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Title: The role of topography and plant functional traits in determining tropical reforestation success

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ABSTRACT

1. Early establishment and sapling growth is a key phase in ensuring cost-effective reforestation success in relation to biodiversity outcomes. Therefore species selection must consider the interaction between plant functional traits and the often-challenging and heterogeneous biophysical environment of degraded landscapes.

2. In this study, we examine how microtopography (slope) results in spatial heterogeneity of soil nutrients, especially phosphorus (P) in a degraded tropical pasture landscape in Queensland, Australia. We then explore how this small-scale heterogeneity influences the growth of two native tree species, *Cardwellia (C.) sublimis* (Proteaceae) and *Flindersia (F.) brayleyana* (Rutaceae), which differ in key nutrient-acquisition strategies.

3. The proteaceous *C. sublimis* was found to be buffered from possible P limitation in degraded soils due to its effective P acquisition by cluster roots. In contrast to *C. sublimis*, which showed no difference in growth after 5 years across a range of soil conditions, *F. brayleyana* was found to be highly responsive to soil conditions with increased growth in low-slope, higher P availability areas. The ability of *F. brayleyana* to take advantage of high soil P levels, including the development of leaves with higher P concentrations, resulted in an apparent switch in competitive fitness between these two species across a landscape gradient.

4. *Synthesis and applications.* In a detailed study of a landscape reforestation experiment in North Queensland, Australia, we demonstrate that site edaphic factors can vary within tens of meters due to topographic relief, and that species respond differently to these conditions. We therefore show the need to consider both the spatial heterogeneity of edaphic factors and the belowground functional traits of potential reforestation species when planning reforestation programs.

Keywords: *Cardwellia sublimis*, cluster roots, edaphic factors, *Flindersia brayleyana*, functional traits, organic matter, phosphorus, rainforest, slope, topography

Introduction

Landscape restoration of degraded and deforested land offers a critical contribution to addressing the global challenges of climate change and biodiversity decline. In the Anthropocene there has been a dramatic decline in forest cover (Malhi et al. 2014), with a net loss of 3.1% over the last 25 years (MacDicken 2015, FAO 2016). Moreover, this net decline obscures a potentially greater concern - the lack of functional equivalency between primary forest being lost and areas undergoing either natural or assisted forest regeneration. This lack of functional equivalency may slow the convergence of restored forests towards the primary condition, and may result in the emergence of alternative stable states and the arrested succession of 'restored' forest landscapes (Sarmiento 1997, Zanne and Chapman 2001, Veldman et al. 2015).

The development of best practice guidelines for the restoration of species-rich tropical forests presents a unique challenge for land-managers. The planting of mixed-native species provides direct benefits for biodiversity, forest products and bush foods (Wishnie et al. 2007, Nguyen et al. 2014), in addition to increasing carbon storage (Díaz et al. 2009, Kanowski and Catterall. 2010). Similarly, the use of diverse plantings adds complexity and community resilience to environmental perturbations, such as future climate change (Kanowski et al. 2008, Paquette and Messier 2010, Nguyen et al. 2014). However, given the practical limitations of native propagule collection and establishment, untested growth and survival characteristics of most species (Plath et al. 2011), as well as economic barriers to the use of mixed-species plantations, the use of mixed-native species comprises only a fraction of current reforestation programs (Nichols et al. 2006, Rodrigues et al. 2009, Paquette and Messier 2010). Those programs that do implement mixed-native plantings often select species from across a broad range of successional stages to rapidly provide more favourable conditions for natural recruitment, and restore functional diversity and thereby ecological

function (Redondo-Brenes 2007, Rodrigues et al. 2009, Rodrigues et al. 2011). This approach has further developed to include the targeted selection of local species, populations, and germplasm derived from remnant forests close to reforestation areas, to maintain the floristic and genetic diversity that are key elements of locally adapted natural forest systems (Lesica and Allendorf 1999).

The conditions inherent to many reforestation sites (e.g. poor soil due to past management, high sunlight exposure, competition from grasses or exotic species) represent a distinctly different biophysical environment compared with mature forest stands. Historically many mixed-native plantings have failed to thrive (in the case of plantations) or did not result in self-perpetuating forests, due to the selected species failing to grow under these challenging conditions (Redondo-Brenes 2007, Rodrigues et al. 2009).

