Running head: Beetles and rainforest reforestation

Title: Responses of ground-active beetle assemblages to different styles of reforestation on cleared rainforest land

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Citation details: Grimbacher, P.S., Catterall, C.P., Kanowski, J. and Proctor, H.C. (2007). Responses of ground-active beetle assemblages to different styles of reforestation on cleared rainforest land. *Biodiversity and Conservation* **16**, 2167-2184.

Abstract

Despite increasing efforts to re-establish forest cover in landscapes that have been previously cleared, the relative ability of different styles of reforestation to contribute to conservation and support forest biota is poorly known, particularly for invertebrates. We investigated the use of different types of reforested habitat by ground-active rainforest beetle assemblages on land which had been previously cleared of rainforest, in the tropics and subtropics of eastern Australia. Between five and ten replicate sites within each of five reforestation styles were selected in each region: un-managed regrowth, young mono-species timber plantations, young mixed-species timber plantations, ecological restoration plantings, and old mono-species timber plantations, together with reference sites in pasture and in intact rainforest. Ground-active beetles were sampled using pitfall traps, and assemblages were compared among site-types. In both regions, beetle assemblages in all styles of reforestation were intermediate in species composition between pasture and rainforest. The similarity of beetle assemblages to intact rainforest increased with the age and structural complexity of reforested sites. The most rainforest-like beetle assemblages were from older reforestation sites (38-70 year plantations in tropics, and 30-40 year regrowth in subtropics) and in younger (6-22 years) but floristically and structurally diverse ecological restoration plantings in both regions. Assemblages in younger (5-20 year) sites of regrowth, mono-species timber plantations, and mixed-species timber plantations were more similar to pasture than rainforest. We conclude that achieving high canopy cover and sufficient structural complexity are important factors associated with the restoration of rainforest-like beetle assemblages to reforested sites.

Key words: Coleoptera, colonisation, forest management, habitat complexity, invertebrate, plantation, restoration, stand age, structure, succession

Introduction

The high diversity and unique biota of rainforests are widely recognised (Gaston 2000; Myers et al. 2000), yet moist forests, particularly those in the tropics, continue to be threatened by deforestation and other activities that lead to forest degradation (Wright 2005). Efforts to re-establish tree cover to land previously cleared of rainforest are relatively new (Janzen 1988; Parotta et al. 1997; Catterall et al. 2004) and thus their ability to sustain rainforest biota and potentially alleviate some of the deleterious effects of forest degradation are largely unknown and untested.

Rainforest reforestation styles can differ greatly. Different pathways for restoring forest cover in rainforest landscapes include un-managed regrowth, monocultures of plantation timber, and species-rich ecological restoration plantings (Lamb et al. 1997; Erskine 2002; Kanowski et al. 2003; Catterall et al. 2004). Ecological restoration plantings are diverse and dense plantings of rainforest trees aimed at recreating rainforest. In certain parts of the tropics, agroforestry (mixtures of agricultural crops and trees) plays an increasingly important role in creating forest cover (Lamb et al. 2005). Overall these diverse reforestation methods vary in plant species mix, spacing, stand age, management style and stand area (Lamb 1998; Catterall et al. 2004; Erskine et al. in press). In addition, other attributes such as surrounding landcover, spatial position, soil type, and climate are also likely to influence the colonisation by,

and longer-term persistence of, rainforest biota (Catterall et al. 2004; Kanowski et al. 2005a, b; Catterall et al. in press). Thus the potential for reforested sites to support rainforest-associated biota is likely to vary considerably.

It has frequently been proposed that the high faunal richness of rainforests is strongly influenced by their structural complexity and the diversity of resources which they provide (Kikkawa 1990; Jones and Crome 1990; Kanowski et al. 2003; Catterall et al. 2004), as well as their favourable microclimatic conditions (e.g., Hoffmann et al. 2003). It might therefore be expected that more structurally complex reforestation styles, and those which have greater plant diversity, should be more likely to support a rainforest-like fauna (Kanowski et al. 2005a; Catterall et al. in press).

