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Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation.

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Abstract

Rainforests in eastern Australia have been extensively cleared over the past two centuries. In recent decades, there have been increasing efforts to reforest some of these cleared lands, using a variety of methods, to meet a range of economic and environmental objectives. However, the extent to which the various styles of reforestation restore structure, composition and ecological function to cleared land is not presently understood. In this study, we develop and apply a method for quantifying the structural attributes of reforestation sites in tropical and subtropical Australia. The types of reforestation studied were plantation monocultures, mixed species cabinet timber plots, diverse restoration plantings and unmanaged regrowth. Two age classes of reforestation were examined: ‘young’ (5 – 22 years), incorporating sites from all categories, and ‘old’ (30 – 70 years), in which only monoculture plantations and regrowth were represented. A total of 104 sites were surveyed including reference sites in intact rainforest and pasture. Intact rainforest was characterised by a suite of complex structural features including abundant special life forms (vines, epiphytes, hemi-epiphytes and strangler figs), a dense stand of trees in a range of size classes, a closed canopy, a shrubby understorey and a well-developed ground layer of leaf litter and woody debris. These features were lost on conversion to pasture. While all types of reforestation returned some elements of structural complexity to cleared land, young plantation monocultures, cabinet timber plots and young regrowth had a relatively simple structure. These sites typically had a low density of woody stems, a relatively open canopy and grassy ground cover, and lacked large trees, coarse woody debris and most special life forms. Restoration plantings and old regrowth were more complex, with a high density of woody stems, a relatively closed canopy and shrubby understorey. Old monoculture plantations in the tropics had acquired many of the structural attributes of intact forest, however this was not the case in the subtropics, where plantations were subject to more intensive management. The marked differences in structural complexity between sites suggest that the different types of reforestation practiced in eastern Australia are likely to vary considerably in their value as habitat for rainforest biota.

Keywords: Mixed-species plantation, Monoculture plantation, Restoration planting, Secondary forest, Structural complexity.

1. Introduction

Over the past few centuries, tropical and subtropical rainforests have been cleared on a vast scale (Richards, 1996; Whitmore, 1997). There is widespread concern that the remaining areas of rainforest may eventually lose much of their biodiversity due to factors associated with habitat loss and fragmentation (Terborgh, 1992; Adam, 1994; Turner, 1996; Laurance and Bierregaard, 1997; Brooks et al., 1999). There is also widespread belief that reforestation can reverse some of the environmental damage wrought by clearing, for example by increasing the amount of habitat available to forest biota, facilitating the dispersal of biota between remnant forests and buffering remnants from surrounding land uses (Hobbs, 1993; Lugo, 1997; Parrotta et al., 1997a; Lamb, 1998; Herbohn et al., 2000; Tucker, 2000; Bonham et al., 2002; Hartley, 2002).

A range of approaches to reforestation have been practiced in former rainforest landscapes. For example, large areas of the tropics and subtropics have been planted with monocultures of fast-growing timber trees (Lugo, 1997; Ashton et al., 2001; Lamb et al., 2001). Mixed-species plantations have also been established in some regions, typically on a small scale (Lamb et al., 1997; Harrison and Herbohn, 2001), while other projects have used diverse mixtures of trees and shrubs to restore rainforest to cleared land (Kooyman, 1991; Parrotta et al., 1997b). In addition, extensive areas of cleared land have been allowed to revert to secondary forest, in some cases with the active assistance of landholders, but more commonly through neglect (Janzen, 1988; Brown and Lugo, 1990). These approaches to reforestation vary widely in their costs, potential economic returns and presumably in their value to rainforest biota (Lugo, 1997; Lamb, 1998; Harrison et al., 2000). However, there has yet to be a comprehensive assessment of the capacity of different styles of reforestation to restore structure, biotic composition and ecological function to cleared rainforest lands.

In this paper, we examine the restoration of structural attributes to cleared rainforest lands in eastern Australia under several types of reforestation. The study is part of a broader research project quantifying the biodiversity values of these types of reforestation and associated changes in ecological processes (see, for example, Proctor et al., in press; Tucker et al., in press). We were interested in structural attributes, partly because the structural complexity of rainforest contributes to the availability of resources for wildlife and partly because these attributes are important and distinctive elements of rainforest in their own right (e.g., Terborgh and Weske, 1969; Kikkawa, 1982; Ganzhorn, 1989; Terborgh and Petren, 1991). We hypothesised that the structural complexity of reforested sites would increase with: (i) the diversity of planted species, due to differences in growth rate and architecture between species; and (ii) the age of reforestation, due to the recruitment of species and life forms to sites over time.

2. Methods

2.1 Study areas

The study was conducted in two regions of eastern Australia: the Atherton Tablelands, an upland plateau in tropical north-east Queensland (17^o – 17^o30’ S, 145^o30 – 145^o45 E); and the lowland subtropics of south-east Queensland and north-east New South Wales, between Gympie and Casino (26^o30’- 29^o S, 152^o30’ - 153^o30 E). In spite of latitudinal differences, both study areas experience a similar climate (due to the lower altitude of the subtropical sites), and rainforests in both areas exhibit structural and floristic affinities (Webb, 1968).

Rainforests in eastern Australia have been targetted for conversion to agriculture since European settlement (Webb 1956). In subtropical Australia, lowland rainforests were extensively cleared between 1860 and the early part of the 20^{th} century. Some 40 - 50000 ha of the remaining rainforests were converted to plantations of native conifers between 1930 and 1990 (Lamb et al., 2001). Today, an estimated 340000 ha of rainforests remain in south-east Queensland and north-east New South Wales, less than half the area present at the time of European settlement (Floyd, 1990; Hitchcock, 1991; McDonald et al., 1998). Large rainforest tracts in the region are restricted to mountain ranges and most are now managed for conservation.

Forest clearance in tropical Australia is more recent. Much of the Atherton Tablelands was cleared between 1900 and 1920, although sizeable tracts of rainforest continued to be converted to agriculture until the 1950s. A relatively small area of rainforest on the Tablelands (several hundred ha) was converted to timber plantations between about 1930 and 1970. About 750000 ha of rainforests remain in the Tablelands and elsewhere in the 'Wet Tropics' region of north-east Queensland ($15^{o}30' – 19^{o}$ S), of an estimated 965000 ha present at the time of European settlement (Winter et al., 1987; Collins, 1994). Most of the remaining rainforests in the region are now conserved in the Wet Tropics World Heritage Area, declared in 1988, although many small remnants are in private ownership.

