first three axes, providing six sets of relationships. Details regarding the interpretation of the direction of sign in multivariate analyses that involve more than one process are contained in Hegarty (1980) and Dale et al. (1979–1980) (Table 3).

These results are reflected in an illustration of the location of plots where there were close relationships between understorey regeneration and site characteristics (Figure 10).

Group 4 of Figure 10 consisted of only one plot. It adjoined an intermittent stream which traversed Grid Point 22. This result was a possible aberration because the plot adjoined the Thylogale walking track in an area formerly subject to many fires. The leading species identified there – *Eupomatia laurina* (which forms suckers) and *Synoum glandulosum* – are very often closely associated in ecotonal areas throughout the region.

The strongest correlations between the separately classified and ordinated groups of understorey species and site characteristics, over 15 stages of succession, are summarised in a simplified overview of the results of previous analyses (as illustrated in Figures 7–9) in Figure 11.

The inclusion of site descriptors such as layered canopy, canopy height, and the presence of tufted grass and lantana, all of which are associated with potential successional changes of understorey species groups, has allowed the depiction of the ecological gradient between eucalypt forest and vine forest. In the prolonged absence of wildfires in the survey area, Figure 11 indicates the expected limitations to successional change of understorey eucalypt forest towards vine forest.

Stage 5: Species–Site Relationships Between Understorey and Canopy Species-groups, as Indicators of Factors Limiting Boundary Changes

The previous 15-group results of classification and ordination of the 160 plots had used data for trees in the canopy and understorey strata (Figures 5 and 7), The results were also truncated at the simpler 7-group level, at which the series of groups defined were of more approximately equal size in both sets of results. This facilitated direct comparison of the location of each set of plots within the parallel ecoclines (immediately below), which was then followed by comparison of the results with those obtained separately (Figure 10, Stage 4) using PCA to show site factor – understorey species relationships.

Almost half (75) of the plots were similarly placed in both sequences, and about a quarter (42) of the plots were placed only one stage (±) apart, indicating a slow change to canopy structure. The remaining 43 plots were placed at 2–3 stages (±) apart, defining the locations where the greater discontinuity between the composition of canopy and understorey tree strata reflected the higher chance of future expansion of CNVF across the survey site. There were no greater (±) levels of difference than those mentioned.

A difference of +2, in 31 plots, all located within Stages 1–3 of the 7-group comparison, indicated natural limits to the progress of successional change. These were plots with a mostly eucalypt canopy, predominantly seen in plots on drier, exposed sites where understorey change was sometimes impeded by routine clearing of paths and a weedy or grassy understorey. Of the 31 plots, 27 were located in parts of Groups 1–3 of Figure 10, and the remainder were in areas where the plots had been mechanically disturbed.

Differences of –2 or –3 predicted local expansion of existing CNVF patches. Of the eight plots with –2 difference in position on the separately defined ecoclines, seven were in Groups 3–5 of Figure 10, with an outlier in Group 6, being situated in a gully recovering from frequent fires. The remaining four plots (–3 stages of difference) included three which supported persistent lantana clumps, and one (Plot 84) was at a sharp CNVF-eucalypt interface, still recovering from fires.

Within the records of species present at each of the 7 parallel stages, it was also noted that understorey species diversity reached a maximum in ecotonal Group 4, as more CNVF species began to establish, while canopy diversity had increased steadily from 11 to 73 species between Groups 1 and 7 in the parallel set of results.

Figure 8. Classification of 160 plots into 15 groups based on understorey site characteristics.