Studies of invertebrate succession associated with reforestation of rainforest (Nakamura et al. 2003), and in other habitats (Brändle et al. 2000; Andersen et al. 2003; Davis et al. 2003; Magura et al. 2003), have suggested that habitat structure may, at least initially, be more important than either plant species composition or site age *per se* in providing suitable conditions for colonisation by forest-dependent invertebrates. There is conflicting evidence whether agroforestry and timber plantations (of native or exotic plants) can sustain invertebrate assemblages comparable to those found in native tropical forests (Estrada et al. 1998; Lawton et al. 1998; Watt et al. 2002; Stork et al. 2003; Schulze et al. 2004; Harvey et al. 2006; Lachat et al. 2006), and this variety of findings may be, at least in part, a consequence of variation in the nature of the plantations. For example, it has been suggested that only a small subset of the rainforest beetle fauna is able to persist in plantations which have simple physical structure and limited plant diversity (Chung et al. 2000; Davis et

al. 2001). However, it is difficult to separate the effects of plant diversity and structural complexity because these two are usually correlated (Kanowski et al. 2003).

In the present study, we compare attributes of beetle assemblages (abundance, species richness and species composition) among a range of different reforestation styles in tropical and subtropical eastern Australia, where clearing of rainforest has largely stopped and reforestation is increasing. Beetles make up a significant component of the invertebrate biota of rainforests (Stork 1988), and are involved in many ecological processes including nutrient cycling, pollination, herbivory, seed predation, and arthropod predation. Their taxonomic and ecological diversity are well known (Nielsen and Mound 2000; Lawrence et al. 2000), and studies of beetle assemblages have provided insights into the environmental changes associated with tropical forest degradation (Didham et al. 1998; Estrada et al. 1998; Lawton et al. 1998; Chung et al. 2000; Davis et al. 2001; Basset et al. 2001; Grove 2002; Grimbacher et al. 2006). We conducted comparisons of beetle assemblages across landscape-scale site networks that included reference sites in pasture and intact rainforest. Other taxa and vegetation attributes have also been studied at these sites (Proctor et al. 2003; Kanowski et al. 2003, 2005a, 2006; Catterall et al. 2004; Wardell-Johnson et al. 2005).

The present paper focuses on the following questions: (1) are there particular styles of reforestation that encourage or limit the development of rainforest-like assemblages of ground-active beetles? (2) Are conditions that support rainforest-associated beetle species more closely associated with physical structure or with plant species richness of sites?

Methods

Study area

The study was conducted in two site-networks located in tropical and subtropical eastern Australia. Tropical sites were located on the Atherton Tableland, an upland plateau (500-900 m in altitude) in northeast Queensland (17°-17°30'S, 145°30'-145°45'E), and the subtropical sites were located in the coastal lowlands (10-400 m) between Gympie and Casino in southeast Queensland and northeast New South Wales (26°30'-29°S, 152°30'-153°30'E). The two regions share similar climates and rainforest characteristics (Webb 1968). In the subtropics, large tracts of rainforests were cleared for agriculture and forestry from around 1860, whereas in the tropics, most rainforest clearing occurred after 1900 (for more details see Kanowski et al. 2003; Catterall et al. 2004). In both regions, rainforest clearing has largely ceased and a range of reforestation styles is now practised. These include monoculture timber plantations, mixed-species plantations, species-rich ecological restoration plantings, and unmanaged regrowth (Lamb et al. 1997; Erskine 2002; Kanowski et al. 2003; Catterall et al. 2004; Erskine et al. in press).

Study design

Within each region, sites representing the most common reforestation styles were compared with reference sites in pasture and intact rainforest. Pasture sites were used as reference sites because these represent the starting point of reforestation, and

because pasture is the typical matrix surrounding rainforest and reforestation sites.

Reforested patches were a minimum of 2 ha in size, with most over 4 ha.

There were 50 sites in the tropics and 54 in the subtropics. All types of reforestation were planted onto pasture or commenced as pasture, except old monoculture plantations, which were established by clearing rainforest and then replanting.

Specific site-types were as follows. 1) Pasture: actively grazed by cattle (5 sites per region). 2) Regrowth (5 sites per region): in the tropics, 10-20 years old and dominated by grass, shrubs and scramblers; in the subtropics, 30-40 years old and dominated by the woody invasive exotic plants camphor laurel *Cinnamomum camphora* and privet *Ligustrum lucidum*. 3) Young monoculture plantations (5 sites per region), 5-15 years old, of hoop pine *Araucaria cunninghamii*. 4) Young cabinet timber plantations (5 sites in tropics, 10 sites in subtropics), 5-10 years old, containing mixtures of 5-20 species of native rainforest cabinet timbers, *Eucalyptus* species and exotic timber trees (e.g., cedar *Cedrela odorata*, teak *Tectona grandis*). 5) Ecological restoration plantings (10 sites in tropics, 9 sites in subtropics), 6-22 years old, containing diverse (20-100 or more species) plantings of native rainforest species at much greater densities than either monoculture plantations or cabinet timber plots. 6) Old monoculture plantations (10 sites per region), 38-70 years old, mainly hoop pine but a few of kauri pine *Agathis robusta*, Queensland maple *Flindersia brayleyana*, and red cedar *Toona ciliata*. 7) Rainforest (10 sites per region), relatively undisturbed forest (no logging activity within the last 20 years).

