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RESEARCH ARTICLE

Comparing the recovery of richness, structure, and biomass in naturally regrowing and planted reforestation

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The clearing of natural vegetation for agriculture has reduced the capacity of natural systems to provide ecosystem functions. Ecological restoration can restore desirable ecosystem functions, such as creating habitat for animal conservation and carbon sequestration as woody biomass. In order to maintain these beneficial ecosystem functions, restoration projects need to mature into self-perpetuating communities. Here we compared the ecological attributes of two types of restoration, "active" tree plantings with "passive" natural forest regeneration ("natural regrowth") to existing remnant vegetation in a cleared agricultural landscape. Specifically, we measured differences between forest categories in factors that may predict future restoration failure or ecosystem collapse: aboveground plant biomass and biomass accrual over time (for regrowing stands), plant density and size class distributions, and diversity of functional groups based on seed dispersal and growth strategy traits. We found that natural regrowth and planted forests were similar in many ecological characteristics, including biomass accrual. Despite this, planted stands contained fewer tree recruit and shrub individuals, which may be due to limited recruitment in plantings. If this continues, these forests may be at risk of collapsing into nonforest states after mature trees senesce. Lower shrub density and richness of mid-story trees may lead to lower structural complexity in planting plots, and alongside lower richness of fleshy-fruited plant species may reduce animal resources and animal use of the restored stand. In our study region, natural regrowth may result in restored woodland communities with greater conservation and carbon mitigation value.

Key words: carbon sequestration, climate change, diversity, functional traits, plant biomass, size class distribution

Implications for Practice

- Aboveground biomass acquisition was similar in planted and naturally regrowing reforestation stands, and regrowth over 30 years old exhibited aboveground biomass similar to uncleared stands.
- Planted and naturally regrowing stands exhibited lower species richness than uncleared vegetation. In plantings, we observed lower richness of two important functional groups: mid-story trees and plants with fleshy, bird-attracting fruits.
- Planted reforestation stands had lower densities and diversity of shrubs and tree recruits than similarly aged natural regrowth.

Introduction

Agricultural development has resulted in profound landscape transformations, particularly the replacement of woodland and forests with cropland and pasture (Vitousek et al. 1997). Restoring some wooded vegetation on cleared land can increase the levels of ecosystem functions and services (Loreau & Hector 2001; Foley et al. 2005) to aid in the conservation of biological diversity and carbon sequestration in biomass to mitigate climate change (Jordan et al. 1988; Fensham & Guymer 2009; Mansourian & Vallauri 2014; Barral et al. 2015). In order for these benefits to be fully realized and persist over time, reforestation projects that aim to restore wooded vegetation need to result in resilient, self-perpetuating communities (Dixon et al. 1994).

Predicting if restored plant communities will become self-sustaining over time is a challenge, particularly in forests and woodlands, because even the oldest reforestation projects are immature relative to mature vegetation (Ngugi et al. 2011; Brudvig 2017). In addition, while definitions of success in restoration vary (Ruiz-Jaen & Mitchell Aide 2005), young projects often fail to meet vegetation growth and structural

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targets (Suding et al. 2004; Suding 2011; Wilson et al. 2011). Complete failure of restoration projects can result in the community collapsing into an alternate state that may be difficult to reverse (Suding et al. 2004). The resulting community may also be of far lower conservation and carbon value (e.g. a woodland collapsing into a community composed of invasive grasses) than if the project were successful (e.g. Vitousek 1991; Spracklen & Righelato 2016). To avoid this, management guidelines for forest restoration suggest that projects should maximize plant diversity, structural complexity (Lindenmayer et al. 2016), and subsequent plant recruitment (McDonald et al. 2016*a*).

Incorporating these management guidelines into active restoration involving planting or seeding can be expensive and labor-intensive (Birch et al. 2010; Holl & Aide 2011). There is evidence that managing naturally regenerating forests ("natural regrowth") is more economical than active restoration (Birch et al. 2010; Evans et al. 2015) and may produce similar restoration outcomes (Crouzeilles et al. 2017; Meli et al. 2017; Jones et al. 2018). Underperformance of active restoration may be because biased subsets of species from the community species pool are included, potentially omitting species with important functional roles. This may result in a system vulnerable to collapse or invasion (Mouillot et al. 2011). To address this, recent methods for designing restoration assemblages have incorporated the use of plant functional traits (e.g. Laughlin 2014; Laughlin et al. 2018).

Functional traits are measurements made on species and individuals that correlate with underlying physiological processes (Violle et al. 2007). Functional traits are useful for quantifying the function of communities, and high functional diversity has been linked to the provision of ecosystem functions and services (Roscher et al. 2012). For measures of functional diversity to be applicable to restoration outcomes, they need to be measures of ecosystem functions and species' ecological strategies that are relevant to the growth and persistence of the restored community (Cadotte et al. 2011). The persistence of a restored community may be limited by the recruitment of new plants (Suding 2011; Monie et al. 2013). In particular, seed dispersal by animals is an ecosystem function of high conservation concern, as the mutualism between plants and dispersers is vulnerable to disruption (Ruxton & Schaefer 2012). As well as this, the functional diversity of traits related to growth strategy, stress tolerance, and maximum carbon storage (e.g. specific leaf area [SLA], wood density, and maximum height; Gibert et al. 2016) may be important for maintaining community biomass and carbon stocks over time (Häger & Avalos 2017).