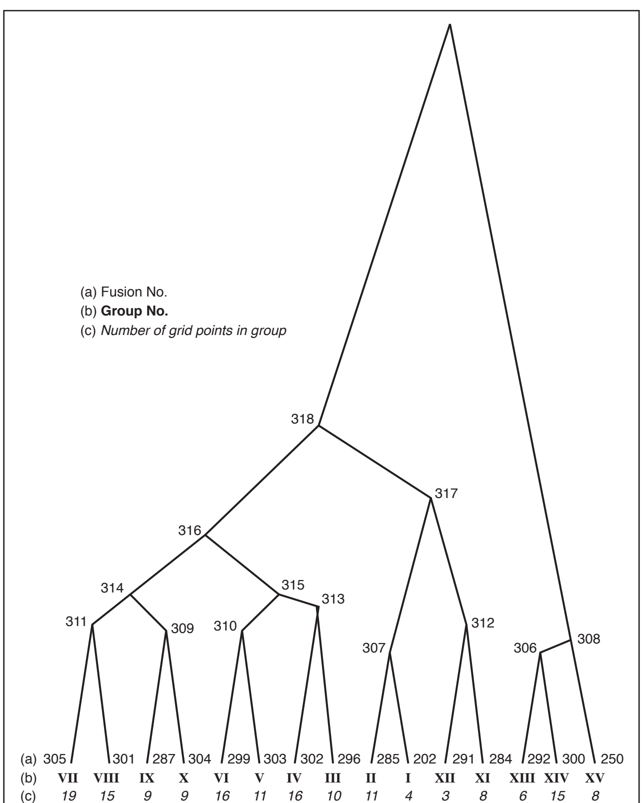


Figure 9. Ordination of classified groups of site characteristics at the 15-group level.

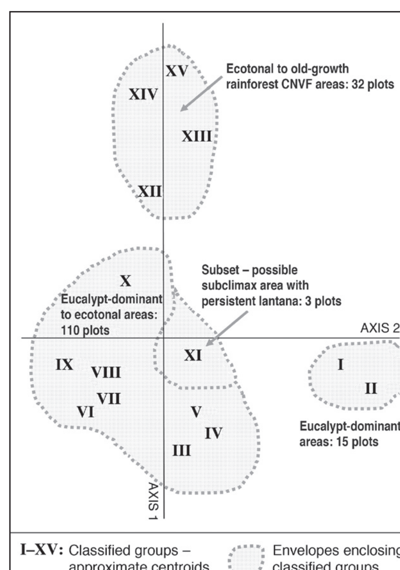


Table 3. Understorey leading species and site (habitat) relationships in the Mt Nebo survey site.

Type	Species recorded	Comments on species-habitat relationships
Type 1 (16 plots)	*Allocasuarina torulosa* *Eucalyptus siderophloia* *Eucalyptus propinqua*	On recently burned sites, grassy but stony, flat uplands; north-easterly convex slopes with eucalypt-dominated canopy. Regeneration of canopy trees at understorey level was very poor. *Allocasuarina torulosa* was marginally most successful. Recently burned sites had also been burned frequently. Low correlations for species indicate very low survival rate of understorey species. Canopy was floristically depleted; no effective regeneration.
Type 2 (6 plots)	*Lophostemon confertus* *Eucalyptus propinqua*	On areas last burned some years previously, with scrambling vines, grasses, deep eucalypt litter and locally dense *Lantana*. Canopy consisted of eucalypts and brush box as co-dominants. Only two species clearly regenerate strongly in this habitat. Other species of this group were less well related to site factors.
Type 3 (12 plots)	*Callistemon salignus* *Denhamia celastroides* *Acalypha nemorum* *Cupaniopsis parvifolia*	On concave, south-east-facing slopes, with soils derived from andesite or basic sedimentary rock, below a semi-open canopy. These species were associated with 14 other species of tree and shrub beneath a rather species-poor sclerophyll canopy, somewhat obscuring the separation of Types 3 and 4.
Type 4 (1 plot)	*Synoum glandulosum* *Eupomatia laurina*	On moister soils on straight mid- or south-west-facing slopes. Hornfels-derived soils, ferny in the understorey, with moderate build-up of eucalypt forest litter. Interpretation of Type 4 was complicated by its single record and its similarity to the next type of association (Type 5), which contained the same species.
Type 5 (15 plots)	*Cryptocarya glaucescens* *Cordyline* spp. *Polyscias elegans* *Guioa semiglauca* *Synoum glandulosum* *Eupomatia laurina* *Archontophoenix cunninghamiana*	On ferny, concave slopes with moist soils. Sclerophyllous upper canopy, with sub-canopy of vine forest species, on hornfels or basic sedimentary rock. All species of Types 4 and 5 regenerate near rainforest margins. Some may persist within rainforest during extended periods of stability (cf. Type 3 species that prefer less-shaded conditions).
Type 6 (30 plots)	*Cleistanthus cunninghamii* *Actephila lindleyi* *Cryptocarya macdonaldii* *Argyrodendron trifoliolatum* *A. actinophyllum* *Alangium polyosmoides*	Tall, layered, closed rainforest canopy, with rainforest litter, lawyer vines and ferns. Relatively high soil moisture, on stony outcrops of basic sedimentary rock. Species are all common to the more mature vine forest understorey. Rarer species were not highly correlated with local site factors (as in previous types). Type 6 combined species of several different associations within the most mature patches of rainforest, although the sample was not large enough to allow further definition of these.