2.2 Study design

The reforestation styles examined in this study are those most commonly practiced in former rainforest landscapes in eastern Australia: i.e., monoculture timber plantations, mixed species plantations, diverse restoration plantings and unmanaged regrowth (Lamb et al., 1997; Herbohn et al., 2000; Erskine, 2002). The restoration of structural attributes to these sites was assessed by comparison with reference sites established in pasture and intact rainforest.

We sought to obtain 5 – 10 replicate sites of each type within each region to capture variation in site history, management and landscape context. In selecting sites, we controlled for altitude and geology, factors known to influence the structure and composition of rainforest assemblages

(Webb, 1968; Kikkawa, 1982; Tracey, 1982). The tropical sites were located at mid-elevations (500 – 850 m a.s.l.) and, with few exceptions, on basaltic soils. Rainfall at these sites ranged from 1300 – 3000 mm per annum. The subtropical sites were located in the lowlands and foothills (10 – 400 m a.s.l.), on basaltic and metasedimentary soils, with rainfall between 1100 – 2000 mm per annum. The different site types were well interspersed except in the subtropics, where most monoculture plantations were located in the drier parts of the study area. Replicate sites in each treatment were generally a minimum of 1 – 10 km apart, but this degree of spatial separation was not possible for monoculture plantations, which were restricted to a few locations (most sites were from two State forests in the tropics, and from three State forests in the subtropics). Some sites in monoculture plantations were only a few hundred metres apart, although closely adjacent plantations differed in species or time of establishment.

Our study targetted the oldest and largest examples of reforestation available in each region, with potential study sites identified from a database of over 600 reforestation projects, forestry department maps and local knowledge. Nevertheless, most cabinet timber plots and restoration plantings were relatively young and small. We restricted the study to sites at least 5 years old, by which time canopy closure could reasonably be expected in the denser plantings. Most sites surveyed in the study were at least 4 ha, although a few sites as small as 2 ha were included to obtain sufficient replicates in some treatments. Two age classes of reforestation were examined: 'young' (5 – 22 years), incorporating monoculture, cabinet timber and restoration plantings, as well as regrowth in the tropics, and 'old' (30 – 70 years), in which only regrowth (subtropics only) and monoculture plantations were represented. The resulting design in the tropics included 5 pasture sites, 5 regrowth sites, 5 young monoculture plantations, 5 cabinet timber plantations, 10 restoration plantings, 10 old monoculture plantations and 10 forest sites (a total of 50 sites). In the subtropics, the site network was similar, except we surveyed 10 cabinet timber plantations and 9 restoration plantings (a total of 54 sites).

Monoculture timber plantations

Monoculture plantations were selected from two age classes: 'young' (5 – 15 years, median age 10 years), chosen to match the age of the cabinet timber plots and restoration plantings, and 'old' (38 – 70 years, median age 60 years), representing plantations at or near commercial maturity. Where possible, we chose plantations exhibiting a range of understorey development characteristic of each region, although the choice of sites was constrained by harvesting schedules and other management requirements of the State forest agencies.

In the tropics, sites were located in plantations of hoop pine *Araucaria cunninghamii* (n = 3), kauri pine *Agathis robusta* (n = 4), Queensland maple *Flindersia brayleyana* (n = 2) and red cedar *Toona ciliata* (n = 1). Plantations were located in Wongabel and Gadgarra State Forests, except for one young plantation on private land. In the subtropics, all sites were located in plantations of *Araucaria*, although one old plantation had also been underplanted with *Flindersia*. Plantations in south-east Queensland were located in State Forest near Imbil, except for one site on private property. Plantations in New South Wales were located in Toonumbah and Pikapene State Forests, except for one site on private property.

All the old plantations within State Forests had been established within existing rainforest, which was cleared and burnt prior to planting (Fisher, 1980; Keenan et al., 1997). Typically, narrow strips of rainforest 80 – 100 m wide were retained around plantations to act as fire breaks. Young plantations were second rotation (i.e., established after clearfall of an old plantation), except for two sites (one in each of the tropics and subtropics) established on cleared pasture. Plantations were established at densities of about 1000 stems per ha. In young plantations, weeds were controlled by slashing, poisoning and grazing. In the old plantations, competition from regrowth and weeds was controlled by hand for the first few years after establishment. Subsequent management of old plantations varied between regions and between species. Subtropical plantations (all *Araucaria*) were typically thinned on several occasions, to about 400 stems per ha, whereas tropical *Araucaria* plantations had experienced a single thinning. Plantations of *Flindersia*, *Agathis* and *Toona* in the tropics had not been thinned.

Mixed-species cabinet timber plantations

The cabinet timber plantations surveyed in the study were 5 - 10 years old (median age 7 years). In the tropics, plantations were established by the Community Rainforest Reforestation Program (CRRP) (Vize and Creighton, 2001). Plantations typically comprised a mix of Australian rainforest and *Eucalyptus* trees, not necessarily from local provenances, and some exotic cabinet timber trees. Trees were planted at about 1000 stems per ha on rows 5 m apart. Plantations were maintained for two years by the scheme, but subsequent maintenance was the responsibility of landowners and varied between sites. Trees in most plots were pruned and the grassy ground cover controlled by grazing, slashing and/ or herbicide along rows.

The cabinet timber plots surveyed in the subtropics were established by a range of individuals and organisations. Nevertheless, most resembled the CRRP plantations, with a small number of cabinet timber species planted at relatively low densities, and a grassy understorey controlled by grazing, slashing and/ or herbicide along rows. Subtropical rainforest trees, as well as some rainforest trees from north Queensland and some *Eucalyptus* trees, were included in these plots.

Restoration plantings

The restoration plantings surveyed in the study were 6 – 22 years old (median age 9 years). In the tropics, we surveyed restoration plantings established by the community group, Trees on the

Evelyn and Atherton Tablelands, in conjunction with the Centre for Tropical Restoration, and the Wet Tropics Tree Planting Scheme. Plantings used a diverse mix of trees and shrubs (generally 20 – 100 species, mostly local species and provenances), planted at high densities (c. 6000 stems per ha) (Lamb et al., 1997; Vize and Creighton, 2001; Tucker et al., in press). Weeds were controlled by hand or by poisoning, but trees were generally not thinned or pruned.

In the subtropics, we surveyed restoration plantings established by a range of individuals, landcare groups and government agencies. Consequently, the plantings tend to be variable in design and management, although the majority were high density plantings of a diverse mix of rainforest trees and shrubs, similar to plantings in north Queensland (Kooyman, 1991; Nagle, 1991; Lynch, 1998). Variants included the use of *Eucalyptus* and *Acacia* as well as rainforest species at three sites, and the use of an assisted regeneration technique – i.e., intensively weeding exotics, while relying on the natural recruitment of native species from a nearby remnant – to restore rainforest at one site (Woodford, 2000).

