Functional trait representation differs between restoration plantings and mature tropical rainforest

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ABSTRACT

The planting and attempted restoration of tropical forest landscapes is increasing rapidly across the globe. Two limiting aspects of large-scale forest restoration are the demand for appropriate quantities of seeds and seedlings of native species, and the ability to facilitate succession in planted sites. Species functional traits such as seed type, tree size, germination time, and wood density may influence the quantity of seedlings that can be produced for restoration, and the potential of these seedlings to persist and facilitate site succession. Therefore, it is important to understand the species composition and functional trait representation of restoration plantings. We explored the species composition and functional trait representation of 846 restoration plantings in the Australian Wet Tropics containing > 465,000 seedlings from 599 species, using seedling supply records from six nurseries over a six year period (2012–2017). Despite restoration plantings in the Australian Wet Tropics containing an impressive number of species, just 52 species contributed over half of all individual seedlings. We found that species with small animal-dispersed seeds and low wood density were more abundant, on average, and had greater representation in restoration plantings than in mature rainforest. Despite this, we did not find evidence that restoration plantings had a diminished capacity to grow tall or sequester carbon as there was no significant difference in the relative abundance of tall tree species or species with high wood density. Small seeded and fast growing species may be cheaper to produce in nurseries and may accelerate site succession as these characteristics are associated with pioneer and early successional species, however these traits are also associated with higher mortality rates. Understanding how functional trait representation influences the success of restoration plantings will require further insight into temporal aspects of site succession.

1. Introduction

Deforestation has resulted in substantial loss and fragmentation of the world's tropical forests (Hansen et al., 2013; Taubert et al., 2018), reducing their ability to support biodiversity (Allnutt et al., 2008) and provide ecosystem services (Portela & Rademacher, 2001; Chazdon, 2008). Loss and fragmentation of tropical forests reduce population sizes (Brook et al., 2003; Ewers & Didham, 2006), gene flow (Hamilton, 1999; Ewers & Didham, 2006), and dispersal potential of both flora and fauna (Laurance et al., 2004; Hadley & Betts, 2009; Cole et al., 2011), exacerbating their vulnerability under changing climatic conditions and

limiting migration to more suitable regions. Additionally, deforestation substantially impacts many ecosystem services provided by tropical forests including carbon cycling (Baccini et al., 2017), water cycling (Webb et al., 2005; Mahmood et al., 2013; Schlesinger & Jasechko, 2014), temperature regulation (Mahmood et al., 2013), and soil maintenance (Hartanto et al., 2003). In this context, ecological restoration is a useful tool for expanding and connecting habitat patches in fragmented landscapes to retain biodiversity value and provision of ecosystem services (DeFries et al., 2010; Hansen et al., 2013; Taubert et al., 2018).

Numerous global initiatives, such as the Bonn Challenge, recognize

the importance of tropical forest restoration and are establishing pledges to restore 350 million hectares by 2030 (Chazdon et al., 2017; Dave et al., 2019). The sheer scale of plant material required to meet these initiatives is daunting. For example restoration projects in India and Ethiopia in 2019, planted 220 million trees and 350 million trees, respectively. However, it is not only the quantity of plant production that is important, but what species are selected and the implications this may have on plant survival, site succession, and the future ecological function of these restored forests. For example, Brancalion et al. (2018) compared the functional traits of planted and mature Atlantic forests in Brazil, and found that species with small animal-dispersed or wind-dispersed seeds were far more abundant in planted forests than in mature rainforest. Although species with these characteristics are common in naturally recovering forests (Goosem et al., 2016), planting millions of trees with similar traits could have important implications for successional trajectories because it may "inadvertently homogenize" plant communities across the landscape (Palma & Laurance, 2015).

Despite the potential for functional trait representation to influence recovery trajectories and biodiversity in tropical forest restoration, studies examining this are rare. After almost three decades of restoration activity in the Australian Wet Tropics, no studies have yet explored the ecological implications of planting composition. The aim of this study was to assess the relative abundance of species used in restoration plantings for both individual plantings, and the pool of all restoration plantings. Additionally, we aimed to compare species abundance relative to functional traits with direct influences on ecological function of restoration plantings, and the relative representation of these functional traits between restoration plantings and mature rainforest. The functional traits of seed type (size and dispersal mode), maximum height, wood density, and germination time were selected for comparison and binned into discreet functional groups based on previous ecological literature and available data. Two key questions were formulated: (1) How does seedling abundance at the level of individual plantings, and the pool of restoration plantings, differ between species and functional groups? (2) Does the relative representation of functional groups differ between restoration plantings and mature forest? We expected that species from functional groups associated with increased seed and seedling production (small seeds, shorter germination times, low wood density) would have higher abundance in restoration plantings, and that this reduction in the relative abundance of large-seeded, slow-growing species would result in a lower abundance of large tree species.