Replicate sites in each treatment were generally a minimum of 1–10 km apart, and the different site-types were generally well interspersed. The main exception was

monoculture plantations (young and old), which were restricted to a few locations (most sites were from two locations in the tropics, and from three locations in the subtropics). Some monoculture plantations were only a few hundred metres apart, although closely adjacent plantations differed in species or age. In the subtropics, most monoculture plantations were also located in the drier parts of the study area.

Almost all sites were located on basalt-derived soils; however, in the subtropics many of the timber plantation sites were located on non-basalt soils which were also in drier parts of the landscape. Other factors thought to influence rainforest biota, such as altitude, were controlled as far as possible (see Catterall et al. 2004). Further details of the study design and of the styles of reforestation involved are reported in Kanowski et al. (2003) and Catterall et al. (2004).

Beetle sampling and identification

Within each site, a 100 m transect was established, along which ten pitfall traps were set at 10 m intervals. Each pitfall trap consisted of a plastic vial (5 cm diameter, 120 ml), sunk flush with the ground with the edges partially covered with leaves and sticks. Wire screens (~3cm diameter holes) were placed over traps to prevent interference from vertebrates. Raincovers (10 X 10 cm flat plastic sheets) were set 2 cm above each trap to reduce water and debris entering traps. Pitfall traps were operated for three days with a diluted solution of methanol and a few drops of detergent. In the tropics, sites were sampled in April-May 2001, whereas in the subtropics, sites were sampled during March 2001. The sampling of different site-

types within each region was temporally interspersed to control for variability due to weather.

All adult beetles were dry mounted, identified to family using keys from Lawrence et al. (2000), and then sorted to morphospecies. Species were also identified, where possible, with reference to specimens held at the Queensland Museum (QM, Brisbane), and all individuals were counted. Voucher specimens are held at the Australian School of Environmental Studies, Griffith University, Brisbane, Australia.

Data analysis

Species-specific counts of individuals were summed across all pitfall traps at each site. These data were used to compare total richness and abundance among site-types, and for analyses of assemblage composition, indicator taxa and habitat correlates with beetle variables. Sampling efficiency was assessed using EstimateS (Colwell 2000) by generating species accumulation curves for each site-type and across all site-types combined. Analyses were grouped into four sections:

(a) *Richness and abundance*. The abundance and species richness of beetles were compared among all site-types with one-way ANOVA's, and post-hoc LSD tests, using the GLM procedure in the SAS (Version 8) computer package (SAS Institute 1999). To best conform to assumptions of normality, abundances were ($\log_{10} + 1$) transformed while species richness data was square root-transformed.

(b) *Assemblage composition*. The similarity of beetle assemblages between sites was determined using the Bray-Curtis metric with ($\log_{10} + 1$) transformed data.

Multidimensional scaling ordination (MDS) was used to represent the patterns of similarity in beetle species composition among sites, using the computer package PRIMER (Plymouth Marine Laboratory 2002). Differences among site-types in species composition were statistically tested with analysis of similarity (ANOSIM, 9,999 permutations) using PRIMER.

(c) *Indicator taxa*. In order to assess the 'success' of the different types of reforestation in restoring rainforest beetle assemblages to cleared land, it was necessary to identify taxa associated with the reference conditions. For well-known fauna such as birds, the habitat affinity of species can usually be obtained from published natural history observations. However, for most invertebrates, including beetles, such data are rarely available and habitat affinity must be determined from surveys of reference conditions (see, Catterall et al. 2004; Kanowski et al. 2005a). In the present study, we used the indicator value (IndVal) procedure of Dufrêne and Legendre (1997) to identify beetle species that characterised the reference conditions of either pasture or rainforest, based on relative abundances and site fidelity in rainforest (10 sites) compared with pasture (5 sites). The statistical significances of the indicator species analyses were assessed using randomisation, and no other site-types were included in these analyses. This resulted in sets of species considered to be either significant "pasture indicators" or "rainforest indicators". The richnesses of pasture and rainforest indicator species were then compared among all site-types with one-way ANOVA's.