It remains unclear whether naturally regenerating and actively planted restoration can provide similar benefits to conservation and carbon sequestration in agricultural landscapes, and whether these benefits will be realized in the long term (Morrison & Lindell 2011). In this study, we compared naturally regrowing vegetation ("regrowth") and planted reforestation stands ("plantings") to mature vegetation ("remnant") in a transformed agricultural region. We compared these vegetation types in terms of biomass accrual over time, size class distributions based on biomass, and functional richness of traits related to seed dispersal and growth. We also used differences between vegetation types to draw conclusions about the potential magnitude and persistence of carbon sequestration and biodiversity benefits of each vegetation type. Specifically, we asked:

(1) Does the accrual of standing biomass in natural regrowth and planted stands differ over time, and how does their standing biomass compare to remnant vegetation?
(2) Do regrowth, plantings, and remnant stands have similar plant densities and size class distributions?
(3) Do regrowing and planted stands contain similar levels of species richness, and are all plant functional groups from remnant vegetation represented?

Methods

Study Region

All forest stands were located in South East Queensland, Australia (Fig. S1), 150–200 km northwest of Brisbane, across the boundary of two biogeographic regions: South East Queensland and Brigalow Belt South (Thackway & Cresswell 1995). This region is subtropical by latitude, and abridges the Great Dividing Range. Coastal areas receive over 1,000 mm of annual precipitation, while the western side of the range receives circa 500–750 mm (Fig. S1; Lloyd 1984). Temperatures are similar across the study region, with a mean annual maximum of 25.20°C (SD = 0.82°C), and a mean annual minimum of 11.65°C (SD = 0.83°C).

Land clearing has occurred in South East Queensland since settlement in the early 1800s, but accelerated in the 1940s and 1950s (McAlpine et al. 2002). Only an estimated 40% of the original vegetation cover in our study region remains (Wilson et al. 2002). Preclearing vegetation was forest or woodland with an open canopy of 20–30-m-tall sclerophyllous tree species (Lucas et al. 2014), particularly *Corymbia citriodora*, *Corymbia trachyphloia*, *Eucalyptus crebra*, *and Eucalyptus pilularis*. Understories contained a mixture of shrub species, including *Geijera parviflora* and a number of nitrogen-fixing *Acacia* species (such as *Acacia leiocalyx* and *Acacia disparrima*). Study sites occurred across three major geologies: loamy and sandy plains (Tertiary and early Quaternary), and soils derived from acid-volcanic (primarily Mesozoic to Proterozoic granite) and metamorphic (Permian and older) bedrock (Wilson & Taylor 2012). These geologies were classified into "land zones" using Queensland's Regional Ecosystem Framework (Wilson & Taylor 2012) (Table S1).

Forest Inventory Data. The data used in our study were collected from sample plots in stands of four different vegetation categories: uncleared vegetation ("remnants": 84 plots in 22 stands), environmental reforestation plantings ("plantings": 44 plots in 16 stands, from 5 to 13 years old), and naturally regrowing forest, divided into two age categories: "young regrowth" (≤20 years since abandonment: 46 plots in 15 stands, 4 to 19 years old) and "old regrowth" (>20 years since abandonment: 27 plots in 10 stands, 21 to 71 years old). Planting and regrowth stands were all on land that was forest or woodland prior to being cleared. While initial species mixes and management is unknown, plantings were established in a single planting event using tubestock of multiple native trees and shrubs, and were planted for ecological restoration, or for alternate purposes such as carbon sequestration. Livestock were excluded from planted stands during establishment, but many stands experienced occasional livestock grazing as a method of weed and fire management.

Data were collected in 2009 (except one stand that was sampled in 2010) by two not-for-profit organizations: Greening Australia (9,299 plant individuals in 198 plots) and Greenfleet (37 plant individuals in three plots). Sample plot sizes varied, but were on average 625 m^2 (SD = 39 m^2). Plots contained an average of 52.4 plants (SD = 23.5). Remnant plots had an average of 64.1 (SD = 27.0) plants, planting plots had 37.3 (SD = 12.6), young regrowth plots had 48.0 (SD = 17.2), and young regrowth plots had 48.6 (17.0). Trees and shrubs in sample plots were identified to species (87.9%) or genus (12.4%): across all plots, 9.2% of plants were dead at time of measurement. In total, the study plots contained stem diameter measurements on 9,336 individual plants from 68 species, 30 genera, and 20 families.

Aboveground Biomass Estimation. Using a diameter measuring tape, stem diameters were measured on all trees and shrubs within each plot. The height of diameter measures varied between sites, based on the heights of surveyed plants and the height that they branched or forked (breast-height [130 cm above the ground], or either 50 cm or 10 cm). Stem diameters were combined and expressed as a single-stem diameter ($\text{De} = \sqrt{\sum \text{Di}^2}$, where Di represents the diameter for each stem of a multi-stemmed plant: see Paul et al. 2013). Where required, relationships between stem diameters at different heights were used to convert diameters measured at 130 cm for trees, or 10 cm for shrubs, as per protocol in Paul et al. (2013). Aboveground biomass (herein "biomass") of each plant (kg) was estimated from its stem diameter by applying an existing species- or life-form-specific allometric equation. The allometric equations are listed in Paul et al. (2013), which were developed by harvesting 3,139 trees and shrubs for aboveground biomass, and were validated by measuring plot-level biomass at eight contrasting sites to test the accuracy of prediction of aboveground biomass per hectare.

Functional Traits. Our study included four continuous functional traits, calculated as mean values for each species: SLA (mm^2/g), wood density (g/cm^3), seed mass (mg), and maximum height (m). These traits were chosen as they are commonly available for a large number of species, and correlate directly with relative growth rate (SLA and wood density), represent size at maturity (maximum height), or affect dispersal distances and early growth and survival (seed mass) (Perez-Harguindeguy et al. 2013; Gibert et al. 2016). Functional trait values were obtained from the TRY plant database (Fonseca et al. 2000; Shipley 2002; Green 2009; Poorter et al. 2009; Onoda et al. 2011; Pierce et al. 2013) and Australian state herbarium records.