Old-field regrowth

In the subtropics, we surveyed secondary forest that had developed on abandoned farmland following the decline of the dairy industry in second half of the 20th century. This regrowth was dominated by woody weeds, notably camphor laurel (*Cinnamomum camphora*) and privet (*Ligustrum lucidum*) (Dunphy, 1991). In the tropics, where the decline of the dairy industry was more recent, patches of regrowth comprised dense clumps of vines and scramblers, including the exotic lantana (*Lantana camara*), growing amongst rank pasture with a few rainforest trees and shrubs. Regrowth sites were approximately 10 – 20 years old in the tropics and 30 – 40 years old in the subtropics.

Reference sites

Reference sites were chosen to match a similar range of environmental conditions as the reforested sites. In the tropics, forest reference sites were located in complex notophyll or mesophyll vine forest, the characteristic forest types on basalt on the Atherton Tablelands (Tracey, 1982). Three reference sites were located near the margin of extensive rainforest (contiguous with rainforest > 100000 ha in extent) and seven in remnants 40 – 400 ha in size. In the subtropics, seven forest reference sites were located in complex notophyll vine forest on moist sites on basalt, and three in Araucarian notophyll/ microphyll vine forest on drier sites on metasediments (Floyd, 1990). Three of the sites were located in large remnants, 150 – 250 ha in extent, which were contiguous with extensive forest (rainforest and eucalypt forest), and the remainder in remnants 4 – 50 ha in size, the largest available remnants within the target range of altitude and geology. All forest references sites may have been subjected to selective logging in the past century, but logging does not appear to have occurred on any site within the last two decades. Pasture sites were located on farms used to graze beef or dairy cattle.

2.3 Target variables

We surveyed a range of structural attributes at each site including canopy cover, the basal area and abundance of woody stems in a range of height and diameter categories, the frequency of special life forms, understorey and ground covers, and the quantity of leaf litter and woody debris (Table 1). Each attribute was assessed on five quadrats located at 20 m intervals along a 100 m x 30 m (0.3 ha) transect at each site, the values pooled or averaged to obtain a site measure. Canopy cover was estimated visually by one observer. The relative accuracy of canopy cover estimates was assessed by comparison with digital photographs of the canopy at 52 of the subtropical sites, using the method of Engelbrecht and Herz (2001); the results of both methods were highly correlated (r = 0.96, d.f. = 50, $P < 0.001$). Attributes were surveyed on a single visit to each site, except for leaf litter, which was surveyed twice. Tropical sites were surveyed in October/ November 2000 (with a second litter collection in April/ May 2001) and subtropical sites in February/ March 2001 (with a second litter collection in November 2001).

The data colected are presented in two ways: first, as comparisons of the mean values of attributes across site types, and second, as multivariate analyses of the relationships between sites based on all measured attributes (n = 32). Separate analyses were conducted for each region. Multivariate analyses were based on the Gower distance metric. Variables were range-standardised prior to analysis. Classification of sites used an unweighted pair-group mean average algorithm; ordination was by hybrid non-metric multidimensional scaling (Faith et al., 1987). Vectors of structural attributes which were significantly associated with patterns in the ordinations were displayed using a principal axis correlation (PCC) procedure. To simplify interpretation, some closely related attributes were combined for this procedure. These included measures of the abundance of (i) shrubs (all size classes combined), (ii) vines (all size classes combined), and (iii) trees (combined into three diameter classes: small (< 20 cm DBH); medium (20 – 50 cm DBH) and large (> 50 cm DBH)). Multivariate analyses were run on PATN (Belbin, 1993).

3. Results

3.1 Structural attributes of intact rainforest

Mature, intact rainforest in both the tropics and subtropics was characterised by a suite of complex structural features including abundant special life forms (vines, hemi-epiphytes, epiphytes and strangler figs), a closed canopy, a high density of woody stems in a range of height and diameter classes, a shrubby understorey with some ferns and herbs, and a well-developed layer of leaf litter and woody debris (Fig. 1). The majority of woody stems were small diameter trees. Large diameter trees (> 50 cm DBH), while an obvious feature of intact rainforests, comprised 2-5% of stems at most sites.

3.2 Structural attributes of reforested sites

Woody stems

The structure of the woody vegetation varied markedly between the different styles of reforestation (Fig. 1). Young monoculture plantations, cabinet timber plots and young regrowth sites invariably carried many fewer trees than intact forest, whereas stem density in most restoration plantings and old regrowth was similar to intact forest. In the tropics, old plantations had a similar density of woody stems to intact forest, whereas subtropical plantations carried fewer stems than intact forest, particularly in the smaller size classes.

In general, the basal area of woody stems increased with the density of planted stems and the age of reforestation. Cabinet timber plots and young plantations tended to have lower values for basal area than the more densely-planted restoration sites. Nevertheless, the basal area of all young reforested sites was relatively low, as these sites consisted mainly of small diameter trees. In contrast, medium and large diameter trees were well represented in old plantations and old regrowth, and the basal area of these sites was similar to intact forest.

The development of woody regrowth under old plantations varied between the tropics and the subtropics. Most tropical plantations had a well-developed midstorey of rainforest trees, with a density and size-class distribution similar to intact forest (on average, 2250 ± 340 stems < 20 m high per ha), whereas subtropical plantations tended to have a much sparser midstorey (1160 ± 360 stems < 20 m high per ha; $t = 2.15$, d.f. = 18, $P = 0.045$). However, the density of woody regrowth appeared to vary between the different species used in the tropical plantations, although small sample sizes preclude rigorous comparisons. For example, the density of woody regrowth under plantations of the broadleaf species *Flindersia* at Gadgarra, in the tropics, was about twice that under plantations of native conifers at nearby sites (3850 - 4130 stems < 20 m high per ha in two *Flindersia* plantations, compared with 2170 ± 170 stems < 20 m high per ha in three *Araucaria* and two *Agathis* plantations). Additionally, the density of woody regrowth also appeared to vary between localities in the tropics. For example, the density of woody regrowth under *Agathis* plantations was higher at Gadgarra than at the drier Wongabel site (1960 - 2780 stems < 20 m high per ha, compared with 890 - 920 stems < 20 m high per ha, respectively).

Special life forms

Most special life forms were much less common in reforested sites than intact forest (Fig. 1). Strangler figs were absent from almost all reforested sites, while epiphytes, hemi-epiphytes and robust vines were rare in reforested sites, except in old plantations in the tropics. However, thorny scramblers were often abundant in reforested sites, particularly young regrowth, young and old plantations and some of the restoration sites in the subtropics (notably, sites dominated by *Eucalyptus* and *Acacia* and the assisted regrowth site). Small diameter vines were also moderately common in regrowth, restoration sites and old plantations.