Consideration of plant-functional traits can provide a conceptual framework to help guide species selection to better ensure reforestation success. Functional traits are characteristics that group species according to their resource use and life-history strategy, and often represent inherent trade-offs between fast growth and low mortality in resource-poor environments (Wright et al. 2010). However, identifying species (or trait combinations) capable of growth and survival in a degraded landscape is not as simple as extrapolating from their performance in mature forests (Ruiz-Jaen and Potvin 2011, Martínez-Garza et al. 2013). Determining the functional traits that predict vital growth rates within the conditions inherent to reforestation programs, will help inform successful species selection (Paine et al. 2015, Martínez-Garza et al. 2016).

Nutrient-acquisition strategies and the morphological and biochemical adaptations of roots (e.g. mycorrhizal associations, N₂ fixation and proteoid or cluster roots) represent functional traits that may be especially important for determining a species' ability to

establish in degraded soils. The advantages of microbial inoculation of the rhizosphere (Dixon et al. 1984, Chanway 1997), and the inclusion of N₂-fixing species in tropical reforestation efforts (Batterman et al. 2013) are well established. However, in general, little consideration has been given to plant root adaptations to low soil phosphorus (P) availability. This is despite P being thought to limit plant growth in strongly weathered tropical (Vitousek and Sanford 1986, Hedin et al. 2003) and degraded agricultural soils (Nesper et al. 2015), which are often the focus of reforestation programs.

Topographic relief in the landscape has profound implications for soil formation and soil nutrient availability (Jenny 1941, Pennock et al. 1987). In tropical ecosystems, topographic relief results in striking spatial heterogeneity of soil nutrients (Tiessen et al. 1994a, Townsend et al. 2008, Chadwick and Asner 2016), and this heterogeneity influences the distribution of tree species at the landscape (Condit et al. 2013) and local (i.e. < 1 ha) scales (John et al. 2007). Even subtle changes in microtopography may result in the spatial heterogeneity of nutrients (Xia et al. 2016) and thereby differences in plant performance depending on a species' plant functional traits.

In the present study, we examine how microtopography results in spatial heterogeneity of soil nutrients (especially P) in a degraded tropical pasture-landscape, and how this influences species growth given differences in belowground functional traits. In particular, we focus on two frequently grown native tree species in the Wet Tropics of Australia, Northern Silky Oak *Cardwellia sublimis* F. Muell. (Proteaceae) and Queensland Maple *Flindersia brayleyana* F. Muell. (Rutaceae), which differ in key nutrient-acquisition strategies. In doing so we demonstrate the need to consider both the spatial heterogeneity of edaphic factors and the belowground functional traits of potential reforestation species when planning successful reforestation programs.

Materials and Methods

The study site is located in the southern Atherton tablelands of the wet tropical bioregion of far north Queensland (17.43°S, 145.51°E), Australia, and is part of a reforestation project established and managed since 2011 (Preece et al. 2013, Preece et al. 2015). Mean annual temperature at the site is 19 °C (mean diel temperature range = 9.5 °C) and mean annual rainfall is 1942 mm. The site experiences seasonal weather with the wettest quarter (Jan- March) receiving on average 1021 mm and the driest (July-Sep) 152 mm (Turton et al. 1999). Prior to reforestation, the site was managed as cattle pasture for approximately 70 years, dominated by exotic grass species (i.e. *Melinis minutiflora*, *Urochloa (Brachiaria) decumbens*, and *Setaria sphacelata*) and effectively in a state of arrested succession. Native vegetation adjacent to the planting area is remnant and regrowth, simple to complex notophyll vine forest of cloudy wet highlands on basalt (Regional Ecosystem 7.8.4) (Environmental Protection Agency, 2007).

The study site comprises 50 ha of degraded pasture of which 16 ha are experimental reforestation plots. The experiment is a randomised block design of forestry plantings, divided into 48 experimental plots (with an additional 16 unplanted controls) (50 m × 50 m; 0.25 ha), established in January 2011 (Figure 1). Plot treatments combine three types of species associations (monoculture, 6 species, or 24 species), and two tree-spacing distances of 1.75 m or 3 m. Tree species were selected at a workshop attended by ecologists, local practitioners and nursery managers. The selected species are from six locally important families and represent a broad combination of functional traits (e.g. maximum height, wood density, fruit type, dispersal syndrome and pollination characteristics). Species were selected based upon seed availability, success in propagation and previous experience of survival and growth in reforested pastures (Erskine et al. 2005, Goosem and Tucker 2013). Included within the six species treatment were *Cardwellia sublimis*, *Castanospora alphandii*

(F.Muell.) F.Muell. (Sapindaceae), *Ficus septica* Burm.f. (Moraceae), *Flindersia brayleyana*, *Neolitsea dealbata* (R.Br.) Merr. (Lauraceae), and *Syzygium cormiflorum* (F.Muell.). B Hyland – (Myrtaceae).