In addition to these continuous traits, we also included two categorical traits: nitrogen fixation (binary) and seed dispersal category. We used the dispersal syndromes outlined in Jurado et al. (1991) to group species into four seed dispersal categories: wind-dispersed (seed shape that increases wind resistance), fleshy (obvious flesh, or bird-attracting arils), elaisome (ant-attracting arils), and unassisted (none of the above features).

Data Analysis

All data processing and analyses were conducted in R (R Core Team 2017). Text depictions of all statistical models can be found in Supplement S1.

Comparison of Community Attributes (Biomass, Density, and Richness) Between Forest Stand Categories. We compared three basic community attributes (plot biomass, plant density, and species richness) across four stand categories: remnants, plantings, young regrowth ($\leq$20 years), and old regrowth (>20 years). We calculated plot biomass by summing the biomass estimates for all plants in each plot, and dividing the total by plot area (expressed as Mg/ha). Plant density was calculated by summing the number of plants in each plot and dividing by plot area (plants/ha). We used subsample-based rarefaction to estimate woody plant richness in each plot, as plot sizes and plant numbers differed ($n = 12$, the smallest number of plants contained within a study plot: rarefy function, vegan package [Oksanen et al. 2012]). Dead plants were excluded from rarefaction, and genus identifications were counted as a single additional species per genus.

Sample plots within each forest stand, and stands on the same geology were unlikely to be independent. To account for this autocorrelation, we used linear mixed-effects models, fitting random intercepts to each land zone (geology underlying each forest stand; Table S1) and stands within each land zone, and used stand category as the only fixed effect. We estimated pairwise differences between stand categories using generalized linear hypothesis testing (glht function, multcomp package; Hothorn et al. 2008).

Biomass Accrual Model. To investigate differences in biomass between stand categories in more detail, we modeled biomass of planting and regrowth forests as a function of stand age: time since planting for planted stands, and time since abandonment for regrowth stands. We excluded remnant plots from this model, and young and old regrowth plots were combined into a single "natural regrowth" category. We used a linear mixed-effects model, fit with random intercepts (as above), and three fixed effects: stand age (years), stand age^2 (a quadratic term for possible nonlinear trends), and stand category (planting or natural regrowth). We included interactions between the age terms and stand category in order to estimate the effect of age on biomass separately for plantings and regrowth.

Size Class Distribution Model. To compare differences in plant density across different size classes, we binned the ln-transformed biomass of plants in sample plots into 20 equal-sized bins (Tables S2 & S3). This gave us an abundance of each size class in each plot and we divided these size class abundances by plot area to adjust for different plot sizes. This converted size class abundances into size class densities (plants/ha). We used these size class densities as the response variable in two generalized additive mixed-effects models (gamm function, mgcv package; Wood 2004).

In the first model, we estimated the mean probability of occurrence for each size class in each stand category. We gave all nonzero size class densities a value of one, and modeled this binary response variable using binomial errors and a logit link function. The center of each size class was used as a continuous fixed effect, alongside stand category as a categorical fixed effect (four categories: planting, young regrowth, old regrowth, and remnant). We estimated the relationship between probability of size class occurrence and size class using cubic regression splines (with a maximum of six knots), fitting different splines to each stand category. We fit nested random intercepts to land zones, stands within land zones, and plots within stands.

The second model included only nonzero densities (i.e. the size class densities excluding absences) and was fit with Gaussian errors and an identity link function. We estimated the relationship using the same fixed and random effects structure as listed above.

Richness of Functional Groups. Finally, we examined differences in plot richness by comparing the mean plot richness of different functional groups of woody plants in each stand category. We categorized species into two sets of functional groups using species-level traits linked to particular functions: capacity for seed dispersal and growth strategy. Seed dispersal capacity was approximated using seed mass and seed dispersal category. Growth strategy was approximated using three functional traits linked to relative growth rate: SLA, wood density, and maximum height (Gibert et al. 2016), as well as a binary nitrogen fixation category. We created each set of functional groups using the process outlined in Laliberté et al. (2010). We calculated distances between species in trait space using Gower dissimilarity (gowdis function, FD package; Laliberté et al. 2014), and then grouped species based on distance using Wald's minimum variance clustering (hclust function). This function returns a dendrogram, with species with low dissimilarity clustered together. We then split these species into eight functional groups, with each group consisting of clusters of species; this corresponded to a Wald's distance of 0.3 and 0.5 for the seed and growth functional groups respectively.

To model differences in functional group richness between stand categories, we used generalized linear mixed-effects models with negative binomial errors and a log link function, which accounted for over-dispersion (glmmPQL function, MASS package: Venables & Ripley 2002). Our response variable was functional group richness, and we fitted the model with two categorical fixed effects: functional group and stand category, allowing for interactions to estimate mean plot functional group richness separately for each stand category. Plot area was added to both models as a continuous covariate to correct for differences in functional group richness between small and large plots. We estimated nested random intercepts for land zones, stands within land zones, and plots within stands.

We extracted model estimates and 95% confidence intervals for plotting, and tested for significant differences in functional group richness between remnant plots and the other three categories using generalized linear hypothesis testing (glht function, multcomp package; Hothorn et al. 2008); this test identified functional groups that were significantly over- or underrepresented in regrowing forests in our study region. We conducted this process twice: once using the seed dispersal functional groups, and once using the growth strategy functional groups.