Canopy and understorey cover

Reforested sites generally did not attain the closed canopy typical of intact rainforest (average canopy cover in rainforest reference sites was 93% and 95% in the subtropics and tropics, respectively). Canopy cover was very low in young regrowth (< 10%, on average), low in young plantations (25 - 50%), intermediate in cabinet timber plots (50 – 60%), and relatively high in restoration plantings (75 - 80%), old regrowth (85%) and old plantations in the tropics (85%).

Cover levels were somewhat lower in old plantations in the subtropics (67%), where some plantations had been heavily thinned.

The understorey composition of reforested sites varied strongly with canopy cover (Figs. 1, 2). Sites with a relatively open canopy (young regrowth, young plantations and cabinet timber plots) typically had a grassy and herbaceous understorey. Restoration plantings, which tended to have a denser canopy cover than other young sites, had a much less grassy understorey, although herb cover was similar. Sites with a relatively closed canopy (old plantations in the tropics and old regrowth) generally had few grasses in their understorey. In contrast, grasses, herbs and ferns were a common component of the understorey of old plantations in the subtropics, where the canopy was more open.

Shrub cover in reforested sites also varied with the style and age of reforestation. Shrubs were uncommon in young plantations and cabinet timber plots, intermediate in abundance in restoration plantings and young regrowth, and common in old plantations and old regrowth.

Litter and woody debris

Subtropical sites generally accumulated a greater quantity of leaf litter than similar sites in the tropics, across most site types (Fig. 1). Allowing for this difference, the quantity of leaf litter tended to increase with the age and complexity of reforestation in both regions. Young reforested sites generally had less leaf litter than old plantations, old regrowth and intact forest. Young plantations in the subtropics had about half the litter of intact forest, while young regrowth and cabinet timber plots had 70-75% of the litter of intact forest, and restoration plantings had 85-90% of the litter of intact forest. Young plantations in the tropics had a similar amount of litter as intact forest, a consequence of recent pruning operations at several sites. Old plantations and old regrowth accumulated about as much litter as intact forest.

The volume of coarse woody debris varied primarily with the age of reforested sites. Young plantations, cabinet timber plots and restoration plantings generally had much less woody debris than old plantations and intact forest. Woody debris was largely absent from young regrowth, but debris comprised of small diameter stems and branches was very common in old regrowth. Many old monoculture plantations had high volumes of coarse woody debris, particularly in the subtropics, where a number of sites had been heavily thinned and the forest floor was covered with logging trash. Relictual logs persisting on the forest floor from plantation establishment also contributed to the high volumes of woody debris in some subtropical plantations.

3.3 Multivariate analyses of sites

The relative development of structural complexity in the different reforestation styles is neatly summarised in the ordination plots (Fig. 3). In both the tropics and subtropics, there was a gradient in structural complexity from pasture to intact forest, associated with increasing values of canopy cover, basal area, and the abundance of trees, shrubs, special life forms, leaf litter and woody debris. Most cabinet timber plots, young plantations and young regrowth had few of these complex structural attributes and tended to be clustered with pasture sites. Restoration plantings and old regrowth, having acquired some of the structural attributes typical of intact forest, were clustered in an intermediate position between pasture and forest sites. In the tropics, old plantations had many of the structural elements of intact forest and were clustered with forest sites. However, in the subtropics, old plantations had fewer complex structural features (although high values for certain attributes including ferns, scramblers and woody debris), and were clustered in an intermediate position between pasture and forest.

4. Discussion

All styles of reforestation surveyed in this study introduced elements of structural complexity to cleared land. Nevertheless, most reforested sites were considerably less complex than intact rainforest, lacking many of the special life forms typical of intact forest, as well as large trees and large-diameter woody debris. Of the sites examined, only old plantations in the tropics had developed a structure resembling intact forest, although some elements typical of intact forest, e.g., strangler figs, were missing from these sites.

4.1 Development of structural complexity on revegetated sites

The structural complexity of reforested sites increased with the diversity and density of planted stems. Most young monoculture plantations, cabinet timber plots and young regrowth sites were relatively simple in structure, with a low density of trees, a relatively open canopy and a grassy understorey. In contrast, restoration plantings were more complex, with a high density of woody stems, relatively dense canopy cover and an understorey of herbs and shrubs.

The relative structural complexity of restoration plantings is partly attributable to the diverse range of trees and shrubs used in these plantings, with consequent variation in growth rate and canopy architecture (Lamb 1998). Structural complexity may also be a consequence of the high density of stems used in these plantings (c. 6000 stems per ha), an approach which typically produces a closed canopy within a few years of establishment. Canopy closure suppresses grasses and other weeds, helps maintain a moist microclimate and facilitates the recruitment of mature-phase rainforest trees and shrubs (Kooyman, 1991; Parrotta, 1995; Harrington and Ewel, 1997; Parrotta et al., 1997b; Parrotta and Knowles, 1999). The few young monoculture and cabinet timber plantations which had developed a closed canopy in this study had acquired more structural complexity than other plantings of their type and were clustered with restoration plantings in the multivariate analyses.

Structural complexity also tended to increase with age in reforested sites. For example, young regrowth (in the tropics) had few trees, a relatively open canopy and an understorey of grass, herbs and thorny scramblers. In contrast, old regrowth (in the subtropics) had a relatively complex structure, with levels of canopy cover, basal area, stem density, ground cover and litter comparable to intact forest. While this comparison of young and old regrowth confounds age with region, the rapid recovery of some structural elements in secondary forests, e.g., stem density and basal area, has been reported elsewhere (Aide et al., 2000; Guariguata and Ostertag, 2001).

The development of structural complexity with age is most strikingly evident in monoculture plantations. While most young plantations were simply rows of pine trees with an understorey of grass and weeds, a number of old plantations in the tropics had developed a complex structure relatively similar to intact forest. In part, this is simply a consequence of the maturity of the timber trees, which comprised most of the larger diameter woody stems in plantations and contributed significantly to canopy cover, leaf litter and woody debris. However, many of the other elements of structural complexity (trees in the smaller size classes, shrubs, herbs, ferns, vines and other special life forms) were a consequence of the recruitment of rainforest plants to the plantations.

4.2 Implications for rainforest biota

Rainforests are renowned for their diverse wildlife. Part of the reason for this diversity, at a local scale, is that the complex structural attributes of rainforest provide a range of foraging and sheltering substrates for wildlife (Terborgh and Weske, 1969; Kikkawa, 1982; Ganzhorn, 1989).