Figure 10. Ecological gradient (six stages) showing the location of 78 plots where the results of ordination of understorey tree species groups and those of site factors were best correlated; 82 plots where the correlations were not as clear are not marked.

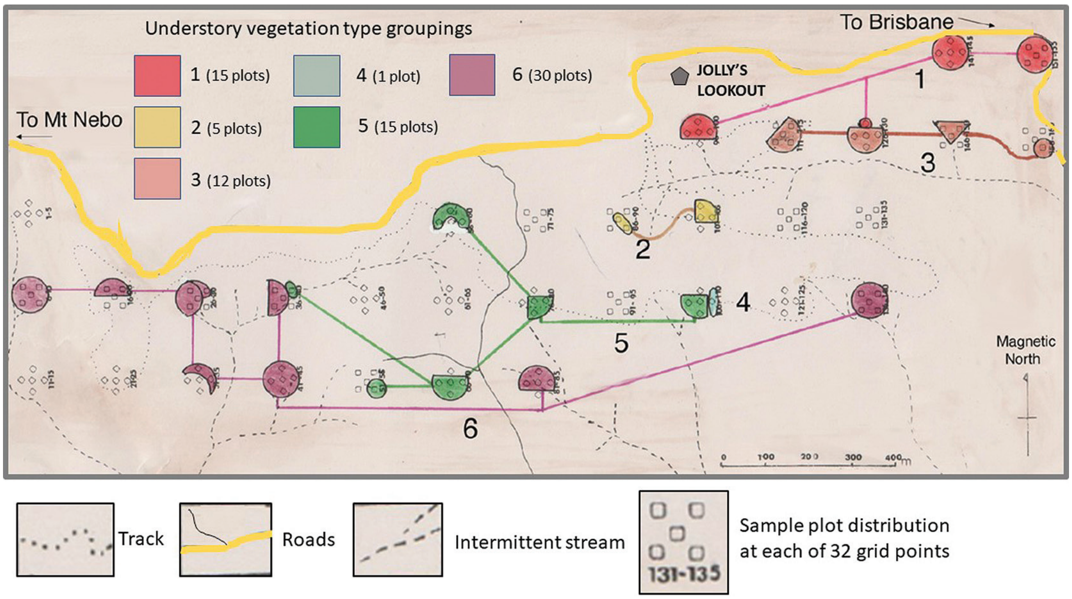
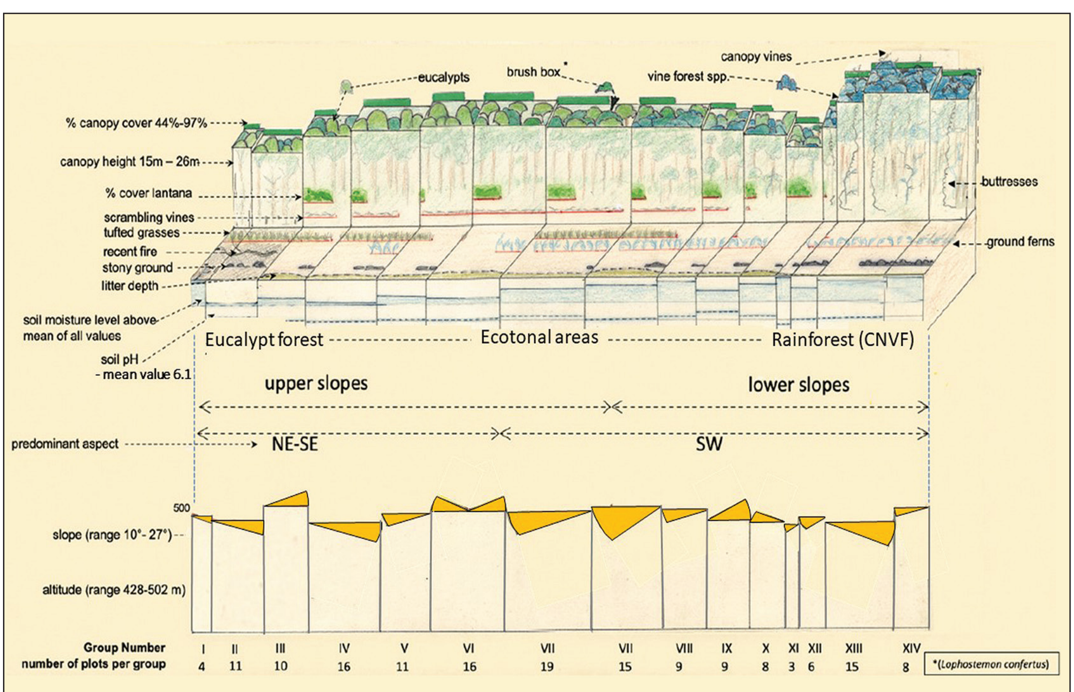


