Conservation of tropical forest tree species in a native timber plantation landscape

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A R T I C L E   I N F O

Article history:
Received 30 July 2014
Received in revised form 26 November 2014
Accepted 27 November 2014

Keywords:
Native Eucalyptus plantation
Production landscape
Papua New Guinea
Dispersal mode
Successional stage

A B S T R A C T

Tropical terrestrial environments are becoming dominated by anthropogenic land-uses, making retention of biodiversity in production landscapes of critical conservation importance. Native timber plantations may represent a land-use capable of balancing production and conservation by potentially supporting understorey plant and tree species otherwise restricted to old-growth forests, with little impact on yield.

In this study we investigated the conservation value of native plantation forests in the lowlands of New Britain, Papua New Guinea. We compared the composition of tree species (> 10 cm DBH) of unlogged forest to those of different aged native Eucalyptus deglupta plantations and intervening (historically logged) secondary forests. We found a high capacity for biodiversity conservation within plantations, with 70% of forest tree species persisting in mature plantations (13-15 years old). However, compositional analyses revealed lower numbers of large individuals (> 10 cm DBH) in both late-successional and non-vertebrate-dispersed species in the plantations, indicating the difficulty of retaining mature old-growth forest trees in production land-uses. Secondary forest protected by conservation reserves was compositionally indistinct to unlogged forest. Our results demonstrate the potential for tropical native timber plantations to contribute to the retention of biodiversity. However, appropriate management is required to ensure the persistence of source populations of old-growth forest tree species. With careful planning a balance between production and conservation can be achieved in lowland tropical regions.

1. Introduction

Deforestation and degradation of tropical forests has precipitated a change in the global composition of rainforest cover, whereby around half of remaining forest cover consists of secondary regrowth and degraded old-growth forests (Chazdon et al., 2009b). Tropical lowland forests experience particularly high levels of deforestation because they occur on flat and fertile soil comparative to other tropical forests, making them valuable for agriculture, logging and agroforestry (Miettinen et al., 2011; Wright, 2010). The loss and degradation of these forests has broad ramifications as they contain over half of the world's terrestrial plant and animal species (Dirzo and Raven, 2003; Sodhi et al., 2010) and play a key role in maintaining global carbon and hydrological cycles (Bradshaw et al., 2007; Houghton, 2012).

Consequently, sustainable management of lowland forests has been identified as a conservation priority (Bradshaw et al., 2009; Gibson et al., 2012).

The needs of local human populations and global demand for forest products means that the full protection of tropical lowland forests is unlikely (Coad et al., 2009). For example, despite being recognised as one of the world’s most significant tropical wilderness areas (Myers et al., 2000), the Southeast Asia–Pacific region has one of the world’s highest rates of deforestation and degradation (Shearman et al., 2012). As such, conservation priorities are shifting from using reserve-based systems to ones targeting sustainable management of multi-purpose landscapes, which attempt to balance biodiversity conservation with production land-uses (Melo et al., 2013). For such approaches to be successful, conservation managers need to understand the capacity of different land-uses to support native biodiversity and the processes which allow persistence of species in heterogeneous production landscapes (Perfecto and Vandermeer, 2010).

Native timber plantations may represent a land-use capable of balancing production and conservation in tropical forests. This is...
because they can potentially support understorey plant and tree species otherwise restricted to remnant forest (Bremer and Farley, 2010), which in-turn would provide for rainforest-dependent fauna (Brockerhoff et al., 2010). By contrast, most agroforests and tree crops are comparatively limited in this capacity (Wilcove et al., 2012). However, the extent to which native timber plantations can support plant communities similar to natural forests is poorly understood, particularly outside of the Neotropics (Chazdon et al., 2009a; Stephens and Wagner, 2007). Given the expansion of timber plantations in the tropics (Carnus et al., 2006) and the push for greater representation of native plantations globally (Davis et al., 2012) it is crucial to gain a better understanding of the contribution that such plantations can make to biodiversity conservation.