For example, many rainforest animals rely on the resources provided by particular structural features (e.g., dead wood: Grove, 2002) or life forms (e.g., strangler figs: Terborgh, 1986). Consequently, the extent to which reforestation returns structural complexity to cleared land is likely to be an important determinant of the value of reforested sites to wildlife. On this basis, we expect that young monoculture plantations, cabinet timber plots and young regrowth will support a lower diversity and/ or abundance of rainforest wildlife than restoration plantings, old regrowth and old plantations.

Of course, structural complexity is only one of the factors which will influence the use of reforested sites by wildlife. For example, the floristic composition of reforested sites is also likely to be important, as many rainforest animals are narrow specialists on particular plant taxa (Stork, 1993; Ganzhorn et al., 1997) or rely on certain types of plants for food (e.g., fleshy-fruited trees and shrubs) (Terborgh, 1986; Green, 1993). Spatial factors such as the area of a reforested patch and its proximity to intact forest would also be expected to strongly influence the use of reforested sites by wildlife (as they do for remnants: e.g., Laurance and Bierregaard, 1997). However, without the development of structural complexity on reforested sites, neither the restoration of floristic diversity nor consideration of spatial factors may be sufficient to ensure that reforested patches provide suitable habitat for rainforest biota.

4.3 Implications for forest management

The observations of this study have implications for the design and management of reforestation projects in former rainforest landscapes. First, it is evident that structurally complex rainforests cannot be restored to cleared lands in a short time-frame (one or two decades). Of the forms of reforestation examined in this study, high-density plantings of a diverse suite of rainforest trees and shrubs develop the most ‘rainforest-like’ structure within the short term. Nevertheless, even this intensive form of reforestation lacks key structural attributes characteristic of intact rainforest. While some of these attributes, such as large woody debris, can be added to reforested sites (e.g., Tucker, 2000), the development of other attributes, such as large diameter trees and vines, is largely a function of time.

Given enough time, less intensive forms of reforestation may suffice to restore structurally complex rainforest to cleared lands. For example, unassisted regrowth may acquire many of the structural attributes of intact rainforest within 50 – 100 years (Aide et al., 2000; Guariguata and Ostertag, 2001; this study). However, secondary forests often have a very different floristic composition to intact rainforest (in our study, for example, old regrowth sites were dominated by one or two species of exotic trees), and hence might be expected to provide relatively poor habitat for specialist rainforest wildlife. Furthermore, in many former rainforest landscapes, the recovery of structural complexity in secondary forests is often suppressed by factors such as the intensity of degradation, repeated disturbance, isolation from intact forest and competition with grasses and weeds (Webb et al., 1972; Hopkins, 1990; Lamb, 1993; Tucker and Murphy, 1997; Holl et al., 2000; Guariguata and Ostertag, 2001).

Timber plantations may also develop a complex rainforest understorey over the longer term, leading to suggestions that plantations may offer a cost-effective means for ‘catalysing’ the restoration of rainforest on cleared and degraded lands (Parrotta, 1993; Keenan et al., 1997; Lugo, 1997; Parrotta et al., 1997a; Lamb, 1998; Ashton et al., 2001). However, plantations do not invariably recruit a rainforest understorey. In our study, for example, the amount of regrowth under plantations varied between regions, and apparently between localities and plantation species. If plantations are to be used to restore rainforest to degraded lands, the circumstances which favour the recruitment of rainforest species to plantations need to be clearly understood.

In our study, the development of a complex rainforest understorey was more pronounced in plantations which were: (i) on wetter sites; (ii) subject to less intensive management; and (iii) comprised of broadleaf rather than coniferous species. These results are consistent with previous studies of plantations in eastern Australia, which have attributed variation in the recruitment of rainforest trees and shrubs to plantations to climatic factors, silvicultural regimes, proximity to intact forest and the attributes of plantation species (Fisher, 1980; Keenan et al., 1997). Unfortunately, these factors are often confounded in the study area. For example, the relatively complex tropical plantations have experienced both a wetter climate and a less intensive management regime than the subtropical plantations. Landscape rainforest cover also differs between the two regions. Similarly, the recruitment of a rainforest understorey to *Flindersia* plantations may be a consequence of favourable attributes of this broadleaf species (e.g., canopy architecture, litter quality: Harrington and Ewel, 1997; Keenan et al., 1997), or simply reflect the benign neglect of these plantations after establishment. Further research is required to elucidate the relative importance of climate, management, species attributes and other factors on understorey development in rainforest plantations.

More generally, we argue that the recruitment of a complex understorey to rainforest plantations in eastern Australia has been favoured by circumstances which are unlikely to apply to the broad-scale restoration of degraded lands. First, these plantations were established by the clear-felling and burning of intact rainforest, a treatment which does not eliminate the soil seed-bank, nor destroy the rootstocks, of many rainforest plants (Stocker, 1981; Hopkins and Graham, 1984). Regrowth of rainforest plants from the seedbank and coppice was a conspicuous feature of these plantations after establishment (Fisher, 1980). In contrast, the rootstocks and seedbank of rainforest trees are usually destroyed by a lengthy pasture phase (Hopkins and Graham, 1984; Uhl et al., 1988; Mesquita et al., 2001).

Second, plantations were usually established adjacent to intact forest, or at least to strips of intact forest which were retained around plantations to reduce the risk of fire. Proximity to intact forest demonstrably increases the recruitment of rainforest plants under these plantations (Fisher, 1980; Keenan et al., 1997). However, seed dispersal is severely attenuated with even moderate levels of isolation from intact forest (Aide and Cavelier, 1994; Holl, 1999). Few seeds of rainforest plants are likely to be dispersed to plantations established in the midst of cleared land.

Third, the most structurally complex plantations surveyed in this study (those in the tropics) had received little thinning or other management after establishment. In contrast, plantations managed for commercial timber production are likely to be regularly thinned and vigorously managed to reduce competition from recruits, with concomitant effects on understorey development.

That is, plantations are unlikely to develop a complex rainforest understorey under the following circumstances: where plantations are established on land that has been used for agricultural production for an extended period, or on land isolated from intact forest, or where plantations are managed primarily for timber production. However, these are just the circumstances that would apply to the rehabilitation of large areas of cleared land with commercial timber plantations. Under such circumstances, the design and management of plantations may need to be modified to facilitate the development and maintenance of a rainforest understorey. Such modifications may include the planting of structurally complex rainforest on part of the plantation estate, reductions in the intensity of management in some areas, and carefully staged harvesting regimes (Lamb, 1998; Hartley, 2002). While these measures may affect timber production, their impact may be reduced by focussing restoration activities on areas which are of marginal commercial value or which have constraints on production, such as steep slopes and stream banks.