Results

Comparison of Community Attributes (Biomass, Density, and Richness) Between Forest Stand Categories

Community attributes varied substantially between different stand categories. Remnant plots contained an average of 155 Mg/ha of aboveground biomass, similar to old regrowth (91.9 Mg/ha), and significantly more than planting and young regrowth plots (25.6 and 49.5 Mg/ha, respectively: Fig. 1A, Table S4). On average, planting plots had lower plant density (495 plants/ha) than remnant and young regrowth plots (1,160 and 1,496 plants/ha, respectively; Fig. 1B, Table S4). Finally, all regrowing stand categories had lower rarefied species richness than remnant stands (4.1 species for remnant stands vs. 2.5, 2.6, and 1.9 for planting, young regrowth, and old regrowth, respectively; Fig. 1C, Table S4).

Biomass Acquisition Model

Stand age was a strong positive predictor of aboveground biomass in regrowing forests, with a significant negative quadratic term for regrowth that suggests biomass acquisition began to slow after 30 years (Fig. 2, Table S5). Aboveground biomass of regrowth plots older than 30 years did not appear to be different to the mean aboveground biomass in remnant plots (Fig. 2). The age range of plantings in our study was relatively restricted (the oldest being 13 years old), but biomass of plantings was similar to regrowth of the same age (Fig. 2).

Size Class Distribution Models

The probability of occurrence of plant size classes was similar between most stand categories. Most plots were highly likely to contain at least one plant in every size category between 2 and 100 kg/plant (Fig. 3A & B). Planted stands differed from young regrowth in that planted stands were less likely to contain a plant between 2 and 30 kg/plant (Fig. 3A).

When we excluded empty size classes and modeled the density of plants within each size class, we found that remnant plots contained circa 70 plants/ha with biomass between 3 and 300 kg/plant (Fig. 3D). Older regrowth was similar to remnants in density across the range of size classes (Fig. 3D). Young regrowth contained far higher average density of small plants (biomass of 3–80 kg/plant) than the other stand categories,

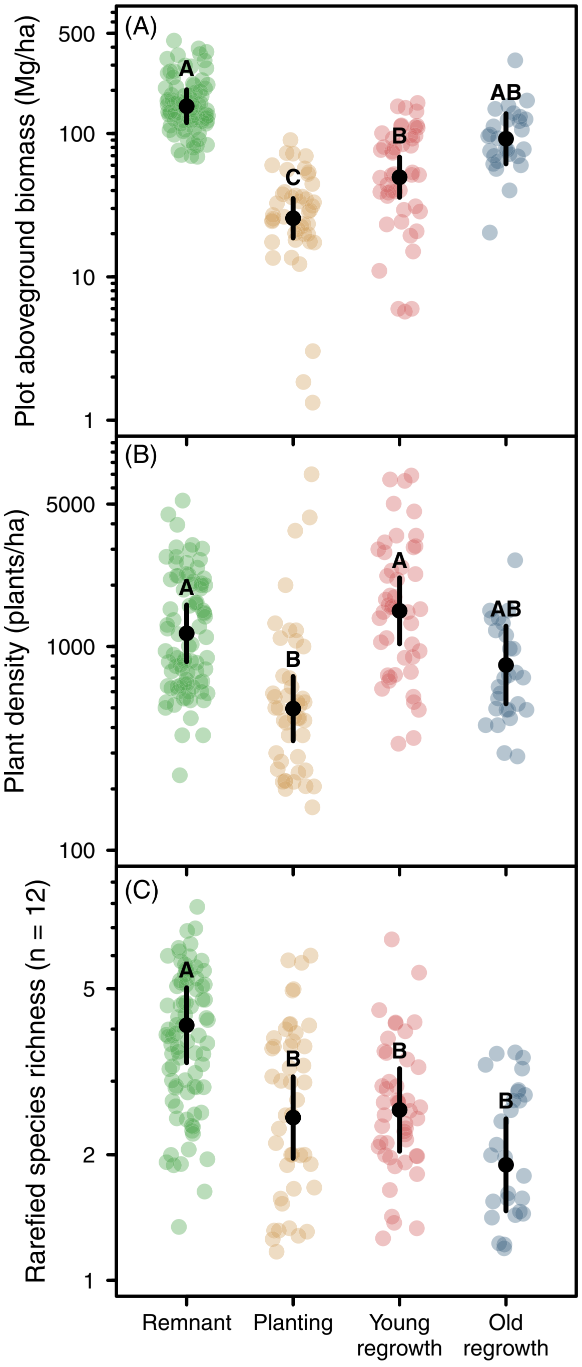

Figure 1. Basic community attribute comparison between different forest stand categories. Regrowth was divided into young (≤20 years) and old (>20 years) regrowth. Background points are values for individual plots, black points are group means estimated from mixed-effects models. Error bars are 95% confidence intervals. Letters indicate significant differences ($p < 0.05$); statistical comparisons between forest stand categories are shown in Table S4. Note that *y*-axes are on a log scale.

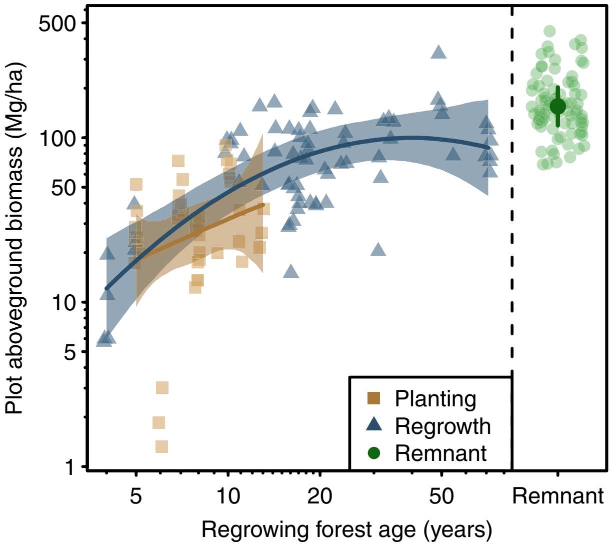

Figure 2. Biomass of regrowing forests (natural regrowth and plantings) over time. Planting growth was positive and linear, while regrowth had a significant negative quadratic term that slowed biomass growth over time (Table S5). Mean remnant biomass was taken from models shown in Figure 1; remnant patches do not have an age since abandonment or planting, and are included in the plot for visual comparison to the modeled trajectories for regrowth and plantings. Shading and error bars are 95% confidence intervals.

especially plantings, which had a far lower average density of plants between 1 and 40 kg/plant (Fig. 3C).