Little is known regarding the functional breadth of forest plant species that can be supported in native plantations. For instance, do plantations support species from multiple forest successional stages, or only early successional species? How is this affected by plantation age? The ecological mechanisms underpinning the ability of species to colonise native plantations are also poorly understood. Examining how species’ traits affect their ability to become established in plantations may provide valuable understanding of the dynamics of understorey composition. For example, following clearing of tropical forests, recruitment of tree communities is largely dependent on ex situ colonisation (Chazdon et al., 2007; Holl, 1999) because most of the seed bank and “seedling bank” (pre-existing seeds stored in the soil and small seedlings) is destroyed during land clearing, particularly when fire is used (Mamede and de Araujo, 2008). Consequently, dispersal mode is likely to be a fundamental trait influencing assemblages post-clearing (Uhl et al., 1982).

Here, we investigate the role that native plantation forests can play in biodiversity conservation in the lowlands of New Britain Island, Papua New Guinea. We assess: (1) the relative ability of different aged Eucalyptus deglupta plantations and intervening secondary forest (historically logged) elements to support tree species of undisturbed forest; (2) the ability of plantations to support a diverse range of successional tree species (e.g. early-, mid-, and late- successional species); and (3) the effects of dispersal mode on establishment in plantations. We include the non-plantation landscape elements in our study in order to comprehensively assess the biodiversity value of this production landscape and to gain insight into processes influencing the persistence of species within plantations (Chazdon et al., 2009a; Gardner et al., 2009). Identifying the conservation value of native plantations will provide vital information for management and the design of production landscapes.

2. Methods

2.1. Study area

This study was conducted in the Open Bay Timber (OBT) operation area on the Gazelle Peninsula, East New Britain, Papua New Guinea (PNG) (Fig. 1). New Britain is an oceanic island, rich in endemism because of its evolutionary isolation (Mayr and Diamond, 2001). The main vegetation type is wet tropical rainforest. Mean annual rainfall is 2000–3500 mm, with a noticeably wetter period between December and March (McAlpine et al., 1983).

Open Bay Timber is one of only two plantation enterprises in PNG cultivating locally native tree species. The focal species, E. deglupta is an evergreen tree native to Indonesia, Timor-Leste, PNG and the Philippines (Ladiges et al., 2003). It is a fast-growing, light-demanding, wind- and water-dispersed species that forms dense, pure stands on river flats and after disturbances such as landslips and volcanic activity (Paijmans, 1973). We have classified it here as an early-successional species (Section 2.4). Before forestry activity at Open Bay (~1950) E. deglupta occurred naturally on river flats and disturbed patches of lowland forest and were eventually replaced by successional processes, culminating in mixed alluvium forest (Paijmans, 1976).

E. deglupta plantations were first established in the 1980’s through conversion of selectively-logged secondary forest, between an elevation of 10–350 m. Plantation management includes clear-fell harvesting, after which remnant logs are left to decompose and fire used to clear weeds prior to seedling planting. Trees are planted on average at a density of ~313 trees/ha (spacing 4 m × 8 m). Manual weed tending occurs from six months-to-three years, and vine cutting from three-to-six years. There is no tree thinning. Plantations are harvested at 15–17 years and Eucalyptus timber products are exported predominantly to Vietnam for use in construction and furniture (veneer).
At the time of the study, *E. deglupta* plantations covered ~14,900 ha (12,000 ha planted area, and ~2900 ha of roads, rivers and tributaries, and temporary employee housing). Plantations were organised into management blocks of broadly different ages (young, intermediate, mature) which were separated into evenly aged compartments. Within a given block, compartments could differ by up to four years in age. The plantation landscape included an area of ~36,400 ha of which ~13% was young plantations (2–6 years), ~4% was intermediate-aged plantations (7–12 years), and ~23% mature plantations (13–15 years), interspersed with secondary forest (selectively-logged before 1992) and unlogged forest (~33% and 26% of the plantation landscape respectively). The broader landscape constituting the timber company's production forest was comprised of a further ~18,000 ha of unlogged forest and ~24,000 ha of secondary forest (selectively-logged before 1998). Riparian buffer zones occur around the two main river systems and their permanent tributaries (the Sai and Toriu Rivers) and are embedded within the plantation matrix (we did not have access to high enough resolution data to estimate their coverage in the landscape). Riparian areas experienced some selective logging before the 1980s, and accessible edges are subject to ongoing timber extraction by locals. Within the operation's bounds a logged-over forest remnant of 382 ha was formally designated a watershed conservation area in 1991.