Figure 11. The ecological gradient of relationships between understorey species groups and associated site characteristics.



Discussion

It was opportune that adaptations of existing statistical methods for analysing patterns in vegetation and other data had recently been developed by CSIRO mathematicians in Brisbane. Most of the methods used herein were developed during the previous decade to define stages of CNVF regeneration on recently bulldozed bare basalt-derived krasnozem soils within old-growth rainforest at higher altitude at nearby Mt Glorious (Williams et al., 1969; Webb et al., 1972; Dale & Williams, 1978; Dale, 2000). However, some common canopy-level CNVF species recorded at Mt Glorious are not found in the Mt Nebo district.

Vegetation Patterns

In this study, separate classification and ordination of species composition in canopy and understorey forest strata revealed groups of species associated with eucalyptus forest, and the early stages of establishment of a transition zone, that were clearly separated from vegetation groups where vine forest species were predominant. Studies by Young (1982), Young & McDonald (1987) and many subsequent classifications (e.g. Neldner et al., 2019) have reported similar rainforest species associations in broader landscapes, but they vary between locations due to differences in elevation, rainfall, soils, recent damage and the period of absence of wildfires.

Changing relationships between the distribution of associated understorey species groups and site characteristics along the observed ecocline foreshadow future change to CNVF boundaries (Figures 10 and 11). The initial stages of the 15-part series of understorey species groups from 160 plots were associated with locations on recently burned, mostly convex, north-easterly-sloping ridgetops, on upper and minor slopes, and places often exposed to hot, windy conditions. These sites were situated on drier, locally rocky soils derived from andesite and hornfels, next to a contact zone affected by intrusions of granodiorite, as described by Gradwell (1955). The observation that "Jolly's Lookout soils are inadequate to support rainforest" (Webb, 1956) was essentially confirmed in the present study. Removal of many nutrients from the dry litter and grass understorey by maintenance burning or wildfires, runoff and wind can be expected. Even lantana did not thrive in such sites, although small local thickets had developed opportunistically and persisted nearby, and some scrambling extensions of branches were recorded in a quarter of all sites.

Later stages of the ecocline depicted in Figure 11 were mostly found on infrequently or never burned sites on sedimentary or adjacent altered rocks situated on lower and concave slopes, such as in shady gullies. In these habitats litter build-ups decomposed more rapidly to mulch beneath a developing closed rainforest canopy. Within-site retention of groundwater from rain and fog also leads to the rapid degradation of soft leaf litter, increases local recycling of soil nutrients, and results in the improvement of soil quality. Soil pH values (range 5.9–6.2) were somewhat lower in rainforest patches than earlier in the ecoclinal gradient. Tommerup (1934) had observed that the vine forest ecotone in the nearby Stanley River catchment "tends to build up its own friable soil as the sere develops, both by the addition of organic matter and by root action on the underlying rocks and clay, whereby soil factors are slowly improved by the advance of the forest itself".

In the absence of pre-1951 details of locations of fires, site factors including visible evidence of past fires combined at each stage to direct the shifting location of the interface (ecotone) between eucalypt and vine forest associations.