(d) *Correlates of beetle richness and composition.* Possible determinants of beetle species richness and composition were investigated by calculating the correlations between a range of beetle variables and eight measurements of each site's physical habitat structure and landscape context. Correlations were tested across young replanted sites only, within each region (N = 20 tropics, 24 subtropics). The beetle variables were: (i) total species richness; and assemblage similarity to (ii) rainforest, and (iii) pasture. A site's assemblage similarity to rainforest or pasture was calculated as its average Bray-Curtis similarity value with all rainforest or pasture sites.

Vegetation attributes assessed were: an index of the volume of woody debris, leaf litter dry weight, an index of grass cover, canopy cover, an index of vegetation structural complexity (Kanowski et al. 2005a), total plant species richness, native plant species richness, and the proportion of the land area supporting rainforest vegetation within 1000m of each site. These were obtained from the database of the QBVR (quantifying biodiversity values of reforestation) project, as described by Catterall et al. (2004). Measurements of plant species richness have been further described by Wardell-Johnson et al. (2005), while all other variables except proportion of rainforest in the landscape within 1000 m were considered in depth by Kanowski et al. (2003, 2005a).

Results

Richness and abundance of beetles

In the tropics, 150 beetle species (morphospecies) and 3165 individuals were captured, while in the subtropics, there were 222 beetle species and 4087 individuals.

Thirteen species occurred in both regions, (found at 1-37 sites in the tropics and 3-45 sites in the subtropics), including five Nitidulidae, five Scolytinae, two Staphylinidae and one Monotomidae. These species dominated captures and collectively accounted for 2332 individuals (73.7%) in the tropics and 2646 individuals (64.7%) in the subtropics. In contrast, a high proportion of species was rarely collected. A total of 68 species in the tropics and 91 in the subtropics were singletons (encountered as one individual), and 23 species (tropics) and 31 (subtropics) were doubletons. Species accumulation curves did not reach an asymptote, either for all site-types combined (Fig. 1a), or for each site-type separately (Fig. 1b).

In both the tropics and subtropics, overall beetle species richness tended to be lower in pasture than in all other site-types (Fig. 2a). In the tropics, the species richness of samples from rainforest sites did not differ significantly from that of all reforested site-types, whereas in the subtropics, species richness in rainforest was similar to that of ecological restoration, (older) regrowth and old plantation sites, and higher than in young monoculture and cabinet timber plantations. The number of singleton and doubleton species followed the same trend as the overall species richness (results not presented).

Overall abundances of beetles in the tropics were significantly lower in (young) regrowth and pasture than in other site-types (Fig. 2b). In the subtropics, beetles were most abundant in rainforest, old plantations, ecological restoration, and (older) regrowth, and least abundant in pasture, with young monoculture and cabinet timber plantations intermediate. Between regions, site-level abundance and richness of

beetles in both pasture and rainforest tended to be slightly greater in the subtropics (sampled in March) than in the tropics (sampled in April-May).

Assemblage composition

In ordinations of the beetle assemblages for both the tropics and the subtropics, pasture and rainforest sites were spaced well away from each other (Fig. 3a,b). In the tropics, the different types of reforestation were generally spread along a gradient between these reference points. However, in the subtropics, old and young monoculture plantations were located to one side of the ordination, rather than within such a gradient. Pairwise ANOSIM tests for both tropics and subtropics showed that most site-types were significantly different from each other in terms of beetle species composition (Table 1).

From the ordination and ANOSIM results combined, the following broad patterns are apparent. In the tropics, pasture and (young) regrowth sites resembled each other in beetle species composition (dissimilarity $R=0.17$, Table 1), and were both very different from rainforest (R values 0.93, 0.96). All reforested site-types differed significantly from rainforest. The younger reforested sites (young plantations, cabinet timber, ecological restoration) were generally similar to one another, and collectively intermediate between pasture and rainforest. Of these young planted site-types, ecological restoration was most similar to rainforest ($R=0.42$). Of all site-types, old plantations were most similar to rainforest ($R=0.27$). In the subtropics, pasture sites were very different from both rainforest and old plantations ($R=0.94$ for both), but rainforest and old plantations also differed moderately from each other ($R=0.54$). Regrowth (older) and ecological restoration were similar to each other ($R=0.06$), and

both were not strongly dissimilar to rainforest (pairwise R values of 0.19 and 0.20, respectively). Young and old monoculture plantations were more similar to each other (R=0.28) than to other site-types. In both the tropics and subtropics, young monoculture and cabinet timber plantations were more similar to pasture than were other replanted site-types