When small plants (<40 kg) in planted and young regrowth plots were grouped into the eight growth strategy functional groups (Table 1), most were recruits of common canopy trees (group 6) and some common nitrogen-fixing shrubs (group 7; Fig. 4). Regrowth plots contained more small plants from all functional groups, including canopy trees and shrubs (Fig. 4). In addition, four common species were well-represented in regrowth tree recruits (group 5), whereas tree recruits in planted plots were dominated by *Corymbia citriodora* (Fig. 4).

Richness of Functional Group

We found that richness estimates of most seed dispersal and growth functional groups were similar across all four forest stand categories (Fig. 5).

Seed Dispersal Functional Group Richness. Two seed dispersal functional groups were absent in some forest stands. The group containing large (>10 g dry weight) unassisted seeds were only present in remnant stands (group 8, Fig. 5A, Table 1). Group 1, which contained plants with small, wind-dispersed seeds, was absent in old regrowth plots. Plantings also contained significantly fewer species with small fleshy seeds (group 4, Table 1) than remnant plots (Fig. 5A, Table S9). Young and old regrowth plots contained fewer species of this group than remnant plots, but the difference was not significant (Fig. 5A, Table S9). Group 4 consisted of species with obvious fruit and seeds containing red or yellow arils that are attractive to birds (Table 1).

Growth Functional Group Richness. Plantings and natural regrowth included species from almost all growth and structure functional groups; the only missing group was the

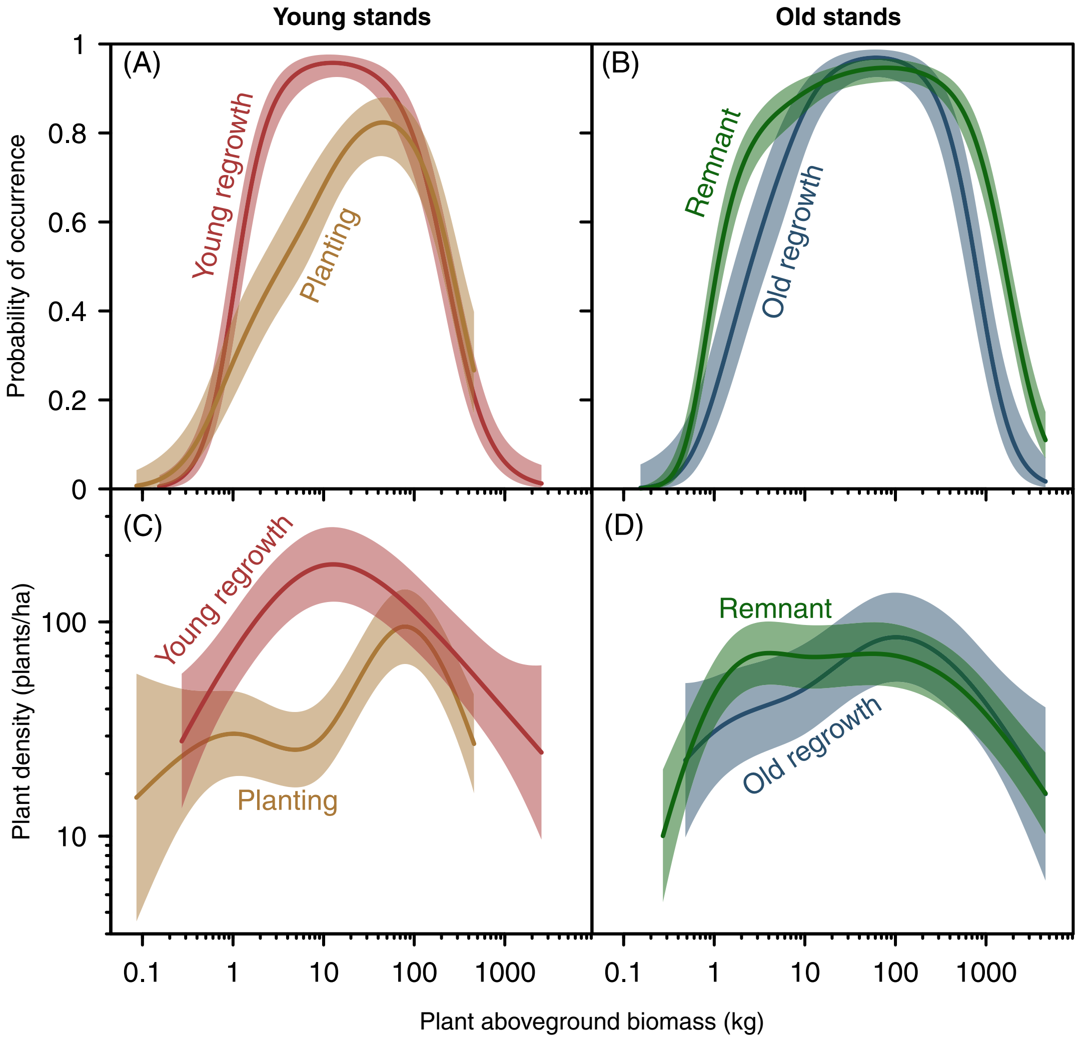

Figure 3. Occurrence probability (A and B) and average density (C and D) of plants of given biomass (grouped into 20 size classes) across four forest stand categories (remnant, plantings, young [≤20 years], and old regrowth [>20 years]). Plants in each plot were grouped into 20 equal-sized ln-transformed biomass bins ("size classes"), and used to estimate the probability of occurrence and mean density of size class distributions using two generalized additive mixed-effects model (see Tables S6 & S7); shading behind splines are 95% confidence intervals. Forest stand categories are split into (A and C) young and (B and D) old stands for visual clarity only: all categories were modeled together in each model. Note *x*-axes in all plots and *y*-axes in (C and D) are on a log-scale.