2. Methods

2.1. Study area

The Wet Tropics biogeographic region of north-eastern Australia, henceforth referred to as the 'Australian Wet Tropics', encompasses an area of ~ 900,000 ha of tropical forest (Kanowski et al., 2003), that spans 450 km of north-eastern Australia (Fig. 1). The region represents an area of significant floral and faunal biodiversity with a high level of endemism (Williams et al., 2009), and is considered an area of Outstanding Universal Value (UNESCO, n.d.). To date, the Australian Wet Tropics has experienced significant deforestation and fragmentation, including forest loss of around 20% since 1880 (Kanowski et al., 2003). Loss and fragmentation of habitat is a key threat to many of the regions species including the Southern Cassowary (Westcott et al., 2014), a keystone species that disperses many rainforest plant species (Bradford & Westcott, 2011). Additionally, the Australian Wet Tropics contains many important climate refugia (Reside et al., 2013), and restoration of much of the region will be crucial for the persistence of numerous species under climate change (Maxwell et al., 2019).

With help from government sponsorship schemes, restoration plantings are carried out on private and public land in the region by restoration nurseries and more than forty different landcare,

conservation, catchment management, landowners, and school-based groups (Catterall & Harrison, 2006). While large-scale farm forestry projects exist, individual restoration plantings are typically small, diverse plantings on land previously cleared for agriculture, with the aim of filling gaps, increasing remnant area, or establishing habitat connectivity (Catterall & Harrison, 2006). The majority of these restoration plantings are provided with plants from government and community supported nurseries.

### 2.2. Restoration seedlings and reference forest

Our study explored the species composition and functional traits of 465,400 seedlings produced over a six year period (2012–2017) from five government funded and/or not-for-profit nurseries (and a sixth nursery from 2017 to 2018). We examined 846 records of seedlings supplied by the nurseries for restoration plantings conducted over the study period. A total of 599 plant species were produced by the nurseries, of which 515 species were trees. Only tree species, which made up 94% of individual seedlings, are included in the following analyses. The seedling supply records examined in this study contained an average of 530 seedlings ($\mu = 530.28$, $\sigma = 629.33$) from 27 species ($\mu = 27.67$, $\sigma = 23.12$). Additionally, we estimated the regional rainforest species pool and determined its functional composition using 20 permanent tree plots in mature rainforest sites that span latitudinal and elevational gradients (Bradford et al., 2014; Tng et al., 2016). The mature rainforest plots included 18 0.5 ha plots and 2 1.0 ha plots, with each plot containing an average of 582 stems $\geq$ 10 cm diameter at breast height ($\mu = 582.80$, $\sigma = 135.81$). In total 11,256 adult trees from 447 species were identified. While individual restoration plantings often consisted of seedlings from multiple supply records, we treated each supply record as an individual study unit as supply records contained a similar number of seedlings as the mature rainforest plots contained adult trees.

2.3. Functional trait selection

We examined species functional traits that were important for both nursery seedling production, and the success and ecological function of restoration plantings. Seed size, dispersal syndrome, and tree size (here measured as maximum height) have been shown to influence seed production (Greene & Johnson, 1994; Moles, et al., 2004). As wood density is negatively correlated with seedling growth rates (Charles, et al., 2018) it, along with germination time, influences seedling production rate. Additionally, seed size and wood density are both negatively correlated with growth and mortality rates in trees (Nascimento, et al., 2005; Poorter, et al., 2008; Chave et al., 2009; Charles et al., 2017). Seed dispersal syndrome and tree size contribute to ecosystem function of restoration plantings through the provision of fruit resources and habitat. Maximum height was also used as a surrogate for carbon storage potential as it has been shown to be a strong positive correlate of aboveground biomass (AGB) (Feldpausch et al., 2011; Feldpausch et al., 2012), and sufficient data to estimate maximal aboveground biomass following Brancalion et al. (2018) was available for only 44.27% of species, making up just 51.29% of individuals.