In the almost five years since establishment, bi-annual monitoring of mortality and growth has highlighted significant variation in the success and growth among species and across plots (Figure 2). The two out of six-representative species found to follow a normal distribution in height were *S. cormiflorum* (a putative ectomycorrhizal species) and *C. sublimis* known to develop proteoid roots (Weston 2007). In stark contrast, *F. brayleyana* displays the largest range and significant skew in its height distribution (Figure 2). To investigate what may be driving this observed variation in growth across the landscape, we examined how topographic relief and changing edaphic conditions have different implications in two contrasting species, *F. brayleyana* and *C. sublimis* due to their belowground functional traits.

Both *F. brayleyana* and *C. sublimis* are endemic rainforest species of the wet tropics of Queensland, and are highly regarded for their timber (Erskine et al. 2005, Australian Tropical Rainforest Plants, Edition 6 2010, online Lucid key www.keys.trin.org.au, accessed 2nd May 2017). *C. sublimis* has proteoid cluster roots typical of the Proteaceae (Figure 3), a morphological adaptation often associated with phosphorus-impooverished soils (Shane and Lambers 2005, Lambers et al. 2015). Cluster roots are ephemeral rootlet structures that release carboxylates to mobilize otherwise recalcitrant soil P (Shane and Lambers, 2005), allowing Proteaceae to exploit even the highly recalcitrant organic P form, phytate (Steidinger et al. 2015). Proteaceae are commonly non-mycorrhizal (Lambers et al. 2015b), with studies in local natural systems showing 0% occurrence of arbuscular mycorrhizae (AM) in saplings of five species of Proteaceae including *C. sublimis* (Gehring and Conell 2006). In contrast, *F. brayleyana* a member of Rutaceae does not exhibit cluster root

formation, instead relying upon AM associations to facilitate nutrient exchange at the soil-plant interface (Gehring and Conell 2006, Richardson et al. 2009).

Remote sensing

Before the establishment of the reforestation planting, we captured both orthorectified true colour images and a digital surface model (DSM) of the study site using a SkyCam UAV Kahu drone (<http://www.kahunet.co.nz/kahu-uav.html>). The drone was fitted with a modified Sony Nex5 sensor, which collected RGB imagery with 80% forward and 60% side overlap. The resulting images were processed using Pix4D Mapper (Version 1.1.30) to generate an orthomosaic image and the DSM (4.5 cm ground sampling distance). The DSM was processed using ArcGIS (V10.3.1) to provide an estimate of the change in slope across each reforestation plot and between planted rows within our focal plot (Figure 1).

Landscape sampling

To examine the implications of landscape position on tree growth and establishment, we used growth inventory data from all reforestation-plots. Thirty-two (0.25 ha) plots were established in 2011 that contained both *F. brayleyana* and *C. sublimis* planted as part of two species mixes (6 or 24 species) and two planting densities (Preece et al. 2013). In July 2013 the central quarter (0.0625 ha) of each plot was surveyed and the surviving stems measured for height and diameter at 10 cm. We further selected only plots with at least three *F. brayleyana* or *C. sublimis* surviving in the central subplot which resulted in 25 plots containing *C. sublimis* and 24 containing *F. brayleyana*. As growth had not resulted in canopy closure at this time, the influence of both planting density and species mix on early sapling growth was not considered. Species average heights were compared with average plot slope derived from the DEM, using a simple linear model weighted by the number of surviving stems in each plot.

Focal plot sampling

To examine the mechanism behind differences in growth observed with changing topography (Figure 4), we selected a focal plot among the 32 mixed-species reforestation plots (Figure 1). The focal plot was selected because its gradual and uniform change in slope (Figure 1) allowed for sufficient numbers of surviving individuals to be present in each row with each pair of rows perpendicular to the dominant slope representing a distinct soil catena.