2.2. Study design

Areas within the OBT production landscape were classified into one of four modified elements reflecting the main forest types present (Fig. 2):

1. Young plantations, 2–6 years after planting (20 sites).
2. Mature plantations, 13–15 years after planting (2–4 years prior to harvest) (50 sites).
3. Secondary riparian, vegetation within riparian buffer zones ~20 years since selective logging (14 sites).
4. Secondary remnant (conservation area), vegetation within a 382 ha forest remnant 16–25 years since selective logging (10 sites).

These modified elements were compared to a fifth, reference element of unlogged lowland hill forest adjacent to the OBT operation area (unlogged forest; 48 sites). Intermediate-aged plantation blocks were not surveyed because those that were arrayed in large enough blocks for survey at the time of the study were confounded by their proximity to transient villages.

2.3. Site selection

We used logging maps to select survey areas that had the highest interior-to-edge ratios of even-aged vegetation to control for contextual noise and edge effects (riparian buffer areas were necessarily linear and thus characterised by edges). Survey areas occurred below 400 m a.s.l. to avoid variation associated with elevation gradients (Paijmans, 1976). Survey areas within a particular forest element were spread across the geographical extent of the element to ensure sampling across the variation in topography and soil type manifest in the region. Plantations, unlogged forest, and the secondary riparian element occurred in discrete patches across a large, accessible region within the landscape. This allowed us to sample elements which were interspersed amongst other land use types, thus reducing the potential influence of spatial clustering driving results. However, this was not the case for secondary remnant forest.

We established point transects in each landscape element, stratifying transect number according to the size of the element. Transects were between 1.2 and 2.4 km in length depending on logistical constraints and element area, and were separated by a
minimum distance of 1 km. Where access was only possible on foot, transects were manually cut into the forest. Survey sites were located 100 m perpendicular to such transects and sites were positioned ≥200 m apart from one another to enhance independence. Elsewhere, transects were located along logging roads and survey sites were positioned at least 150 m from the road to reduce edge effects.

2.4. Data collection

At each survey site (n = 142), a 30 m line from the central survey point was marked in each of the cardinal directions resulting in a square vegetation plot of 1800 m². All trees ≥10 cm diameter at breast height (DBH) were tallied, and species, size (DBH); mortality status, and phenology (fruit/flower present) were recorded. Plots of 1800 m² are unlikely to capture all tree species occurring within diverse tropical lowland forest. Consequently, we use these data to compare relative species density and composition between treatments (landscape elements) and discuss broader species richness trends in regard to rarefaction curves.

The successional stage and mode of dispersal for each species was defined using data collected from several sources (Table S.1). Successional classes generally followed the description in van Valkenburg and Keeney (1994): (1) early-successional species (light-demanding (heliophilic), early maturing species (<5 years) with a relatively short life-span (<80 years) (e.g. Macaranga species)); (2) mid-successional species (heliophilic species but with shade tolerant life-cycle stages (e.g. Octomeles sumatrana), and species which can tolerate shade in earlier developmental stages (e.g. Canarium indicum)); and (3) late successional species (species that are relatively slow-growing, and tolerant of shade through all developmental stages (e.g. Celtis rigescens)).

Trees often have more than one mode of seed dispersal (Nathan and Muller-Landau, 2000), so we classified species according to their primary mode of dispersal: animal dispersed (birds, bats and some arboreal and ground mammals); or non-vertebrate dispersed (wind, water or gravity) (Paijmans, 1976). Where information regarding dispersal mode was not available at species-level, dispersal mode was inferred from genus-level knowledge (Table S.1).

2.5. Data analysis

2.5.1. Tree species richness, density and composition

All data analysis was performed in the statistical computing program R (R Core Team, 2013). To observe the accumulation of species richness within each landscape element we conducted rarefaction analyses using the function ‘specaccum’ in R package ‘vegan’ (Oksanen et al., 2013). Accumulation curves were calculated based on both (i) survey sites (using the ‘exact’ method) and (ii) individuals sampled (using the ‘rarefaction’ method).

We modelled species density (sensu Gotelli and Colwell, 2001) for each element using generalised linear mixed models (GLMMs) in the ‘lme4’ package (Bates et al., 2013). Our response variable was the total number of species recorded at each site, and was modelled as a Poisson distribution. Each transect was specified as a random effect to account for non-independent error structures associated with potential clustering of study sites (Zuur et al., 2011), and the landscape element that sites were located within (i.e. young plantation, mature plantation, etc.) was specified as a fixed effect. Landscape elements were considered an important influence on species richness where 95% confidence intervals (CI) for parameter estimates did not overlap zero when compared to the reference element (unlogged forest).