2.4. Functional trait data

We collated a functional trait database for the 599 species produced in nurseries and the 447 tree species present in mature forest reference plots from published sources (Zanne et al., 2009; Kanowski et al., 2010; Hyland et al., 2010; Cooper & Cooper, 2013) and nursery records. Species germination times for 209 plant species were provided by Queensland Parks and Wildlife Service Lake Eacham Nursery. These species were commonly produced in nurseries and comprised 41% of produced species and 74% of produced seedlings. Seed size, seed dispersal, and maximum height estimates were available for all tree
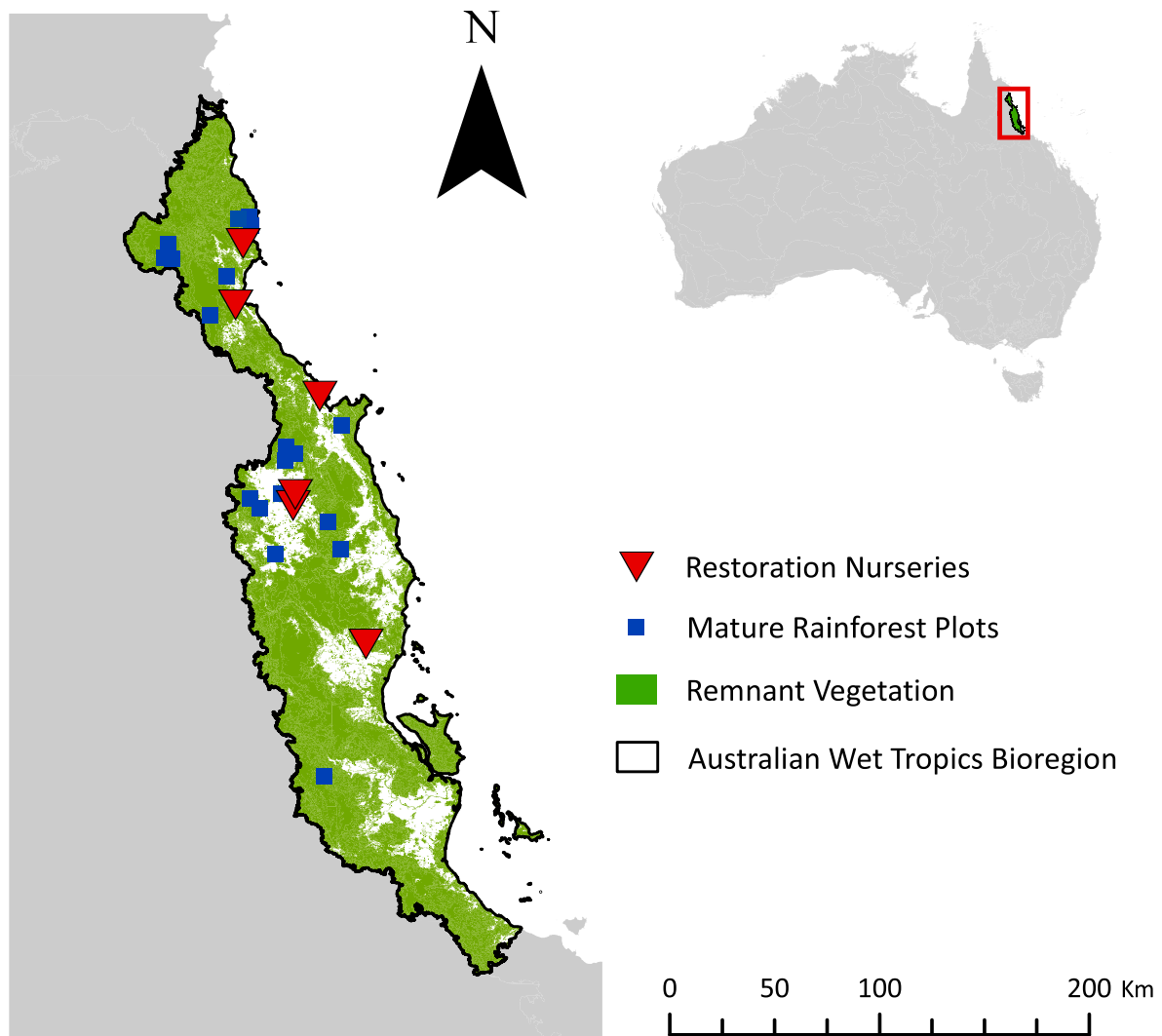
Fig. 1. The distribution of remnant vegetation in the Australian Wet Tropics and the location of nurseries and mature rainforest plots that were examined in this study.

species used in restoration. Wood density was available for 90% of species found in seedling supply records, which contributed over 99% of individuals. Wood density measures were available for 94% of individuals present in mature forest plots, and we were able to confidently estimate the wood density class for a further 3%, resulting in wood density class information for 97% of individuals. We considered the estimated wood density class of a species to be confident when the mean plus or minus the standard deviation of wood density values for conspecifics fell within a single wood density class. Functional traits were binned into discrete classes, based on previous literature where possible, to preserve relative interspecific differences while reducing the influence of error and uncertainty when reporting only the mean value for traits that experience intraspecific variation between individuals and ecotypes (QPWS, unpublished data; Sungpalee et al., 2009; Lönnberg and Eriksson, 2013). Species with animal-dispersed seeds were categorized in the size classes used by Brancalion et al. (2018): as small- (width $<$ 6 mm), medium- (6 mm $<$ width $<$ 12 mm) or large-seeded (width $>$ 12 mm); and seeds with abiotic dispersal were categorized as either wind-dispersed or other (gravity dispersed, water dispersed). Species were categorized by their maximum heights using classes modified from Korning & Balslev (1994) as either understory trees (height $<$ 20 m), subcanopy trees (20 m $<$ height $<$ 30 m), canopy trees (30 m $<$ height $<$ 40 m) or emergent trees (height $>$ 40 m). Additionally, species were

categorized by wood density using classes from Kearnside (1998) as having low density (density $<$ 0.5 g cm^{-3}), medium density (0.5 g cm^{-3} $<$ density $<$ 0.7 g cm^{-3}), or high density (density $>$ 0.7 g cm^{-3}). Finally, species were categorized by their mean time till 50% of seeds were germinated (GD50) as taking less than one month, between one and two months, or more than two months. Species were binned by aforementioned germination times as previous literature and the unpublished data used in this study indicate that the majority of tropical tree species take between 15 and 60 days to germinate (Norden et al., 2009; QPWS, unpublished data).