This study indicates how the several eucalypt tree species of the canopy stratum of ecotonal areas changed almost exclusively to *Eucalyptus saligna*, which increasingly co-existed with the more widespread, earlier-establishing *Lophostemon confertus* (brush box) as canopy species, throughout the ecotone (Figure 11; Table 2). It then became uncommon inside the small old-growth rainforest patches, where the upper stratum was characterised by emergent epiphytic figs, buttressed trees, and the few species of tall vines which are characteristic of such areas (Hegarty, 1988, 1989, 1991). Increasing shade during the development of a layered canopy discouraged regeneration of most weedy species, including lantana, and of small-seeded plants such as tufted grasses. Constant disturbance of the litter layer by foraging birds such as noisy pittas (*Pitta versicolor*) was another deterrent to their germination.

The site–species relationships described above extend and complement information regarding those defined by previous studies across broader landscapes with differing site characteristics, such as those by Laidlaw et al. (2011, 2015) and Hines et al. (2020). Factors such as altitude, soil derivation and climatic variation were more variable in such studies than within the compact, intensively sampled Mt Nebo survey area. The results which appear to be most similar, and comparable in some respects to those of this study, are those from the 500–600 m level of an altitudinal gradient of CNVF in the Lamington region of South East Queensland (Laidlaw et al., 2011). However, the species array and site factors such as soil derivation differ somewhat from those found at Mt Nebo.

Influence of Wildfires on CNVF Succession in the Survey Area

Crown fires, which are the most damaging form of wildfires, are not as frequent in subtropical forests as in temperate regions (Webb, 1968). However, lightning during thunderstorms, which mainly approach Mt Nebo from the south-west, can result in spot, or more extensive, fires.

A long-time Mt Nebo resident, Miss Mary Hall (pers. comm., 1979) recalled seeing open grassland in areas of the village, which had been replaced over 60 years by a mixed community including rainforest species and woody weeds, mostly exotic, with lantana the most widely found. Some evidence of old, unrecorded fires was observed deep in areas that now support mature ('climax') vine forest communities. Aboriginal use of fire in the area has not been well recorded.

Since control burning of forest compartments to the south began about 17 years after the extensive fire of 1951, no wildfires had entered the survey site. In ridgetop areas closest to the southern side of Mt Nebo Road, regeneration from a wildfire in 1968 (which burned about half the survey site) had been increasingly of rainforest species beneath an existing shady rainforest canopy, rather than new establishment of eucalypt species by seed from the adjoining steep north-facing slopes.

Long-term observations of subtropical rainforest regeneration elsewhere, such as those of Lahey (1960), recount the ability of rainforest pioneers to expand the boundaries of their parent community in the absence of fires. Webb (1977) cited work by Hopkins (1975), who summarised rainforest succession in the Lamington area. It was postulated that it would take 15–50 years to form an early secondary canopy, 100 years to an intermediate stage, and 200–300 years to form a very tall, mature canopy including species of *Argyrodendron*, *Syzygium* and *Cryptocarya*, classified in this report (Table 2) as typical of the small patches of old-growth vine forest at Mt Nebo. However, many prominent rainforest canopy species in the Lamington area, at the higher elevations, were not present at Mt Nebo or Mt Glorious.

The failure of regeneration of hoop pines (*Araucaria cunninghamii*) in the survey area, despite several relict specimens in unburned CNVF, and the nearby presence of mature specimens, tends to confirm a very long absence of fire in the oldest CNVF patches. Hoop pine is very sensitive to fire (DAF, 2017). The layout of the grid points in the survey had bypassed the location of a few surviving remnants of a former planting in a grid pattern near the Boombana section. Tommerup (1934) had noted that hoop pines regenerate poorly on the majority of non-rainforest soils, which are "devoid of decaying organic matter". Regarding *Eucalyptus saligna*, almost the only eucalypt which survives as a canopy emergent in Mt Nebo CNVF, a local resident (the late Mr Darcy Kelly) had worked to expand a local private rainforest. He observed (pers. comm., 1979) that it took two years to become established from seed that fell on bare soil, e.g. following a fire, and to rise through and persist above the shrubby lantana, which establishes more quickly on the same sites. In the present study, *E. saligna* was the only local eucalypt found to have established in the ecotone adjoining sclerophyll forest. *E. grandis* occupies a similar position in some nearby forest areas.