We used Poisson GLMMs to compare the density of species grouped according to (i) successional stage and (ii) dispersal mode per site. Response variables represented the total number of species belonging to each category that occurred at each site. Each transect was assigned as a random effect, and the landscape element as a fixed effect. Pairwise comparisons between elements (with unlogged forest as reference category, and secondary remnant as reference category) were corrected for family-wise error using a Bonferroni correction to adjust significance levels (Quinn and Keough, 2002). All mixed models were tested for overdispersion, and for autocorrelation using Moran’s I statistic (Bivand, 2014).

To assess differences in tree species composition across elements, we applied a novel model-fitting method of multivariate generalised linear models (GLMs) to our tree species basal area and count data (Wang et al., 2012). This method directly models the underlying mean–variance relationship in the abundance data rather than using distance based measures of community dissimilarity/similarity (Warton et al., 2012). As such, the approach is useful for assessing treatment effects on community composition because it better detects the influence of treatments on rare species (Warton et al., 2012). This was important for our study because the lowland rainforests are hyper diverse with patchy dominance by any one species (Mueller-Dombois and Fosberg, 1998; Paijmans, 1976).

Models were fitted using the ‘manyGLM’ function in package ‘mvabund’ in R (Wang et al., 2012, 2013). We built models based on the number of individuals of species at sites (counts), specifying a negative binomial error distribution. Landscape element was included as a single categorical predictor. To determine whether landscape elements had a significant effect on tree community assemblage, the data were resampled using parametric bootstrapping, with likelihood ratio employed as the test statistic (Wang et al., 2012). To compare pairwise significance among landscape elements we ran the resampling step twice, first with unlogged forest as the reference factor and second with the secondary remnant forest as the reference factor. The significance of landscape elements on individual species abundances was corrected for family-wise error between species using Holm’s multiple testing procedure (Wang et al., 2012). These significance values were used to identify which species were having a differentiating effect among elements, and abundance plots comparing these species among elements were used to distinguish the element(s) in which they were comparatively most localised (Warton, 2008). In this way we were able to determine species characteristic of certain land-covers.

Multivariate data are difficult to test for autocorrelation (Ramage et al., 2013). Here we attempted to determine whether any spatial autocorrelation remained unexplained by the categorical predictor by including an interaction term (transects × elements) in our models following Wang (2012).

3. Results

3.1. Tree species richness, density and composition

In total, 95 tree species with DBH ≥10 cm were recorded across all elements in the plantation landscape. Accumulation of species across sites was similar for unlogged forest and secondary remnant and riparian elements as evidenced by their rarefaction curves and overlapping confidence intervals (Fig. 3). Accumulation of species in mature plantations was lower than unlogged and secondary forest (although still quite high), and young plantations were depauperate compared to all other elements (Fig. 3). The slightly steeper accumulation curves of both secondary forest elements compared to the curve of unlogged forest (Fig. 3a) appears to be mostly caused by an increased stem density in secondary forest elements
as exemplified by the greater similarity in rarefaction curves of these three forest elements (Fig. 3b). Comparisons between species densities among elements (alpha diversity) supported the overall species richness results, demonstrating that species densities were similarly high in both unlogged (Fig. 4, $S = 27.60 \pm 0.29$) and secondary elements, but were significantly lower in mature and young plantations (Table 1, $p < 0.05$).

Tree species composition differed significantly among landscape elements (multivariate GLM, $p < 0.001$). All modified elements differed in composition from unlogged forest except the secondary remnant for which there was no significant difference (although the $p$-value was close to significance, $p = 0.052$).

Univariate analyses of species’ relative abundance found 38 species were the main drivers of compositional differences among landscape elements (i.e. occurring in different abundance among elements, $p_{adj} < 0.05$, Table S.2). The majority of these trees were late-successional, animal-dispersed species (Fig. 5). We did not detect any significant interaction between landscape elements and transects ($p = 0.06$). This indicates that the effect of landscape element on species composition was not strongly affected by the transect that the site was on (i.e. spatial autocorrelation was unlikely to significantly affect results, Wang et al., 2012). However, we recognise that $p = 0.06$ is close to the cutoff for significance, and thus results need to be interpreted in light of potentially some (relatively weak) spatial structuring in the data.