Indicator taxa

Indicator species analyses produced one ‘pasture indicator’ species in the tropics and three in the subtropics. The first of these, the broadly-distributed nitidulid *Carpophilus* sp.1 responded in a similar manner to reforestation in both regions, being particularly abundant in cabinet timber sites (Fig. 4a). The other pasture indicators (detailed responses not shown) were another nitidulid (*Carpophilus* sp. 2) and one anthicid (genus unknown). Indicator species analyses produced two ‘rainforest indicator’ species in the tropics (both Staphylinidae; *Quedius metallicus*, and genus unknown) and five in the subtropics (two Staphylinidae: *Quedius metallicus*, and *Hesperus haemorrhoidalis*, two Nitidulidae: *Stelidoba variabilis*, and *Epuraea occularis*, and one Curculionidae: Scolytinae, genus unknown). The staphylinid *Quedius metallicus* had similar abundance in rainforest in both regions (Fig. 4b), was consistently absent from pasture, and in all reforested site-types it showed intermediate abundance (with some between-region variation in the pattern). Across all indicator species, and all site-types, the mean richness of both pasture and rainforest indicators was intermediate between these two reference conditions in both regions (Fig. 4c,d). The patterns of rainforest indicator beetle richness differed between regions mainly with respect to regrowth, with the (older) subtropical

regrowth being more forest-like than the (younger) tropical regrowth. For pasture indicators, cabinet timber sites tended to have high values in both regions.

Correlates of beetle richness and composition

Correlations between beetle variables and site characteristics within the younger replanted sites showed that overall beetle species richness was significantly positively correlated with leaf litter dry weight in both regions, and also with canopy cover and structural complexity in the subtropics (Table 2). Rainforest beetle species composition (average Bray-Curtis similarity to rainforest sites) had strong positive correlations with canopy cover and plant species richness in both regions (Table 2). In the subtropics, both the rainforest beetle species composition and the species richness of rainforest indicators were significantly positively correlated with leaf litter dry weight and structural complexity, and negatively correlated with grass cover (Table 2). These correlations were weaker in the tropics.

There were also complex patterns of inter-correlation among the site characteristics themselves. In particular, structural complexity was highly correlated with plant species richness ($r=0.75$, 0.80 for all plants and native plants respectively in the tropics; 0.71 , 0.76 in the subtropics). Canopy cover was highly correlated with species richness of all plants ($r=0.83$) and native plants ($r=0.84$), and with structural complexity ($r=0.88$) in the tropics, with slightly lower values in the subtropics (0.58 , 0.57 , 0.75). Leaf litter dry weight had significant positive correlations with canopy cover, structural complexity, and plant richness of all plants and native plants in the subtropics ($r=0.58$, 0.75 , 0.42 , 0.47), whereas in the tropics these correlations were low ($r=0.00$, 0.00 , -0.15 , -0.12). This pattern was a consequence of relatively high

levels of leaf litter (and of woody debris) in most of the tropical young monoculture plantations (the result of recent pruning of the timber trees), in spite of their low canopy cover, structural complexity, and plant species richness.

Discussion

Sampling efficiency

Despite the reasonably large numbers of individuals captured, both the species accumulation curves and the high proportion of species found at only one site suggest that we did not sample all species present. However our aim was not to compile a species inventory at either the site or habitat scales, or to compare diversity between regions. Rather, we set out to discover the extent to which beetle assemblages differed among site-types within each region, using a standard sampling regime. Constraints on logistics, sample processing and taxonomic knowledge mean that ecological researchers must often choose between increasing either the number of spatial replicate sites or the intensity of sampling within a site (Catterall et al. 2004). In this study, a priority was to achieve adequate spatial replication. Ground-active beetles showed measurable assemblage-level responses to most differences in reforestation style and age, in spite of the incomplete site-level sampling of beetle species. Also, it seems unlikely that the results of species richness comparisons would change greatly if sampling were more comprehensive, since the species accumulation curves for different site-types showed no signs of crossing (Fig. 1).

However, the measurement of reforested sites' progress towards a rainforest-like beetle assemblage in the tropics may have been affected by the lower catch rate of beetles in the tropical rainforest reference sites, when compared with the subtropics (Fig. 2). This lower catch could have been a consequence of the difference in sampling months (tropics April-May, subtropics March) as well as a lower leaf litter dry weight (7.1 tons/ha in tropical rainforest reference sites compared with 10.5 in the subtropics; Kanowski et al. 2003). Whatever the cause, sparser sampling of beetles in the tropical forests resulted in a smaller number of indicator species. More intensive sampling at each site could reveal further rainforest indicators, by providing more reliable abundance measures for the common species.