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Table 1. List of structural variables surveyed on 104 reforested and reference sites in former rainforest landscapes in eastern Australia.

Target variable and units	Methodology [a]	Quadrat radius
Basal area (m^2 per ha)	Angle-count method (Avery and Burkhart 1995).	-
Woody stems (per ha)	Count of stems in 4 diameter classes (2.5–10, 11–20, 21–50, >50 cm DBH) and 4 height classes (2–5, 6–10, 11–20, >20 m)	5 m
Canopy cover (%)	Visual estimate of projective cover of vegetation above 2 m above ground.	10 m
Shrub cover (index, 0 – 25)	Frequency of woody vegetation, including seedlings, with stem <2.5 cm DBH., in 5 x 0.5 m radius subplots per quadrat. Assessed in 3 height classes: (i) <1 m, (ii) 1–2 m, and (iii) >2 m.	10 m
Understorey cover (index, 0 – 25)	Frequency of (i) grass, (ii) herbs, and (iii) ferns in 5 x 0.5 m radius subplots per quadrat.	10 m
Strangler figs (index, 0 – 5)	Occurrence of mature strangler figs.	10 m
Epiphytes (index, 0 – 5)	Abundance of clumping epiphytes (e.g., basket ferns) on 4 point ordinal scale (1 <0.001 m^3; 2 = 0.001 - 1 m^3; 3 >1 m^3).	10 m
Hemi-epiphytes (index, 0 – 5)	Occurrence of hemi-epiphytic (stem-clasping) plants (Webb et al. 1976).	10 m
Vines (index ,0 – 5)	Occurrence of vines. Assessed in 3 stem diameter classes: (i) wiry (<1 cm), (ii) slender (1 – 5 cm), (iii) robust (>5 cm).	10 m
Scramblers (index, 0 – 5)	Abundance of scrambling, multi-stemmed thorny shrubs (e.g., *Lantana*), assessed on 4 point ordinal scale (1 = present, 2 = common, 3 = impenetrable).	10 m
Leaf litter (t per ha)	Dry weight of leaves and dead plant material including stems <2.5 cm diameter on ground, collected from two random 0.0625 m^2 subplots per quadrat. Average of wet and dry season samples after 3 days at 70^{o}C.	10 m
Woody debris (index, unbounded)	Contacts with dead wood >2.5 cm diameter on 10 m line per quadrat, assessed in 3 size classes: 2.5–10, 11–50, >50 cm diameter, converted to an index of volume by weighting counts by relative cross-sectional area of each size class.	10 m

[a] All variables were assessed on 5 quadrats per site.

Figure captions

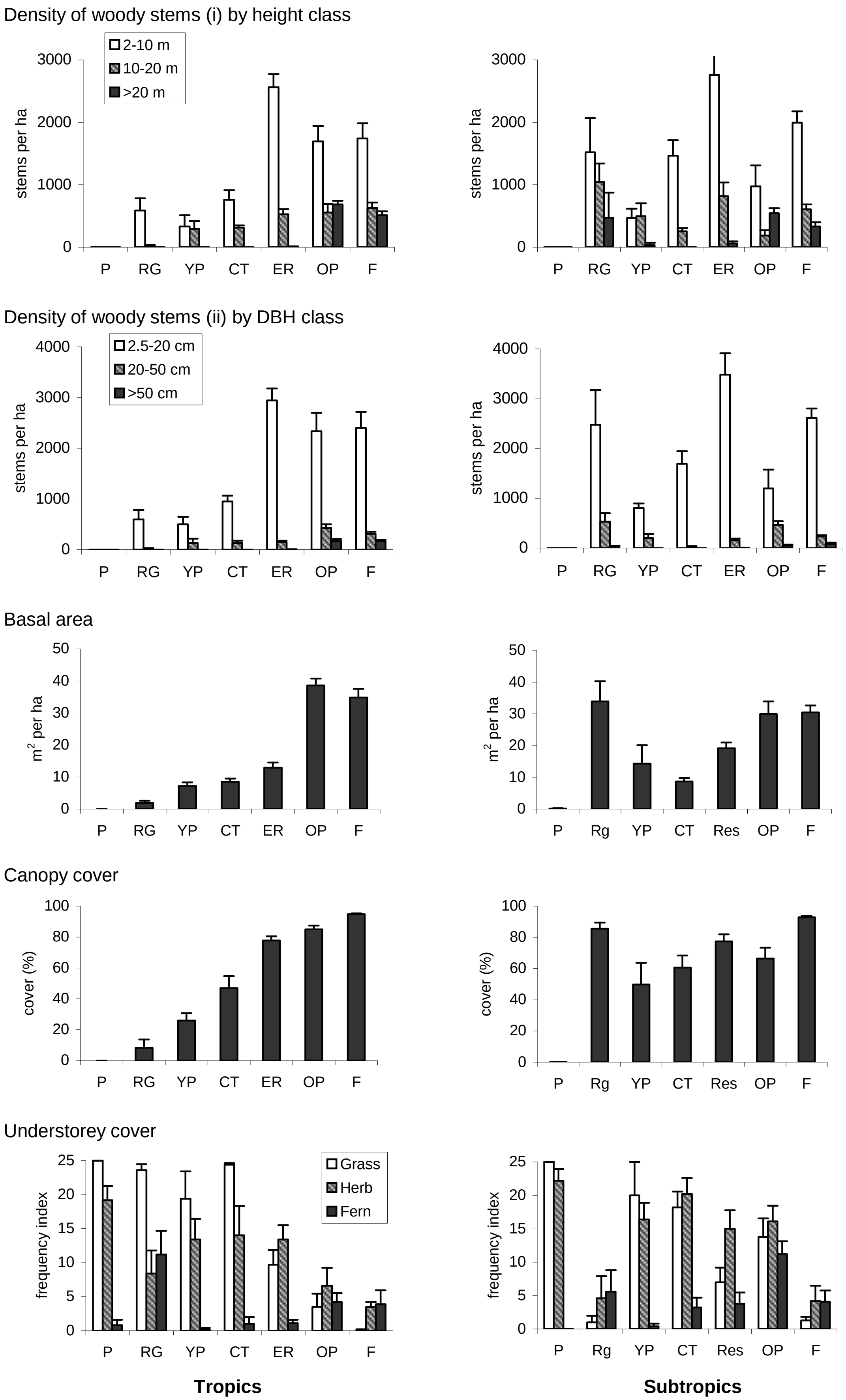
Fig. 1. Structural attributes (mean, SE) of reforested and reference sites in former rainforest landscapes in eastern Australia. P = pasture; RG = regrowth; YP = young plantations; CT = cabinet timber plots; ER = restoration plantings; OP = old plantations; F = intact rainforest.