2.5. Analysis

We compared the relationship between functional trait groups and species abundance using a Negative Binomial GLM (log link) with seed type, maximum height class, germination time, and wood density included as fixed effects. We utilized a GLM to test the differences in abundance as all functional traits influenced a species' abundance simultaneously and species' abundances were non-normally distributed. To account for substantial variation in landscape-level species abundance, both between and within functional trait groups; and the simultaneous influence of multiple functional traits, estimated marginal means were reported for each functional trait group. Comparisons of the mean abundance of groups for each functional trait were conducted
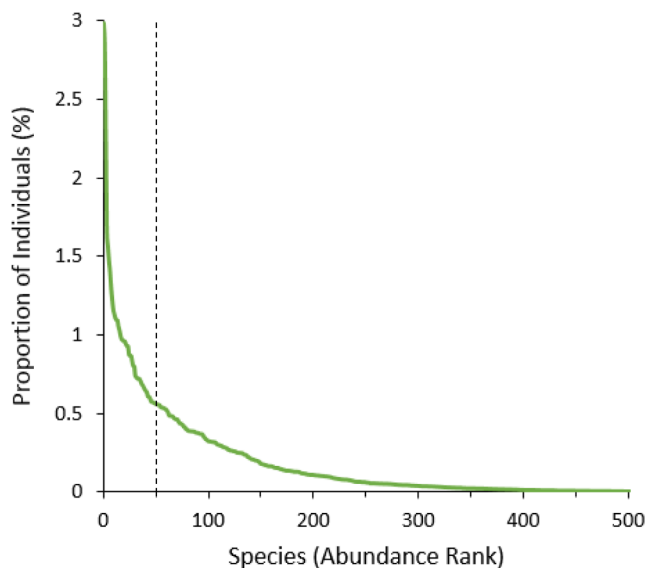
Fig. 2. A rank abundance curve of all tree species (n = 515 species) used in rainforest restoration plantings in the Australian Wet Tropics from 2012 to 2016. The most abundantly planted species (n = 52 spp.) account for > 50% of plants and are indicated by the dashed line.

using sequential Bonferroni pairwise tests. Additionally, we compared relative abundance of functional groups in mature rainforest plots with a subsample of the seedling supply records (n = 124). Seedling supply records were subsampled to reduce bias potentially introduced by comparing plots with substantially different sample sizes. The subsample included only seedling supply records containing between 427 and 737 seedlings (within one standard deviation of the mean adult tree number in mature rainforest plots). Comparisons of the relative abundance of species with different seed types, maximum heights, and wood densities between seedling supply records and mature rainforest were conducted using Mann-Whitney U tests.

3. Results

3.1. Species diversity and abundance

Over a six year period, rainforest restoration in the Australian Wet Tropics incorporated a highly diverse selection of 515 tree species, making up 435,435 individual seedlings. The abundance of species produced in nurseries was extremely uneven (Fig. 2) with the 52 most abundant species comprising > 50% of all individual plants produced (the 20 most abundant species are reported in Table A1). Hence, the overwhelming majority of species had low abundances across the pool of seedling records, with the 312 least abundant species combined contributing only 10% of individuals. Although a percentage of species achieved high abundance when pooling all seedling supply records, mean abundance at the scale of individual records was relatively uniform, with a species' total abundance having only a minor influence (Fig. A.1; Nagelkerke Pseudo-R^2 = 0.14, p < 0.001).

3.2. Functional trait abundance

For restoration species, seed type, germination time, and wood density were significantly correlated with abundance; however, height class was not (Fig. 3). Tree species with small animal-dispersed seeds had higher mean abundance than large-seeded animal-dispersed species, and the highest total abundance – making up nearly half of all seedlings within the records (Fig. 3a). When accounting for other functional traits, there was no significant difference in mean abundance between trees of differing heights (Fig. 3b). Despite this, canopy trees were the most speciose life

form, and hence had the greatest proportional representation in seedling supply records. Species with high wood density had significantly lower mean abundance than species with low and medium wood densities (Fig. 3d). Species with germination times of less than one month had significantly higher abundances than species with germination times longer than 2 months or species where germination time data was not available (Fig. 3c). Almost half of the species included in seedling records (n = 292) had no data on germination time; however these species contributed only 26% of all individuals produced.

3.3. Functional trait representation

When comparing the composition of seedling records to mature forests with respect to seed size and dispersal mode we found that tree species with small animal-dispersed seeds had substantially higher abundances in seedling supply records than in mature forests (Fig. 4A). Consequently, large-seeded animal-dispersed species were relatively lower in abundance compared to mature forests. Conversely, tree species with medium-sized animal-dispersed seeds, wind-dispersed seeds, or species with other dispersal modes did not differ in their relative abundances between seedling supply records and mature forests. To ensure subsampling of seedling supply records did not affect the comparisons we also compared the subsample of seedling supply records to the entire pool of records. The subsample of seedling supply records showed no significant difference in the relative abundance of any seed types when compared to the entire pool (Fig. A.2A).

To assess potential vegetation structure and carbon stocking potential of restoration plantings we compared representation of species from different tree height classes and wood density classes between seedlings in the supply records and adult trees in mature rainforest. We did not find a difference in relative abundances of any tree height classes between seedling supply records and the mature rainforest plots (Fig. 4B). As mature rainforest plots only recorded trees with a DBH ≥ 10 cm, understory trees may be underrepresented in this comparison, however it would likely not impact the comparison as non-woody species and woody species with a maximum height of < 5 m were excluded from analysis of seedling supply records. Additionally, while we found that species with low wood density had greater relative representation, we did not find any difference between the relative representation of species with medium or high wood densities between restoration seedling records and mature forest plots (Fig. 4C). However, a greater proportion of individuals in mature rainforest plots did not have available data on wood density, which introduces a degree of uncertainty to this result. The subsample of seedling supply records used as a comparison to mature rainforest plots had greater relative representation of sub-canopy trees than the total pool of records, but did not differ in any other height class (Fig. A.2A), or for any wood density classes (Fig. A.2B).