### 3.2. Successional stage and species composition among elements

The unlogged forest was primarily composed of late-successional species (67%), followed by mid-successional (25%), and early-successional (~10%) species across all sites. The composition of the secondary remnant element, while not significantly different from unlogged forest, did contain a higher proportion of early- and mid-successional differentiating species (Fig. 5). The secondary riparian and secondary remnant elements differed in their composition (multivariate GLM, $p < 0.006$, Table S.2), even though both elements had a similar species density of trees belonging to each successional class (Fig. 4). The secondary riparian element was comprised of a greater proportion of individuals belonging to early- and mid-successional differentiating species, and the secondary remnant had a greater proportion of late-successional individuals (Fig. 5). Cumulatively across all mature plantation sites 70% of tree species found in the unlogged forest were recorded, however, in mature plantations they were sparsely distributed: 24 were found in significantly lower abundance compared to unlogged forest (Fig. 5). Fig. 5 shows the occurrence of recruited trees in mature plantations, with most individuals representing early-successional and mid-successional, heliophilic classes. Young plantations contained very few trees aside from *E. deglupta* (Fig. 3) leading to either an absence or lower abundance for all species except the invasive exotic, *Muntingia calabura* (cherry), including a complete absence of any late-successional trees.
Table 1
Model results of species density for all tree species, and species densities grouped according to successional type and dispersal mode. Emboldened figures represent values whose 95% confidence intervals do not overlap with zero with unlogged forest as reference group (intercept).

<table>
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<th>Response variable</th>
<th>Landscape element</th>
<th>Coef</th>
<th>SE</th>
<th>z value</th>
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</table>

Fig. 5. Composition of differentiating species (found to occur in significantly different number among elements), grouped by successional class and mode of dispersal; Eucalyptus deglupta is not shown. LS = late successional; MS, mid-successional; ES = early-successional; NVD = non-vertebrate-dispersal; A = animal-dispersed.

3.3. Dispersal mode and species composition among elements

Typical of wet tropical forests where the majority of woody plants are vertebrate-dispersed (Jansen and Zuidema, 2001 and refs. therein), >93% of the species found in unlogged forest were animal-dispersed. The species densities of dispersal modes were similar for both secondary remnant and riparian elements (Fig. 4, Table 1), although the number of non-vertebrate-dispersed individuals was proportionally greater in the riparian element (Fig. 5). The species density of animal-dispersed trees was significantly lower on average in mature plantation sites compared to unlogged forest (Fig. 4, Table 1). This was because, although 75% of animal-dispersed trees were recorded across all sites in mature plantations, they occurred in comparatively sparse distribution. Similarly, species density of non-vertebrate-dispersed species was also significantly lower in mature plantations (Table 1), however this was caused by an even lower representation of non-vertebrate-dispersed species found in unlogged forest (only 50%), also sparsely distributed. The eight tree species recorded within the young plantations were comprised of animal-dispersed species that were patchily recruited (e.g. Macaranga spp., Endospermum medullosum) and non-vertebrate-dispersed species (e.g. O. sumatrana, Alstonia scholaris) that occurred as large remnant individuals in a few sites (Figs. 4 and 5).

4. Discussion

The ability to conserve biodiversity in production landscapes will be critical to biodiversity conservation in the 21st century. Here, we have shown that native timber plantations and secondary logged forests support a substantial proportion of forest tree biodiversity. Native plantations supported 70% of forest tree species, and the number of tree species in unlogged and secondary forest elements was similar. However, clear differences were evident in the species composition of unlogged forest and most modified elements, and these were related to the attributes of species (namely, species’ successional stages and modes of dispersal). While modified landscape elements can be species-rich and play a role in maintaining biodiversity in tropical regions, the retention of secondary and unlogged forests within production landscapes remains critical for preserving populations of the full suite of tree species.
4.1. Species richness and composition of landscape elements

Both secondary forest elements, and the secondary remnant forest in particular, demonstrated a high conservation value, as evidenced by the presence of a similar number of tree species in common with unlogged forest. This finding is consistent with the high species richness observed in other selectively-logged tropical forests after relatively short fallow periods (Gibson et al., 2012; Hall et al., 2003; Putz et al., 2012). In some cases, this comparably high richness has been the result of an increased number of early- and mid-successional species after selective-logging, at the expense of late-successional species, therefore masking compositional differences between forest types (Sheil and Burslem, 2003). By contrast, we found no significant difference in composition between the secondary remnant and unlogged forest in this study, although the secondary remnant displayed a trend towards higher abundance of early- and mid-successional species.