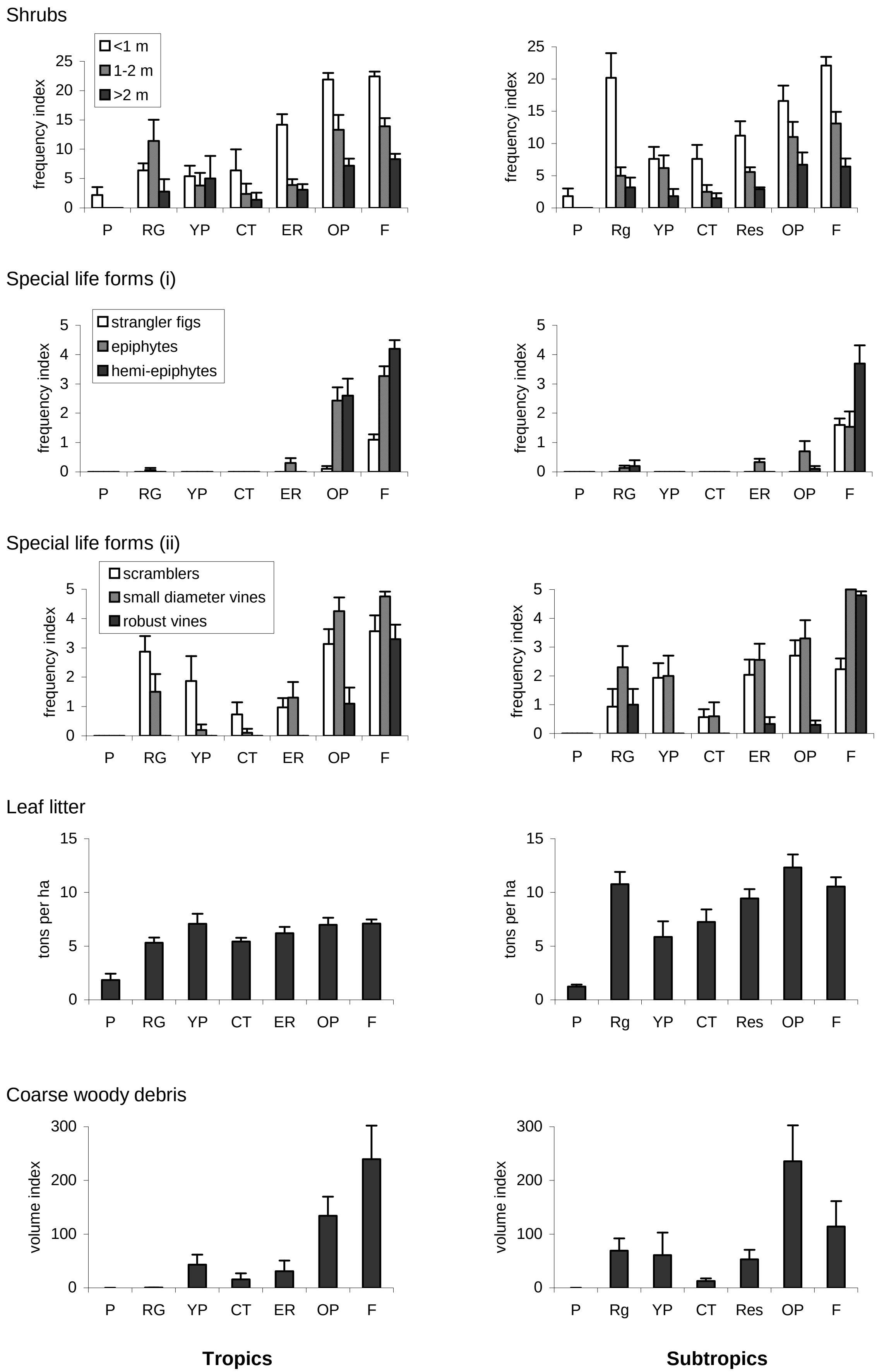
Fig. 2. Relationship between canopy cover and grass cover in reforested and reference sites in former rainforest landscapes in eastern Australia. Points show mean values (± SE) for each site type in the tropics and subtropics (n = 14).

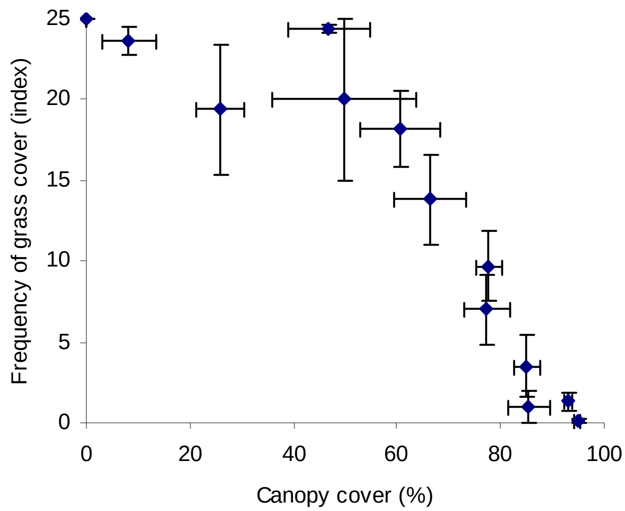
Fig. 3. Multivariate analysis of reforested and reference sites in former rainforest landscapes in eastern Australia: a) tropics (n = 50 sites); b) subtropics (n = 54 sites).

(i) Ordination of sites by 32 structural attributes (tropics: stress = 0.15; subtropics: stress = 0.19). The solid lines enclose sites grouped together by classification to the two-group level.

(ii) Principal axis correlation showing vectors of structural attributes significantly associated ($P < 0.05$) with patterns in each ordination. For example, sites to the left of the both ordinations are associated with increasing values for grass and herb cover, and decreasing values of canopy cover and other structural attributes.