4. Discussion

We found that seedling supply records for plantings in the Australian Wet Tropics to be some of the most speciose when compared to previous studies, in Australia and globally, at the level of both individual plantings (Palma & Laurance, 2015) and across the entire region (Brancalion et al., 2018). Relative abundance of tree species was highly variable, however, species possessing functional traits associated with greater seed supply and faster seedling production (such as smaller seeds, shorter germination times and lower wood density) were, on average, more abundant. When compared to mature rainforest, we observed that tree plantings in the region had greater abundances of small-seeded animal-dispersed species, however, this did not result in a lack of tree species capable of reaching large sizes or tree species with high wood densities.

In line with our findings, Brancalion et al. (2018) found that small-seeded species were more abundant in restoration plantings in the Brazilian Atlantic Forest despite differences in restoration cost structures between the two regions. For restoration plantings in the Australian Wet
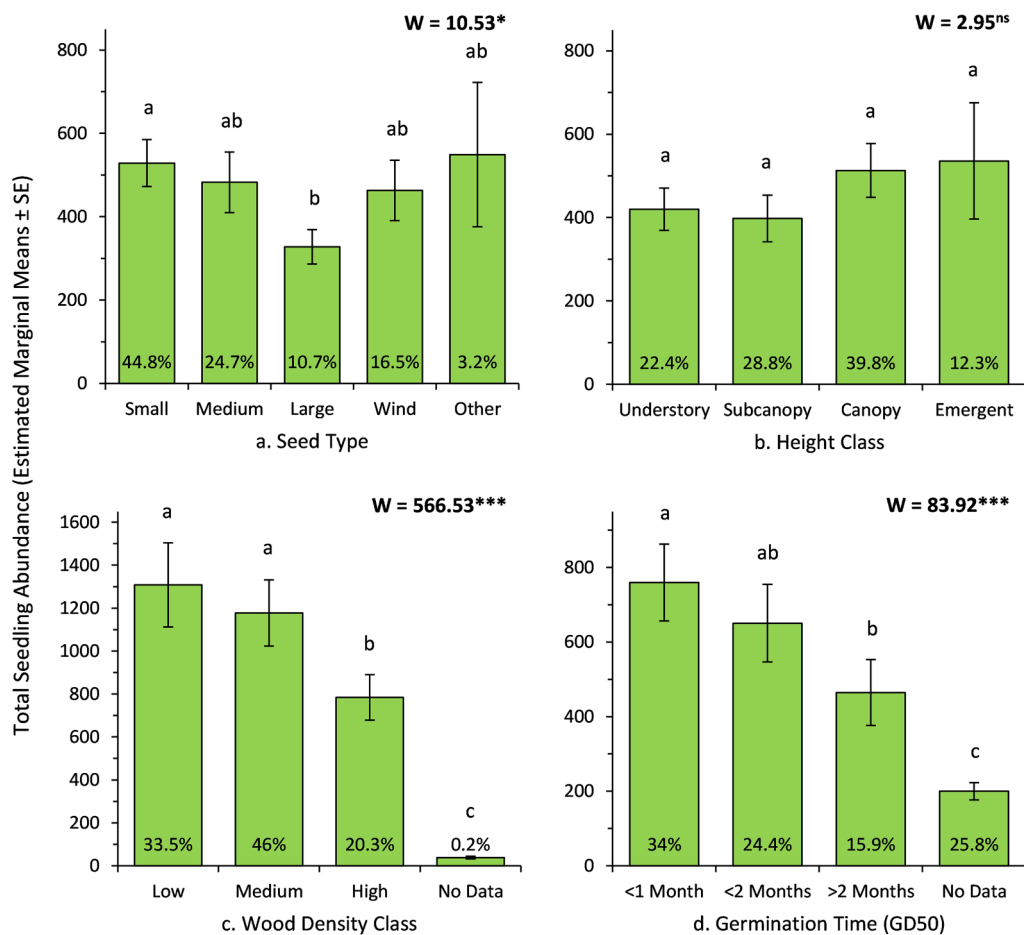
Fig. 3. A comparison of the relative abundance of seedlings produced in nurseries and their functional traits, from the Australian Wet Tropics in the years 2012–2016. Seedling supply records show that most plants produced for restoration have: (A) small- (diameter < 6 mm) to medium-sized (6 mm < diameter < 12 mm) animal-dispersed seeds, (B) potentially grow to forest canopy (20 m < height < 30 m) tree heights, (C) have low (< 0.5 g cm3) to medium wood density (< 0.7 g m3) and (D) germinate within 2 months from collection. Estimated Marginal Means were calculated from abundance data using a Negative Binomial GLM with the Wald Chi-Square stat (W), significance is based on bonferroni pairwise tests * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ns = non-significant.
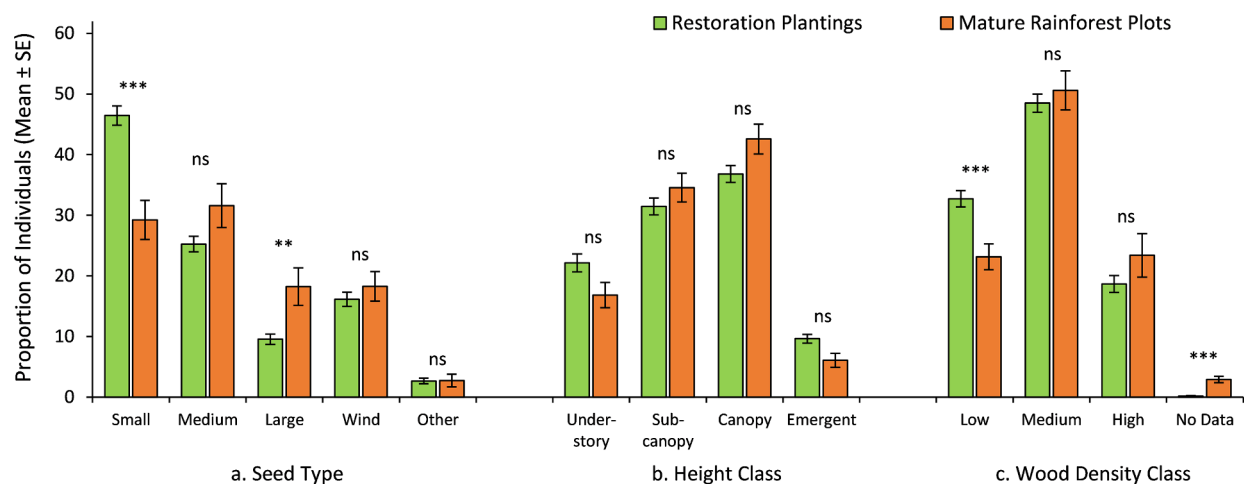
Fig. 4. A comparison of the representation of functional groups in seedlings provided for restoration plantings and trees in mature rainforest plots in the Australian Wet Tropics. Restoration plantings have significantly more individuals with small seeds and lower wood density compared to mature forests. We used Mann-Whitney U tests to examine proportional data on seedlings generated from a subsample of nursery supply records from 2012 to 2016 (n = 124) and mature forest communities from 20 long-term forest plots (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ns = non-significant).