Compositional similarity between the selectively-logged, secondary remnant element and unlogged forest may be explained by the low density of commercial timber species in PNG’s forests, and hence, a history of lower intensity harvesting disturbance compared to other tropical countries (Bonnell et al., 2011; Johns, 1992). The secondary remnant had also been left fallow and free from human disturbance since its designation as a conservation reserve over 16 years prior to this study. Another factor may be the evolution of these forests in conjunction with regular volcanic disturbances, and one of the longest histories of anthropogenic modification in the world (over 30,000 years) (Lenfer et al., 2010). These regular disturbances may have resulted in the filtering of more disturbance-tolerant plant assemblages—an observation which has been made of forests on neighbouring Melanesian islands (Bayliss-Smith et al., 2003). Therefore, the unlogged forests in this study may resemble secondary forest more closely than studies in other regions experiencing different biogeographic processes and disturbance histories.

Selectively-logged secondary forests can play a vital conservation role as source pools of forest propagules in production landscapes, if properly managed (Edwards et al., 2010). However, the selectively-logged, riparian elements that are subject to ongoing local timber extraction, had a lower abundance of late-successional species compared to the secondary remnant, exhibiting a diminished conservation value. Significant decline in the biodiversity value of secondary stands experiencing continuing disturbance has been well documented (Chazdon, 2003; Gibson et al., 2012; Laurance, 1997), and it is equally likely here that without adequate protection from further modification, the biodiversity value of secondary elements will continue to decline.

Mature plantations demonstrated high cumulative species richness, recruiting 70% of forest species across all sites, although occupation of sites by E. deglupta resulted in their sparse distribution (low site-level richness) compared to non-plantation elements. Comparison of tree species richness with other tropical plantation studies is confounded by differences in the age of plantations studied, the life-stage measurement of woody plants (seedling, sapling, tree), and the study site’s baseline forest species richness. Nevertheless, the mature E. deglupta plantations contained a similar or greater proportion of native rainforest tree species compared to studies in exotic (Chapman and Chapman, 1996; Lugo, 1992; Parrotta, 1995) and native timber plantations (Keenan et al., 1997; Wardell-Johnson et al., 2005). By contrast, young plantations 2–6 years post-clearfell had a substantially reduced richness of recruiting trees, which is not surprising given that only trees >10 cm DBH were sampled and few recruits would have grown to that size within the time since plantations were established. This highlights the varying contribution of differently aged plantations to the functional composition of trees in a landscape.

4.2. Successional stage is limited by plantation age

Mature plantations were mainly comprised of early- and mid-successional individuals. Most late-successional trees were found in low density, but cumulatively, across mature plantation sites, two-thirds of late-successional species found in unlogged forest were capable of growing to 10 cm DBH in mature plantations. It is possible that even more late-successional species, which were <10 cm DBH, were present in mature plantations. Late-successional trees tend to grow slowly (Laurans et al., 2012), resulting in more individuals occurring as difficult to detect saplings and seedlings (<10 cm DBH). For example, in some other plantation studies, richness of late-successional trees was found to be higher in juvenile stages compared to adult stages (Farwig et al., 2009; Keenan et al., 1997). The richness of late-successional species is best assessed where juvenile tree species (<10 cm DBH) can be identified and recorded. This was not possible in this study and it is therefore likely that we have underestimated richness of these species here. This type of assessment would be especially instructive for those plantations incorporating a restoration role. For the industrial plantations of this study, plantation age is a more influential inhibitor of the density of late-successional trees that can survive beyond juvenile stages.

The ability of E. deglupta plantations to foster a breadth of successional types may arise from its natural role in these forests as a successional catalyst, where it invades disturbed sites, quickly forms mono-specific stands, suppressing weedy plants and creating abiotic conditions resembling intact rainforest (Pajmans, 1973). Additionally, facilitative germination conditions are likely augmented by the low intensity of stand-level management: thinning was unprofitable and rare, and manual weed tending ceased at three years. In many production plantations, high intensity management has inhibited recruitment of mid- and late-successional species (Kanowski et al., 2005; Keenan et al., 1997).