nonnitrogen-fixing shrub species (group 2, Table 1) in older regrowth (Fig. 5B, Tables S8 & S10). This functional group was far rarer in remnant plots than the nitrogen-fixing shrub group (group 7, Table 1), and was composed of several native species (e.g. *Breynia oblongifolia*) as well as the invasive shrub *Lantana camara* (Fig. 5B, Tables S8 & S10). The richness of growth and structure functional groups in remnant and regrowing forest plots was similar for all but one group. This group (group 5) was significantly less rich in plantings than in remnants, and was comprised of 20–25-m tall trees with higher SLA than the group containing dominant canopy tree species (group 6, Fig. 5B, Table 1). Species in group 5 included some of the shorter *Eucalyptus* species (e.g. *Eucalyptus melanophloia*), related genera *Angophora* and *Corymbia*, and a mixture of tree species with fleshy fruit (Table S8).

Discussion

Here we compared naturally regenerating regrowth and reforestation plantings to each other, and with remnant vegetation, across a number of ecological factors, including biomass accrual, plant density, and species and functional group richness. We found that biomass accrual over time was similar in naturally regenerating regrowth and planted reforestation. Our modeled trajectories suggest both regrowing forest types are on track to reach aboveground biomass estimates of remnant vegetation. While natural regrowth and planted stands exhibited lower species richness than remnant stands, in plantings this manifested as lower richness of two common functional groups: fleshy-fruited species and mid-story trees. Plantings also showed low density and richness of shrubs and tree recruits, which may result in trees senescing without replacement and

Table 1. Brief description and example species of functional groupings. Species were grouped by seed mass and seed dispersal category ("seed dispersal": as per Jurado et al. (1991)), and by specific leaf area, wood density, maximum height, and nitrogen fixation ("growth and structure"). See Table S8 for group membership of all study species. Group numbers are used to refer to groups in Figs 4 and 5 and supplementary tables.

Functional Groupings	*Group Number*	*Description*	*Example Species*
Seed dispersal:	1	Extremely light wind-dispersed seeds	*Allocasuarina littoralis*
	2	Light wind-dispersed seeds	*Grevillea robusta*
	3	Seeds with white, ant-attracting arils (elaisomes)	*Acacia fimbriata*
	4	Light fleshy seeds containing obvious fruit or bird-attracting arils (red or yellow)	*Breynia oblongifolia*
	5	Medium fleshy seeds containing obvious fruit or bird-attracting arils (red or yellow)	*Exocarpos latifolius*
	6	Extremely light unassisted seeds	*Eucalyptus tereticornis*
	7	Light unassisted seeds	*Angophora floribunda*
	8	Extremely heavy unassisted seeds	*Castanospermum australe*
Growth and structure	1	Soft-wooded understory trees	*Glochidion ferdinandi*
	2	High SLA low-wood density shrubs	*Alstonia constricta*
	3	Low SLA, high wood density shrubs	*Dodonaea triangularis*
	4	Canopy trees with high SLA and wood density	*Flindersia australis*
	5	Understory trees with low SLA and high wood density	*Angophora subvelutina*
	6	Canopy trees with low SLA and high wood density	*Corymbia citriodora*
	7	Nitrogen-fixing shrubs with relatively high wood density	*Acacia leiocalyx*
	8	Nitrogen-fixing shrubs and short trees with extremely high wood density	*Allocasuarina torulosa*

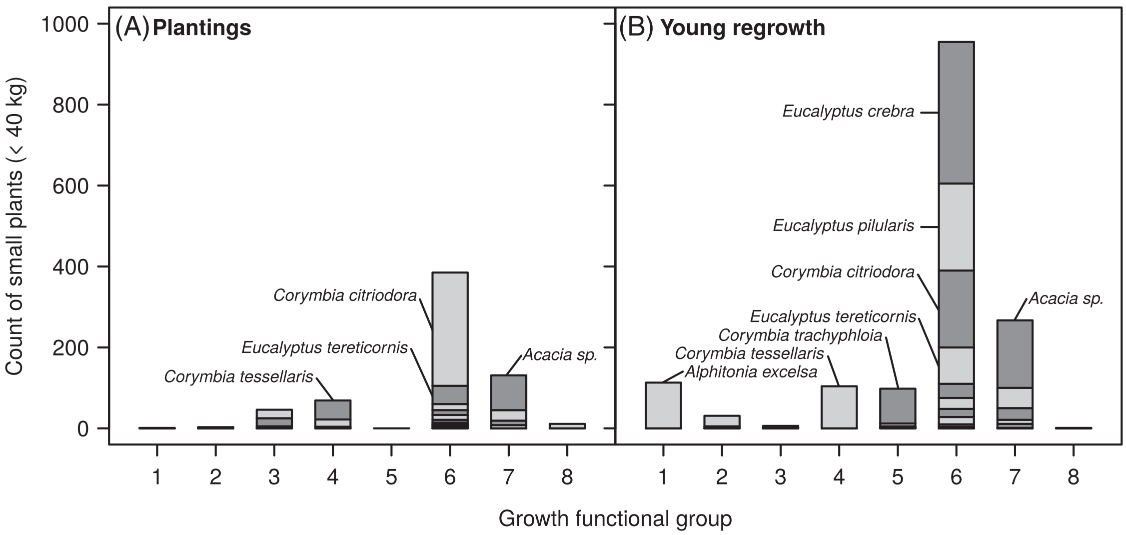

Figure 4. The abundance and composition of small plants (<40 kg) in planted and young regrowth plots. Species are grouped into the eight "growth and structure" functional groups identified using four functional traits: specific leaf area, wood density, maximum height, and nitrogen fixation (Table 1). Species that contributed a large proportion of small plants are labeled.