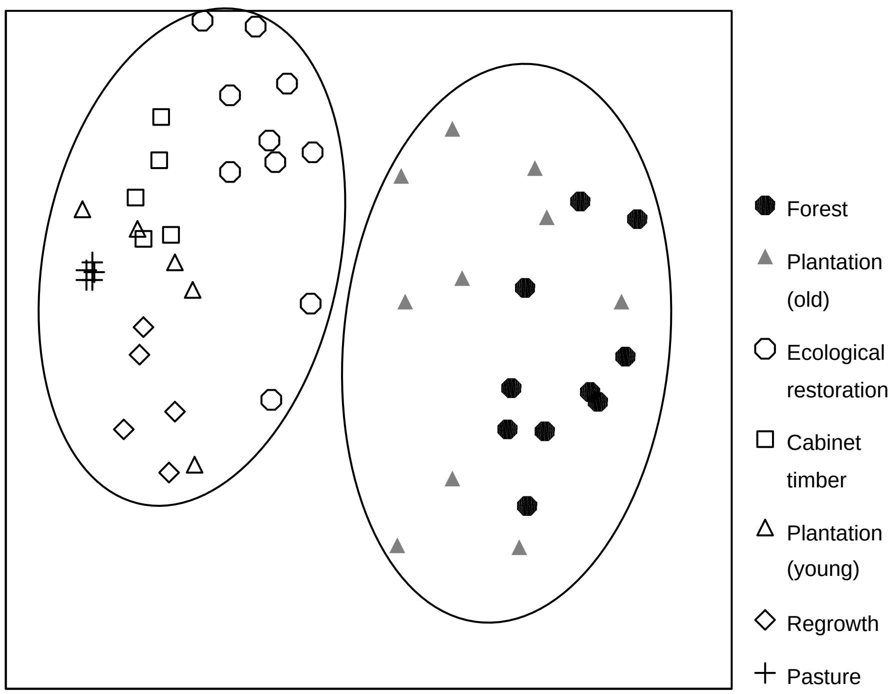

Density of woody stems (i) by height class
2-10 m
10-20 m
>20 m
stems per ha
P RG YP CT ER OP F
Density of woody stems (ii) by DBH class
2.5-20 cm
20-50 cm
>50 cm
stems per ha
P RG YP CT ER OP F
Basal area
m2 per ha
P RG YP CT ER OP F
P Rg YP CT Res OP F
Canopy cover
cover (%)
P RG YP CT ER OP F
P Rg YP CT Res OP F
Understorey cover
Grass
Herb
Fern
frequency index
P RG YP CT ER OP F
P Rg YP CT Res OP F
Tropics
Subtropics


Shrubs
□<1 m
■1-2 m
■>2 m
frequency index
P RG YP CT ER OP F
P Rg YP CT Res OP F
Special life forms (i)
□strangler figs
■epiphytes
■hemi-epiphytes
frequency index
P RG YP CT ER OP F
Special life forms (ii)
□scramblers
■small diameter vines
■robust vines
frequency index
P RG YP CT ER OP F
Leaf litter
tons per ha
P RG YP CT ER OP F
P Rg YP CT Res OP F
Coarse woody debris
volume index
P RG YP CT ER OP F
P Rg YP CT Res OP F
Tropics
Subtropics

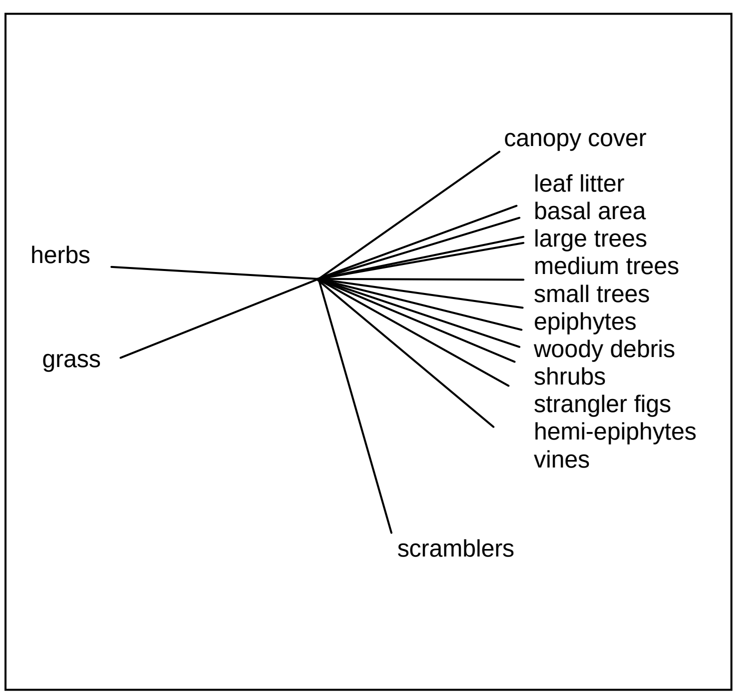

25
20
15
10
5
0
Frequency of grass cover (index)
0
20
40
60
80
100
Canopy cover (%)

a) tropics

(i)

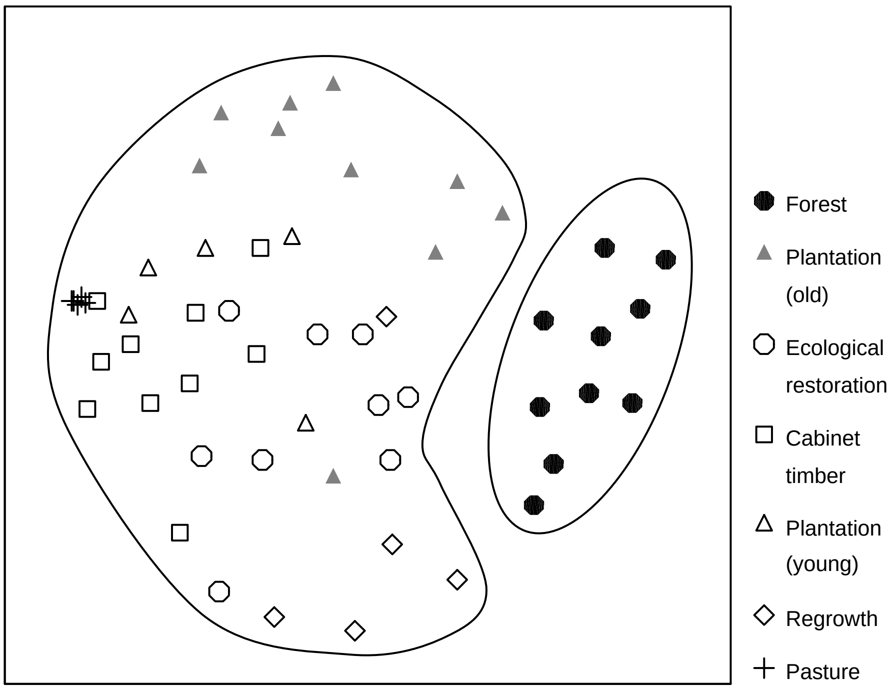


(ii)



b) subtropics

(i)



(ii)