Lophostemon confertus (brush box) was another large tree found very widely across the survey area, persisting as an emergent in CNVF. Florence (1965) observed that brush box, being widely tolerant of variable site conditions, can persist in otherwise very adverse habitats, though its ultimate size is a function of habitat factors, including soil fertility. In a study of fire effects in a comparable area of the

Mackay highlands, containing rainforest and scrub (Hines et al., 2020), it was noted that since a catastrophic fire in 2018, there had been little recovery, and extensive lantana invasion. In combination with other factors, lantana was likely to have exacerbated the extent and severity of fire in those areas. It was also noted (loc. cit.) that fire promoted regrowth of *Alphitonia* and *Acacia* species, but not as quickly as lantana, as was also observed during the present study.

Discontinuities in the Progress of CNVF Regeneration

This section identifies locations where understorey species groups indicate future localised change as they replace the canopy directly above. The results complement and reinforce the connection between site factors and understorey composition, as shown in Figure 10.

The combined results of this study indicate a generally slow, orderly progress towards species change in the absence of fire, though this is still limited by site characteristics. Steady progress towards expansion of rainforest margins can be expected to take place over about half of the survey area in the absence of fire. The greatest discontinuities were found within sections of the ecotone which linked eucalypt forest and CNVF, particularly where there were lantana thickets, had been multiple episodes of damage by fires, or were in the vicinity of CNVF, where shade-intolerant species decline. Although the lantana thickets were evidently slowing or preventing regeneration of all competing species, the results do not indicate the full area of lantana presence, as its many thin, opportunistically rooting extensions are usually close to ground strata, and are below the minimum size for understorey recording. The uneven persistence of lantana, considered as a site factor which may inhibit succession in the ecotone bordering developing CNVF, is indicated in Figure 11.

Conclusions

In the absence of fire, site factors combine unequally during succession to inhibit or promote the expansion of rainforest remnant patches. Where rainforest patches are surrounded by flammable eucalypt forests, pattern analysis tools used and developed by CSIRO for prior studies in a nearby larger, old-growth rainforest (CNVF) allowed comparisons of patterns in three independent sets of data from each plot – canopy trees, understorey trees and shrubs, and site characteristics. This has allowed comparison of successional groups of species at canopy and understorey level, and the definition of relationships between understorey speciation and many site factors in an ecological sequence, which defines, and variably limits, the possibility of extension of patches of vine forest during the prolonged absence of fire.

The most relevant factors influencing the possibility of shifts in vine forest boundaries, apart from fire history, included the direction, and particularly the shape, of slopes (ranging from convex to concave), soil moisture and derivation, the height and openness of the canopy, and more recently the presence of opportunistic woody weeds. All of these factors, and others less clearly associated with the predicted change in position of the ecotone, varied in importance along a 15-stage ecological sequence (Figure 11).

It was difficult to compare the results of this intensive local survey with those of more recent studies that vary with regional location, local vegetation composition, the size of areas surveyed, the arrangements of sample plots and locations, the choice of categories of environmental data, and fire history. However, it is expected that the same successional processes and relationships to site factors defined here could be reliably observed in other similar subtropical Australian locations, depending on the combination of natural features of sites. However, the major determinants of the boundaries of subtropical rainforests will inevitably include the continuing absence of fire.

Exotic trees and shrubs were uncommon within the survey area at the time of the study. However, recently naturalised species were present nearby. Some of these, including *Ochna serrulata*, Kahili ginger (*Hedychium gardnerianum*) and privets (*Ligustrum* spp.), are more tolerant of shade during establishment than *Lantana camara*. In the longer term, predicted changes to temperature and rainfall, if not reversed, are also expected to affect the integrity of this and many similar areas of subtropical rainforest.

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Author Profile

Elwyn Hegarty is a retired botanist, now living in Armidale, New South Wales. Her return to university studies after a long break had been to undertake the study reported here. This was prompted by a desire to understand and use the complicated processes involved in promoting the expansion of patches of rainforest on a nearby family farm, so as to increase its protection from possible wildfires. Following this thesis in the Geography Department of The University of Queensland, she was a Ph.D. student of Emeritus Professor Specht and the late Emeritus Professor Clifford in the Botany Department. This subsequent study unexpectedly led to new opportunities that involved diversion from further ecological research into other equally demanding occupations. It has been a pleasure to remember the excitement of research and discovery during the compilation of this report.