4.3. Dispersal mode drives colonisation in plantations

Of the trees recorded in unlogged forest, mature plantations supported 50% of the non-vertebrate-dispersed species and 75% of animal-dispersed species. This finding likely reflects the lower dispersal capacity of non-vertebrate-dispersed species throughout the landscape (Willson and Crome, 1989). Distribution of animal-dispersed trees in this landscape does not appear to be as limited, and may be explained by the high permeability of the matrix to local animal vectors (e.g. birds, bats). Our contemporaneous studies of forest birds supports this hypothesis: we found just two species restricted to unlogged forest (Pryde et al. unpublished data), and birds, along with bats, are considered the primary tree dispersers in these lowlands (Mayr and Diamond, 2001). Permeability is thought to be enhanced in plantation landscapes because of the proportion of the matrix with a continuity of tree cover (Brockerhoff et al., 2010; Keenan et al., 1997).

The recruitment of most animal-dispersed species in the plantations (albeit, in low abundance) suggests that plantations themselves attract visitation by a range of seed-dispersing species. This is most likely in more mature stages when plantations have a higher tree species richness, however, in young plantations we still observed birds exploiting the perching structure and nectar provided by E. deglupta, a particularly important food resource for the island’s parrot species (Marsden and Pilgrim, 2003). Between three-to-six years of age, E. deglupta can flower and grow to a height of 10 m (Francis, 1988). The fast-growth rates typical of plantation species has been similarly observed to provide structural resources from very early stages (McClanahan and Wolfe, 1993; Parrotta, 1995).
4.4. Conservation and management implications

The results from this study indicate that the combination of native timber plantations set among older secondary forest elements can support high levels of tree species biodiversity. Native timber plantations are rare in many tropical regions and should be considered in preference to exotic plantations due to their enhanced capacity to harbor native biodiversity. We found that older plantations held greater benefit for biodiversity, with young plantations demonstrating a poor capacity to recruit all but a homogeneous assemblage of early-successional tree species. Therefore, temporarily varying harvesting cycles to ensure the highest possible cover of mature plantations through time (and their presence at all times) would increase the biodiversity conservation value of the landscape.

Regenerating secondary forest elements were found to be important refugia for populations of rainforest-restricted species, such as slow-growing, late-successional and non-vertebrate-dispersed trees. Therefore, recognition of their high conservation value is vital, and their protection from future harvesting and further plantation establishment recommended. Open Bay’s high ratio of unlogged forest to cleared area in the broader landscape, and the extensive, old, regenerating secondary forest within the production landscape, have been identified as key contextual characteristics for biodiversity conservation in multi-purpose landscapes (Gibson et al., 2012; Letcher and Chazdon, 2009). Therefore, any future expansion of plantations to meet increasing timber demands should be located on degraded lands, rather than by encroaching into logged-over forest, as is current practice in New Guinea.

Ultimately, the capacity of plantations to contribute to biodiversity in terms of species population sizes and reproductive success will be modest compared to that of unlogged and secondary elements because of clearfell practices and competition from plantation trees (Catterall et al., 2005). Thus, ensuring that old-growth rainforest is retained is critical, to provide refuge for rainforest-restricted species and source pools for species capable of existing in modified elements.

Acknowledgements

This research would not have been possible without the help of forestry workers employed by the Open Bay Timber Company, East New Britain Province, Papua New Guinea, particularly Dionisio Quinones, the late (great) Francis Yendkao, Eddy Kaukia, Steven Taubuso, Hendry Bapo and Albert Keso. We are much indebted to the Kol, Baia, Makolkol and Baining communities for allowing us access to their customary land, embracing us as guests, and for providing field guidance and assistance. We are likewise grateful to the Open Bay Timber Company for permitting us to conduct this study. The field research for this study was supported financially by grants from James Cook University, Australia Pacific Science Foundation, Oregon Zoo Futures Fund and the Skyrail Rainforest Foundation. We thank David Warton and Yi Wang for their assistance with data analysis and two anonymous reviewers for their valuable contribution to the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.11.028.

References