Beetle responses to reforestation styles

Comparisons of total species richness among site-types for both regions showed that many forms of reforestation could rapidly (within 5-15 years) result in a similar species richness of ground-active beetles to that found in rainforest. This agrees with the suggestion by Dunn (2004) that species richness is the most easily restored component of biodiversity. In contrast, the restoration of richness is not the same as the restoration of composition, and all reforested sites differed in beetle species composition from rainforest reference sites, even several decades after reforestation.

In the tropics, old plantations had the most similar species composition to rainforest and this may be due to several factors. First, old plantations were established by conversion of rainforest, unlike all other sites, and most were located in close proximity to remnant forest. Second, old plantations would have had a longer time to

accumulate beetle species through dispersal and colonisation than other reforestation styles. Third, during this time, many rainforest plants had also established in old plantations (Wardell-Johnson et al. 2005), and plant species richness and composition may strongly influence invertebrate assemblage composition (Koricheva et al. 2000; Haddad et al. 2001; Novotný et al. 2002). Fourth, the old plantations also had a well-developed canopy and structural heterogeneity (Kanowski et al. 2003). A number of studies have linked the development of habitat structure to invertebrate successional patterns (Majer and Nichols 1998; Reay and Norton 1999; Brändle et al. 2000; Grove and Tucker 2000; Grove 2002; Andersen et al. 2003; Davis et al. 2003; Magura et al. 2003; Nakamura et al. 2003; Lachat et al. 2006).

In the subtropics, the beetle assemblages in old plantations were less similar to those in rainforest. A number of factors may drive this difference. Old plantation sites in the subtropics tended to be located on more nutrient-poor soils in drier parts of the landscape in comparison to those in the tropics (Kanowski et al. 2003; Catterall et al. 2004). Climate is an important determinant of beetle assemblage composition (Luff et al. 1989; Davis & Scholtz 2001; Verdú & Galante 2002; Blake et al. 2003; Grimbacher et al. 2006), and soil conditions could influence ground-dwelling beetles, through variation in either physical structure or resource availability (associated with differing soil fertility). Also, old plantations in the subtropics had been more heavily thinned by forest managers, and hence were structurally simpler, with less canopy cover (Kanowski et al. 2003).

Vegetation structure and plant species richness typically both increase with site age in reforested sites, making it difficult to separate the relative influence of habitat quality

and opportunity for colonisation (which increases over time) in determining assemblage composition. However, in this study we surveyed several site-types that differed in both plant species composition and structural attributes, but were of a similar age: young plantations, cabinet timber plots and ecological restoration plantings. Of these, ecological restoration had the greatest similarity to rainforest in beetle species composition, indicating that habitat qualities independent of age are important attributes influencing beetle assemblages. Ecological restoration sites also had the highest plant species richness (Wardell-Johnson et al. 2005) and the most rainforest-like structure (Kanowski et al. 2003).

The effects of plant species richness and habitat structure are difficult to separate, and the analysis of correlations between beetle attributes and habitat attributes in the younger replanted sites suggested that both play important roles. However, there are several reasons why structure may be particularly important to the development of ground-active beetle assemblages in the reforested sites. First, herbivorous beetles were rare in these assemblages (1.1% of individuals in the tropics, 3.6% subtropics), and these are the groups most likely to have high specificity for particular host plants (Koricheva et al. 2000; Haddad et al. 2001; Novotný et al. 2002). Second, factors such as shading by the tree canopy, and the amount of leaf litter (or grass, with which it is negatively correlated) are arguably likely to directly impact ground-level organisms, through the provision of resources and the regulation of microclimate. Third, in the subtropical regrowth sites (30-40 years old), beetle assemblages were relatively similar to those of rainforest. These sites also had a relatively forest-like structure (Kanowski et al. 2003), even though their floristic diversity was low, being dominated by a few exotic plant species (Wardell-Johnson et al. 2005). Other studies have

attributed differences in invertebrate assemblages between single and mixed-species stands to habitat structure and resource availability rather than plant species composition (Magura et al. 2000; Scheu et al. 2003; Finch 2005). Working at the same sites as the present study, Proctor et al. (2003) found no correlation between the taxon richness of litter-dwelling mites and plant species richness.