In September 2015 all surviving individuals of *F. brayleyana* ($n = 72$) and *C. sublimis* ($n = 69$) in the focal plot were measured for diameter at breast height (DBH) and total height. Mature leaves (3 leaves per tree per species) and surface soil samples (0 to 5 cm depth, 7.3 cm diameter, 4 cores) were collected and bulked per row pair. Leaves were digested using nitric acid (assisted with peroxide) and analysed for total elemental concentrations (B, Ca, Cu, Fe, Mg, Mn, P, K, Na, Zn) using inductively coupled plasma atomic emission spectroscopy (ICP-AES). Total C and N as well as $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$, were determined using a Costech Elemental Analyser coupled via a ConFloIV to a ThermoFinnigan Delta V PLUS Continuous-Flow Isotope Ratio Mass Spectrometer (IRMS). Soil samples were analysed for basic parameters including moisture content, bulk density (soil mass determined after drying at 105°C), pH (2:1 deionized water), and an estimate of organic matter (loss on ignition at 450°C). Extractable elements (Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, and P) were determined using Mehlich-3 and total elemental concentrations using reverse aqua regia; both solutions were subsequently analysed using ICP-AES as above. Where reported, data represent arithmetic means ± 1 SD. The influence of slope on soil and plant parameters was explored using simple linear models with average row slope as the predictor term. All statistical tests and visualization were made using R (R Core Team 2015).

Results

Variation in growth across the landscape

To test whether distributions in growth rates (Figure 2) were related to differences in how species react to topographical relief we examined the variation in tree height of *C. sublimis* and *F. brayleyana* across all mixed-species reforestation plots. While average growth in both species varied considerably (Figure 4), the mean height of *C. sublimis* after 3 years of growth was independent of plot slope ($F_{1,23} = 2.9$, $p > 0.05$, $R^2 = 0.10$), whereas the mean height of *F. brayleyana* was significantly shorter in steeper plots ($F_{1,22} = 11.1$, $p < 0.05$, $R^2 = 0.30$).

Variation in growth across a slope

Within our focal plot there was an elevation difference of 14 m from 950 to 964 m a.s.l. with the average slope within each row pair ranging from 12.0° to 25.9° (Figure 1c, Table 1). Across the entire plot there was no significant difference in tree height growth or estimated stem volume (D^2h , $p > 0.05$) for *C. sublimis*, with an average height of 3.4 ± 0.4 m and an estimated stem volume of 19.9 ± 8.4 dm³ across all rows. In contrast, *F. brayleyana* displayed significantly lower tree height ($F_{1,12} = 15.3$, $p < 0.01$, $R^2 = 0.52$) and stem volume ($F_{1,12} = 16.6$, $p < 0.01$, $R^2 = 0.55$) in rows with a greater slope. However, a segmented linear regression (R package: segmented) identifies a break point in this relationship at a slope of $19 \pm 1^\circ$ for height, and $15 \pm 1^\circ$ for stem volume, with rates of change reduced at slope angles greater than these thresholds (Figure 5a). The variation in slope across the plot had a direct influence on soil biophysical properties with a strong negative relationship ($F_{1,12} = 23.24$, $p < 0.001$, $R^2 = 0.63$) between slope angle and organic matter (Figure 5b). In *C. sublimis* there was no significant relationship between soil organic matter concentration and tree growth,

while *F. brayleyana* showed a significant increase in growth with increasing organic matter concentration downslope ($F_{1,12} = 16.25$, $p < 0.01$, $R^2 = 0.54$).

Soil biogeochemistry

In the acidic (pH 4.7 to 5.5) basalt-derived soils of the study area the increase in soil organic matter with decreasing slope aspect had multiple implications for soil elemental concentrations and biophysical properties (Table 2). However, in the context of the differential growth response observed in *C. sublimis* and *F. brayleyana*, it is the change in pH and P dynamics that appeared to be the most important factor. Soil pH and total [P] increased significantly with increasing organic matter concentration ($F_{1,12} = 47.1$, $p < 0.001$, $R^2 = 0.78$; $F_{1,12} = 40.77$, $p < 0.0001$, $R^2 = 0.75$, respectively). The increased soil [P] was likely available for plant uptake, with significant increases in both Mehlich-3 extractable [P] ($F_{1,12} = 38.5$, $p < 0.0001$, $R^2 = 0.74$) and in the molar ratio of Mehlich-3 extractable P to (Fe + Al), ($F_{1,12} = 31.5$, $p < 0.001$, $R^2 = 0.70$), this, the Mehlich-3 Phosphorus Saturation Ratio (PSR), being a good indicator of P availability in acidic soils (Khiari et al. 2000).