Tropics, the initial cost of obtaining trees for restoration is generally cheaper than the site maintenance required post-planting (Hunt, 2008). Therefore, species that perform well in exposed early site conditions and have high rates of growth and canopy formation would provide an economic advantage by reducing the duration and cost of site maintenance. Conversely, for restoration plantings in the Brazilian Atlantic forest, the implementation phase of projects is typically more expensive than the

maintenance phase, and inputs more expensive than labour and machinery costs (Brancalion et al., 2019). In this instance, species would be favoured when costs of seed sourcing and seedling production are lower (Brancalion et al., 2018). Despite these differences in cost structures, restoration plantings in both the Brazilian Atlantic Forest and the Australian Wet Tropics had a greater relative abundance of small-seeded species when compared to mature rainforest, suggesting that this may be a general

trend across large-scale forest restoration programs.

The higher abundance of small-seeded species in restoration plantings compared to mature forests is a pattern that has been observed previously in secondary forests in the same region (Goosem et al., 2016). This suggests these plantings may follow a similar successional trajectory to secondary forests; however, the plantings also include medium- and large-seeded species which are rare in secondary forests (Goosem et al., 2016). The inclusion of medium- and large-seeded species, and the abundance of species capable of reaching large sizes may allow restoration plantings to kick-start succession. In fact, previous work has found that restoration plantings in the Australian Wet Tropics grew faster, accumulated more biomass, and accrued more native species than natural regrowth in the same region (Shoo et al., 2015; Shoo et al., 2017). Contrary to our findings, plantings in the Brazilian Atlantic Forest, which also had a greater abundance of small-seeded species, experienced a reduction in large trees relative to mature rainforest (Brancalion et al., 2018). This may be due to previously noted differences in cost incentives in restoration. Alternatively, previous work has shown that replacement of large-seeded species with small-seeded and abiotically-dispersed species would reduce the abundance of large trees in African and Neotropical rainforests, but not in the Australian Wet Tropics (Osuri et al., 2016).

Although restoration plantings in the Australian Wet Tropics did not lack large trees or trees with high wood densities, quantifying the potential biomass accumulation of restoration plantings using maximum height or carbon-stocking potential applies a static measure to a dynamic system. Many large-seeded, animal-dispersed species have slow life history strategies and may take decades or centuries to meet their carbon stocking potential, while small-seeded species may take substantially less time (Moles & Westoby, 2006). Previous work has shown that small-seeded species and species with lower wood density generally have higher growth rates in the early stages of restoration (Erskine et al., 2005; Nascimento, et al., 2005; Poorter, et al., 2008; Coelho et al., 2016; Charles et al., 2017), and can have greater carbon storage than slow-growing species for decades after the initial planting (Shimamoto et al., 2014). Higher growth rates also allow these species to compete with weedy species that often dominate young restoration and early successional sites. Additionally, individual trees in the first generation of a restoration planting are unlikely to reach their maximum size due to environmental constraints, such as soil quality and disturbance, rather than functional traits (Osunkoya et al., 2007; Kellner & Asner, 2009). In fact, Crouzeilles et al. (2016) found that restored forests were on average half the height of, and had half the biomass of, comparable mature forests.