There are several key differences in habitat structure among young plantation, cabinet timber plots and ecological restoration plantings that are likely to have a substantial effect on beetle assemblage composition. Young plantations and cabinet timber plots had relatively low tree densities and tended to have an open canopy that allowed the growth of grasses and herbs, plant forms not usually found in intact rainforest (Kanowski et al. 2003). This is consistent with the greater number of pasture indicator species found in these types of reforestation.

Canopy cover (determined by the amount of foliage held on trees and tall shrubs) is arguably a particularly important habitat attribute. The canopy has a direct role in ameliorating microclimatic extremes (Davis et al. 2003) and in creating the humid conditions required by many rainforest-associated invertebrates (Hoffmann et al. 2003). Furthermore, the extent of canopy cover is also the cause of variation in other structural attributes such as the cover of grass (through shading) and leaf litter (through leaf fall) (Kanowski et al. 2003; Erskine et al. in press). These three aspects of structure were all correlated in this study with beetle variables. Variation in canopy cover within reforested sites is affected by the density, size, and species-specific architecture of trees and shrubs. A high density of planted trees, together with a high floristic diversity, leads to both higher canopy cover and greater structural

complexity in young plantations. Other studies have also found that canopy cover is an important determinant of beetle assemblage composition in reforested sites (Ings and Hartley 1999; Chung et al. 2000; Jukes et al. 2001; Davis et al. 2003; Magura et al. 2003; du Bus de Warnaffe and Lebrun 2004). In the present study, spatial context (amount of nearby rainforest) had a relatively modest influence on the beetle assemblages of reforested sites. Thomas et al. (2001) and Cunningham et al. (2005) also found that isolation had less effect than habitat quality on insect assemblages in remnant or reforested patches.

Implications for site management

This study has shown that a wide range of approaches to reforestation of previously cleared land will result in a more rainforest-like assemblage of ground-active beetles than is found on active pasture. However, it is likely that the potential of a particular method of reforestation to support rainforest beetles will be strongly influenced by both the speed at which it attains canopy closure, and whether a rainforest-like structure can be provided with the mix and density of tree species planted. Further work is needed to fully resolve the relative contributions of floristic attributes (such as plant species richness and composition) and vegetation structure.

Our results have a number of implications for the management of reforested areas. First, reforestation for timber production has limited ability to provide high quality habitat for most beetles that depend on rainforest, at least when plantations are young. Furthermore, management of plantations for timber production over short harvest cycles may be incompatible with the time needed for plantations to develop resources

and conditions that favour rainforest-dependent beetles (see also Grove 2002; Catterall et al. 2004). Second, regrowth that attains a rainforest-like vegetation structure can provide significant habitat for some rainforest species and thus needs to be given more consideration as a potential alternative to other, more expensive, reforestation styles. Third, at least in the first decade of growth, ecological restoration plantings have the greatest "rainforest beetle biodiversity" potential of all reforestation styles, and would therefore be the preferred method if rapid local restoration of biodiversity is the primary objective (and cost is not an obstacle). Incorporating patches of ecological restoration planting within larger-scale reforested areas, such as broadscale timber plantations or regrowth, could greatly increase their contribution to biodiversity (see also Kanowski et al. 2005b).

None of the reforestation styles and ages considered in this study had resulted in complete restoration of rainforest beetle assemblages. Achieving greater faunal similarity to rainforest is likely to depend on the development of resources provided by particular structural attributes such as large trees and large woody debris (Grove and Tucker 2000; Grove 2002). Therefore, even complex restoration plantings cannot provide a short- or medium-term substitute for the retention of intact rainforest. Finally, in our study neither the overall species richness nor the abundance of single indicator species could adequately quantify the response of beetle biodiversity to forest clearing and reforestation. Rather, we advocate the inclusion of species composition measurements in such assessments, since composition is more informative than species richness. Furthermore, analyses based on measures of species composition are less vulnerable to the effects of patchiness or low sampling intensity than analyses based on the abundance of individual indicator species.

Acknowledgements

We acknowledge the numerous landowners for access to sites. Terry Reis provided valuable assistance with field sampling and contributed to the project design together with Grant Wardell-Johnson and Nigel Tucker. Scott Piper conducted the IndVal and landscape forest cover analyses. Peter Hallcoop, Brett Taylor, Richard Pidgeon, and John Holt all assisted with beetle sorting. Geoff Monteith confirmed the species-level identifications. Funding was provided by the Rainforest Cooperative Research Centre. Peter Grimbacher was supported by a Griffith University Postgraduate Research Scholarship.