make plantings vulnerable to collapse to a nonwooded state with lower potential carbon storage (Lindenmayer et al. 2016; Caughlin et al. 2019). Lower shrub density and mid-story tree richness may lead to lower structural complexity in planting plots and, alongside lower richness of fleshy-fruited plant species, may reduce animal resources and animal use of the restored stand (e.g. Morrison & Lindell 2011; Jung et al. 2012). Overall, planted reforestation in our study region may result in communities of low conservation and carbon mitigation value, but further work is required to investigate these patterns as plantings mature.

Biomass Accrual for Carbon Storage

Despite diverging in absolute aboveground biomass, plantings and regrowth forests in our study region appear to be on the same trajectory of biomass accrual. While planted stands are still immature, older regrowth stands appeared to converge on the standing biomass of some remnant plots. The plantings in our study were not old enough to observe a similar pattern, but early biomass accrual was similar between planted and natural regrowth stands. This suggests that both plantings and regrowth in our study region will take circa 30 years to approach biomass similar to remnant plots. Plantings in similar vegetation types

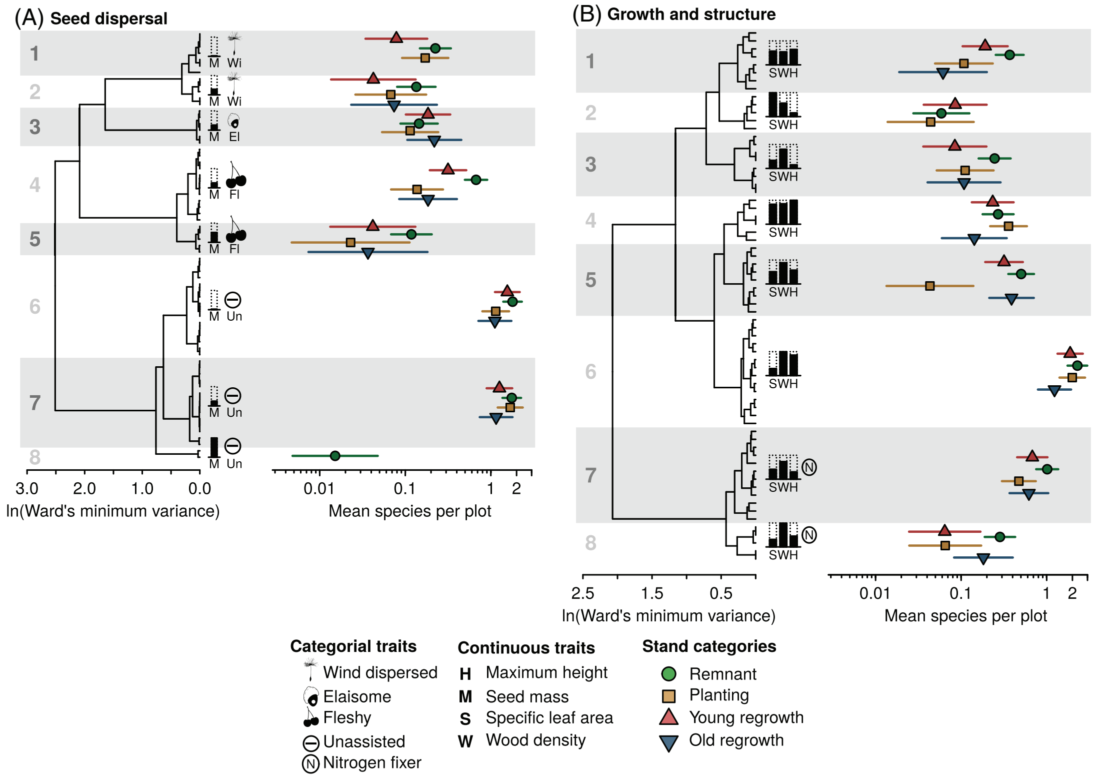

Figure 5. Functional dissimilarity dendrograms, functional groupings (gray shading and numbering), and functional group richness for four vegetation categories (remnant, green circles; plantings, yellow squares; young regrowth [≤20 years], red triangles; and old regrowth [>20 years], blue inverted triangles). Points are mean plot functional group richness in each stand category; lines are 95% confidence intervals. Statistical comparisons between remnant vegetation and other categories can be seen in Tables S9 & S10: functional group membership is shown in Table S8. Functional groups were calculated two ways: (A) by seed dispersal, calculated using seed mass (M) and seed grouping (wind dispersed [Wi], elaisome [El], fleshy [Fl], and unassisted [Un], as per Jurado et al. (1991)) and (B) by growth strategy, calculated using specific leaf area (S), wood density (W), and maximum height (H), as well as nitrogen fixation (binary, indicated by N). Black bars beside dendrograms represent the mean trait values of continuous traits in each group, as a proportion of the greatest group mean.

resembled remnant vegetation after 30–40 years, but lacked ground layers and important structural features (Munro et al. 2009). We identified similar concerns in planted stands in our study.