The use of carbon stocking potential or wood density as a metric also assumes a static site composition, which does not take into account colonization and succession dynamics, or differential reproduction and mortality rates of species. Small-seeded species and species with lower wood density tend to have improved survival in exposed early-site conditions (Gross, 1984; van Ulft, 2004; Erskine et al., 2005; Coelho et al. 2016), reproduce earlier (Moles & Westoby, 2006), provide resources that attract more species of frugivores (Westcott et al., 2008), and have higher recruitment (van Breugel et al., 2007). This suggests that these faster-growing species will increase in abundance relative to slower growing species, and hence contribute more to ecological function and carbon stocking in the early stages of site development. Conversely, as species with small seeds and lower wood density tend to have higher lifetime mortality rates (Nascimento et al., 2005; Poorter et al., 2008; Chave et al., 2009), evidence suggests that restoration plantings will follow typical forest succession patterns, with large seeded species becoming more abundant as the site ages (Tabarelli and Peres, 2002; Goosem et al., 2016). However, the time frame over which succession may occur, and the likelihood of successfully achieving site succession, is influenced by numerous factors unrelated to initial species composition.

With climate change shifting the geographical extent of, and human impacts reducing the size and connectivity of viable habitat for countless species, creating ecologically functional habitat in short timeframes should be the priority. Evaluating the species composition of young restoration sites by some potential end-point ignores the dynamic and time-dependent nature of the ecological processes being reinstated. Despite no previously studied forest restoration site returning fully to reference conditions with regards to habitat structure (Crouzeilles et al., 2016) or biodiversity value (Catterall et al., 2012; Crouzeilles et al., 2016), some ecological processes can be reinstated in relatively short time frames. Processes such as facilitation of faunal dispersal (Paetkau et al., 2009), provision of fruit resources, and seed dispersal (Wunderle Jr., 1997; Reid et al., 2015) for example, may be reinstated in a few years. Other important processes such as soil stabilisation (Cao et al., 2017), and canopy formation and weed suppression (de Souza & Batista, 2004) may also be achieved in relatively short timeframes. While weed suppression can be crucial to restoration success (Holl, 1998; Holl et al., 2000; Standish et al., 2001) it is less attractive to volunteers (Galabuzi et al., 2014), requires long-term commitments (Tischew et al., 2010; Holl & Aide, 2011), and may be a substantial cost to practitioners (Hunt, 2008). As such, a species ability to suppress weed growth and facilitate succession (through fast growth, canopy formation, and production of soil organic matter for example) may be a more important metric for determining value to restoration plantings than maximum size or carbon stocking potential.

To date, the majority of studies on forest restoration have been plot-based with a limited capacity to inform land managers of the broader functional and ecological role of the restored area (Palma & Laurance, 2015). This study along with Brancalion et al. (2018) makes an important contribution by exploring the functional role of restoration plantings at the landscape scale. For example, very few species achieved high abundances in individual restoration plantings (Fig. A.1), however when pooling the seedling supply records across the whole bioregion, a small percentage of species were highly abundant. This relative dominance of a small percentage of species in restoration plantings suggests that despite high species richness, a few species may contribute disproportionately to success and ecological function of restoration plantings. Therefore, understanding the growth and survival of a small proportion of species can give information on long-term dynamics of restored forests, even when species richness is high. While the majority of species contributed only a small percentage of seedlings in restoration plantings at the landscape scale, they may contribute to beta diversity, provide functional redundancy, and promote landscape-level resilience to environmental changes (Fonseca & Ganade, 2001).

5. Conclusion

Species with functional traits promoting greater seedling production and faster growth (small seeds, shorter germination times, lower wood density) were substantially more abundant when analysing seedling supply records for restoration across the Australian Wet Tropics. This resulted in restoration plantings having a greater abundance of seedlings from small-seeded animal-dispersed species than was present in adult trees of mature rainforest within the same bioregion. However, this did not result in a reduction in abundance of large tree species or species with higher wood density. In restoration, greater seed supply and faster growth reduce costs associated with both nursery seedling production and site maintenance in restoration plantings. However, these traits tend to be associated with higher lifetime mortality rates, leading to uncertainties in the successional trajectory and carbon stocking of restoration plantings. Evaluation of the true costs of different species and functional groups in restoration plantings will require better understanding of growth and mortality rates, and ability to facilitate site succession.

CRediT authorship contribution statement

Jayden E. Engert: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing -

Acknowledgements

Declaration of Competing Interest

None.