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Table 1. Pairwise ANOSIM tests comparing beetle species composition among all site-types. R values are presented along with levels of significance.

(a) Tropics (Global R=0.486, P<0.001, N=50)

	Pasture	Regrowth	Young plantation	Cabinet timber	Ecological restoration	Old plantation
Rainforest	0.934***	0.956***	0.566***	0.601**	0.415***	0.274***
Old plantation	0.907***	0.943***	0.352*	0.596**	0.338***	
Ecological restoration	0.740***	0.598***	0.129	0.260		
Cabinet timber	0.468**	0.052	-0.060			
Young plantation	0.572**	0.528**				
Regrowth	0.172					

(b) Subtropics (Global R=0.477, P<0.001, N=54)

	Pasture	Regrowth	Young plantation	Cabinet timber	Ecological restoration	Old plantation
Rainforest	0.943***	0.202	0.601***	0.454***	0.191*	0.542***
Old plantation	0.936***	0.495***	0.280*	0.578***	0.678***	
Ecological restoration	0.914***	0.060	0.695***	0.268**		
Cabinet timber	0.636***	0.074	0.516**			
Young plantation	0.628**	0.322**				
Regrowth	0.808**					

* p<0.05, **p<0.01, ***p<0.001

Table 2. Correlation coefficients between beetle attributes and site-structural and landscape variables for 20 young (5-22 years) replanted sites in the tropics and 24 in the subtropics. Species composition refers to the average Bray-Curtis similarity of each site to either rainforest or pasture sites. Sources of non-beetle variables are given in the methods.

Beetle variables	Woody debris index	Leaf litter (dry weight)	Grass cover index	Canopy cover (%)	Structural complexity	Species richness (all plants)	Species richness (native plants)	Proportion of rainforest within 1000m
Tropics, N=20 sites								
Overall species richness	-0.04	0.64**	-0.11	-0.09	-0.06	-0.13	-0.08	0.28
Pasture indicator species richness	-0.10	-0.07	0.42 ⁺	-0.47*	-0.33	-0.62**	-0.54*	0.14
Similarity to pasture species composition	-0.17	-0.11	0.19	0.11	0.19	-0.06	-0.01	-0.14
Rainforest indicator species richness	0.20	0.25	-0.14	-0.04	-0.07	0.25	0.27	0.28
Similarity to rainforest species composition	-0.01	0.02	-0.22	0.38 ⁺	0.14	0.46*	0.48*	0.20
Subtropics, N=24 sites								
Overall species richness	0.14	0.47*	-0.37 ⁺	0.52**	0.68***	0.27	0.39 ⁺	-0.05
Pasture indicator species richness	0.31	0.14	0.23	0.13	0.14	-0.05	-0.18	-0.18
Similarity to pasture species composition	0.09	-0.08	0.31	-0.02	-0.05	-0.18	-0.30	-0.34 ⁺
Rainforest indicator species richness	0.16	0.42*	-0.57**	0.81***	0.66***	0.35 ⁺	0.41*	-0.12
Similarity to rainforest species composition	0.15	0.51*	-0.71***	0.86***	0.81***	0.56**	0.62**	-0.19

⁺p<0.10, * p<0.05, **p<0.01, ***p<0.001

Figure 1. Cumulative species richness of beetles across (a) all site-types combined, (b) each site-type separately. F=forest, OP=old plantation, ER=ecological restoration, CT=cabinet timber, YP=young plantation, RG=regrowth, P=pasture. Curves are the mean of 50 iterations.

Figure 2. Mean (and SE) (a) species richness, (b) abundance, (per site) of beetles for each site-type. F=rainforest, OP=old plantation, ER=ecological restoration, CT=cabinet timber, YP=young plantation, RG=regrowth, P=pasture. P values (ANOVA) are with each graph. Means with the same letter do not differ significantly ($P>0.05$).

Figure 3. Multidimensional scaling ordinations of beetle species assemblage composition. In a) N=50, b) N=54.

Figure 4. Mean (and SE) of beetles that are either pasture (a, c) or rainforest (b, d) indicators (per site), for each site-type. F=rainforest, OP=old plantation, ER=ecological restoration, CT=cabinet timber, YP=young plantation, RG=regrowth, P=pasture. P values (ANOVA) are with each graph. Means with the same letter do not differ significantly ($P>0.05$).

(a) Tropics

(b) Subtropics

Tropics
(a) *Carpophilus sp.1*

Subtropics

(b) *Quedius metallicus*

(c) Mean richness of pasture indicator species

(d) Mean richness of rainforest indicator species