We found that plantings exhibited a lower richness of mid-story trees than remnant and regrowth stands, as well as very low densities of shrubs and tree recruits. This may represent a decision by landowners or managers to preferentially plant taller, hardier species (e.g. *Eucalyptus* species), or reflect biases in tubestock availability. Biased patterns of growth-form recovery have been commonly observed in active restoration of other vegetation types (Munro et al. 2009; Nichols et al. 2010; Garcia et al. 2016). Our results suggest that, when mature, vegetation structure in plantings may be less complex than remnant stands, which has been shown to reduce the maximum carbon that can be stored as woody biomass (Ford & Keeton 2017).

Despite showing similar biomass gains over time, planted plots contained much lower overall density of trees and shrubs than natural regrowth, linked to an eightfold reduction in the density of shrubs and trees weighing less than 20 kg. These plants had breast-height diameters of less than 10 cm (Table S2). This pattern may be due to several mechanisms. One potential mechanism is lack of recruitment, either because planted trees are still immature, remnant patches are too distant for any meaningful seed dispersal (Matlack 1994), or native seed banks have been exhausted by years of crop or pasture growth (e.g. Middleton 2003). Alternatively, livestock grazing under planted areas may have caused removal or mortality of shrub and tree recruits (Pettit & Froend 2008; Yates et al. 2008; Dorrough et al. 2011; Prober et al. 2011).

We do not have data to support or refute these mechanisms, but the consequences of low densities of shrubs and young trees are clear. If planted trees and shrubs die without replacement, the forest could collapse into a nonforested state, potentially one with low conservation and carbon value (Sherren et al. 2011; Lindenmayer et al. 2016). Modeling suggests that when this occurs, woodlands persist at most for 50 years (Sherren et al. 2011).

Provision of Conservation Benefits

The recovery of faunal communities in restored forests and woodlands has been linked to diversity in plant growth forms and food resources (Garcia et al. 2014). We found that uncleared remnant plots had higher overall richness than planted and regrowth stands. When examined as richness of specific functional groups, natural regrowth plots showed no systemic differences from remnant stands. In contrast, planted stands showed lower richness of two groups common in remnants stands: mid-story trees and fruit-bearing plants.

Mid-story trees contribute to vegetation cover, complexity, and heterogeneity, all of which may affect conservation value of these reforested areas (e.g. Jung et al. 2012). Reduction in habitat complexity can increase the chance of ecosystem collapse into other ecosystem types (Lindenmayer et al. 2016). Loss of tree cover could negatively affect animal species which rely on resources from trees and shrubs. This includes animals using reforested stands as habitat, or as corridors through a heavily cleared agricultural matrix. Diversity of food resources may encourage a diverse mix of animals to occupy and use restored stands, but we feel that potential ecosystem collapse from low plant recruitment and structural complexity may present a larger concern to the conservation potential of ecological restoration in our study region.

While we raise concerns about the permanence of planted reforestation in our study region, we cannot predict the future states of regrowing forests with our results alone. Indeed, restoration outcomes are notoriously variable (Suding 2011), and reliably predicting community attributes, especially functional and taxonomic composition, is a core challenge of restoration ecology (Brudvig 2017; Laughlin et al. 2017). Instead, we used community attributes to identify patterns that may result in reduced ecosystem functions and services over long timescales. This is not a replacement for systematic long-term monitoring, but our findings highlight the importance of considering the long-term implications of current restoration practices (Stanturf et al. 2014).

Our study also excludes some important restoration considerations. In particular, our study used surveyed forest stands that were already established, and active restoration sites were selected by landowners or restoration managers. Natural regrowth stands were only surveyed if they had persisted from land abandonment to time of survey, which is a positive site bias (Reid et al. 2018). This does not invalidate our results, as natural regrowth is only likely to be protected and managed where it occurs, and active management will be biased to locations where passive regeneration is unlikely or infeasible. As well as potential site bias, we also note that we lacked detailed management practice information for restored stands. This prevents us from drawing conclusions about the mechanisms leading to the ecological patterns we observed.

Our results are consistent with other studies showing that, where possible, regrowth offers cost-effective opportunities to deliver conservation and carbon benefits in agricultural regions (Crouzeilles et al. 2017; Meli et al. 2017; Jones et al. 2018). Where active reforestation is required, we suggest that recruitment and recruit survival is a high priority. This may be possible through exclusion of livestock, alternate weed control methods, and follow-up planting. In all, our results accord with Australian and international restoration guidelines. The most successful restoration action results in self-perpetuating ecosystems similar to reference sites (McDonald et al. 2016*a*; McDonald et al. 2016*b*). Current and future restoration efforts must consider potential long-term implications of project design to maximize both ecosystem function and community persistence.

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Data Accessibility

While raw data are held under data agreements, code and minimal data necessary to reproduce all results and figures are available at Zenodo (Staples 2019).

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Description of statistical models.
Figure S1. Distribution of sampled forest stands across the study region of South East Queensland, Australia.
Table S1. Count of forest stands across different land zones.
Table S2. Summary of size class distribution data for plants with diameter at breast height.
Table S3. Summary of size class distribution data for plants with diameter at 10 cm or 50 cm.
Table S4. Summary of generalized linear hypothesis tests comparing basic community attributes between forest stand categories.
Table S5. Mixed-effects model summary of comparison of plot biomass over time between regrowth and planted forest categories.
Table S6. Generalized additive mixed-effects model summary estimating probability of occurrence of plant size classes in four forest stand categories.
Table S7. Generalized additive mixed-effects model summary estimating mean density of plant size classes in four forest stand categories.
Table S8. Functional group membership of species in study region.
Table S9. Summary of generalized linear hypothesis test comparing seed dispersal functional group richness in regrowing forest to remnant plots.
Table S10. Summary of generalized-linear hypothesis test comparing growth and structure functional group richness in regrowing forest to remnant plots.

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