Appendix A

See Figs. A.1 and A.2 and Table A1

Fig. A.1. A comparison between a species' total seedling abundance across all plantings and the mean abundance in a single planting. Regression analysis was conducted using a Gamma GLM (Identity link) with Nagelkerke's pseudo R^2 reported.
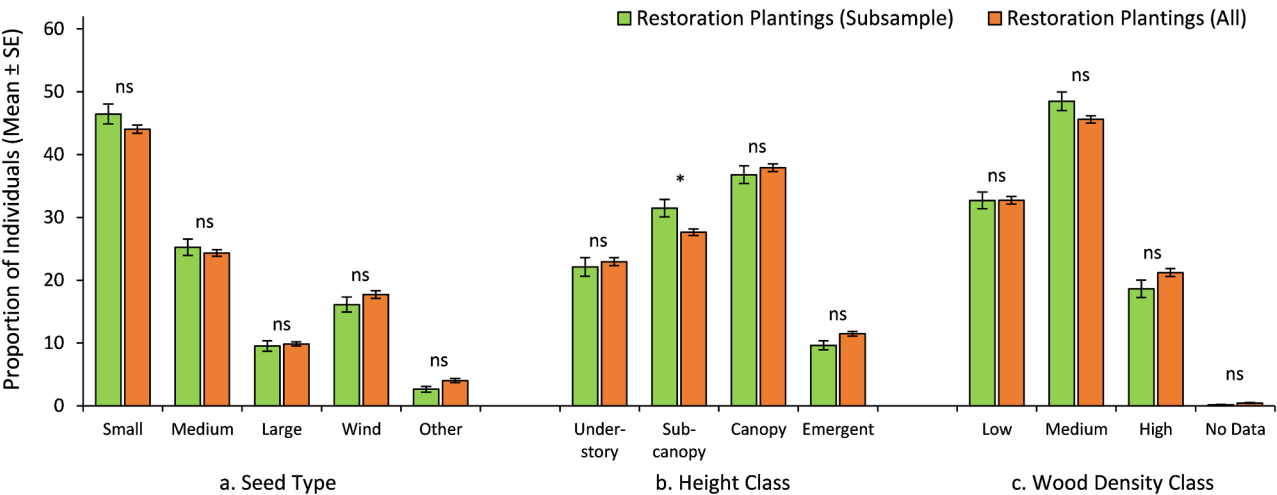
Fig. A.2. A comparison of the representation of functional groups in seedlings provided for restoration plantings from the subsample of supply records and the total pool of supply records. The subsample of nursery records contained more subcanopy tree species than the pool of records, but no other significant difference was found. We used Mann-Whitney U tests to examine proportional data on seedlings generated from a subsample of nursery supply records from 2012 to 2016 (n = 124) and the total pool of nursery supply records (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ns = non-significant).

Table A1

The 20 most abundant species utilized in rainforest restoration in the Australian Wet Tropics. Species with small, medium, and large seed types are species with animal-dispersed seeds.

Binomial	Family	No. of Seedlings	No. of Supply Records	Seed Type	Height Class	Germination Time	Wood Density
Nauclea orientalis F.Muell.	Rubiaceae	12,845	180	Small	Canopy	< 1 Month	Low
Homalanthus novoguineensis (Warb.) Lauterb. & K.Schum.	Euphorbiaceae	12,176	375	Small	Sub-canopy	< 2 Months	Low
Syzygium tierneyanum (F.Muell.) T.G.Hartley & L.M.Perry	Myrtaceae	9599	160	Medium	Sub-canopy	< 1 Month	Medium
Chionanthus ramiflorus Roxb.	Oleaceae	7070	261	Medium	Sub-canopy	< 2 Months	Medium
Melicope elleryana (F.Muell.) T.G.Hartley	Rutaceae	6690	321	Small	Canopy	> 2 Months	Low
Elaeocarpus grandis F.Muell.	Elaeocarpaceae	6319	327	Medium	Canopy	No Data	Low
Melaleuca leucadendra (L.) L.	Myrtaceae	6009	80	Wind	Emergent	No Data	Medium
Alstonia scholaris (L.) R.Br.	Apocynaceae	5565	289	Wind	Emergent	< 1 Month	Low
Atractocarpus fitzalanii subsp. *fitzalanii* (F.Muell.) Puttock	Rubiaceae	5257	176	Medium	Sub-canopy	> 2 Months	High
Ficus congesta var. *congesta* Roxb.	Moraceae	4998	222	Small	Understory	< 1 Month	Low
Cryptocarya triplinervis var. *pubens* B.Hyland	Lauraceae	4870	234	Medium	Understory	< 1 Month	Medium
Terminalia microcarpa Decne.	Combretaceae	4752	184	Small	Emergent	< 1 Month	Medium
Flindersia brayleyana F.Muell.	Rutaceae	4709	231	Wind	Canopy	< 1 Month	Low
Guioa acutifolia Radlk.	Sapindaceae	4693	211	Small	Sub-canopy	< 1 Month	Medium
Alphitonia petriei Braid & C.T.White	Rhamnaceae	4518	164	Small	Emergent	< 2 Months	Low
Neolitsea dealbata (R.Br.) Merr.	Lauraceae	4413	226	Medium	Understory	> 2 Months	Medium
Castanospermum australe A.Cunn. ex Mudie	Fabaceae	4268	205	Large	Canopy	> 2 Months	Medium
Syzygium hemilamprum subsp. *hemilamprum* (F.Muell.) Craven & Biffin	Myrtaceae	4175	133	Medium	Canopy	No Data	Medium
Castanospora alphandii (F.Muell.) F.Muell.	Sapindaceae	4152	237	Large	Emergent	< 2 Months	Medium
Syzygium australe (H.L.Wendl. ex Link) B.Hyland	Myrtaceae	4124	171	Medium	Sub-canopy	< 2 Months	Medium

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