Leaf nutrient composition

The importance of P in determining the differential growth of *F. brayleyana* and *C. sublimis* across the hillslope was apparent in the corresponding leaf nutrient status (Table 3). Phosphorus concentrations in the leaves of *F. brayleyana* ranged from 1.3 to 3.1 mg g⁻¹ and were closely correlated with Mehlich-3 [P] of the soil ($F_{1,12} = 21.9$, $p < 0.001$, $R^2 = 0.62$) and soil organic matter concentration ($F_{1,12} = 18.6$, $p < 0.01$, $R^2 = 0.58$, Figure 6a). In contrast, *C. sublimis* maintained a relatively low and stable [P] in its leaves of 1.3 ± 0.18 mg g⁻¹, with no significant relationship with either bioavailable or total soil [P]. Leaf [N] was significantly different between the two species ($F_{1,23} = 97.4$, $p < 0.001$) averaging 9.2 ± 0.1 mg g⁻¹ and 13.3

$\pm 1.2 \text{ mg g}^{-1}$ in *F. brayleyana* and *C. sublimis*, respectively. However, there was no relationship between leaf [N] and soil organic matter concentration (Figure 6b).

Leaf isotopic composition

The two study species had contrasting leaf $\delta^{13}\text{C}$, both between species generally and in their responses to the soil fertility gradient (Table 3). The mean leaf $\delta^{13}\text{C}$ for *C. sublimis* was $-26.5 \pm 0.5 \text{ ‰}$, whereas for *F. brayleyana* it was $-30.3 \pm 1.1 \text{ ‰}$. Both species had a significant relationship with soil organic matter concentration; however while *C. sublimis* leaf $\delta^{13}\text{C}$ declined significantly with increasing soil organic matter concentration ($\alpha = -0.19$; $F_{1,11} = 5.65$, $p < 0.05$, $R^2 = 0.28$), *F. brayleyana* leaf $\delta^{13}\text{C}$ increased significantly ($\alpha = 0.54$; $F_{1,12} = 16.7$, $p < 0.01$, $R^2 = 0.55$) (Figure 7a). The same pattern was observed for the relationship between leaf $\delta^{13}\text{C}$ and either soil total P or Mehlich-3 extractable P, as is expected given the collinearity among these three measures of soil fertility (Table 2).

Leaf $\delta^{15}\text{N}$ similarly differed between species (Table 3). The mean value for *C. sublimis* was $7.7 \pm 0.6 \text{ ‰}$, and for *F. brayleyana* was $2.2 \pm 1.3 \text{ ‰}$. In both species leaf $\delta^{15}\text{N}$ increased significantly with increasing soil organic matter concentration ($F_{1,11} = 5.61$, $p < 0.05$, $R^2 = 0.28$; $F_{1,12} = 0.79$, $p < 0.001$, $R^2 = 0.78$, respectively) (Figure 7b). Again, this pattern remained unchanged for soil total [P] or Mehlich-3 extractable [P].

Discussion

In monitoring reforestation success in a degraded and complex-topographic landscape, we show how differences in plot slope results in differential tree growth. While no relationship was found between the mean of plot-slope and tree height across all experimental plots for *C. sublimis* (Figure 4), *F. brayleyana* did show a significant trend, with reduced tree heights in plots which had, on average, steeper slopes. In a more closely monitored focal plot we demonstrate how topographic relief affects edaphic properties, which, in turn, leads to this differential growth responses among tree species. Species such as the proteaceous *C. sublimis* have adaptive functional traits to low P conditions (e.g. cluster roots), that provide a competitive advantage on steeply sloping degraded soils. However, a lack of functional trait plasticity in *C. sublimis* (Figure 3) and the inherent costs associated with these traits prevents an increase in growth under ‘high’ nutrient downslope conditions (Figure 5a). In contrast, although *F. brayleyana* growth was clearly constrained by low soil P conditions on the valley sides, growth increased with increasing P availability towards the valley floor (Figure 5a). This ability to take advantage of high soil P bioavailability, including the development of leaves with a higher [P] (Figure 6a), results in an apparent switch in competitive advantage, with *F. brayleyana* trees out-performing (after 5 years of growth) *C. sublimis* in lower slope locations.

The implications of landscape position and slope on soil carbon and nutrient heterogeneity in agricultural landscapes has long been recognized (Gregorich et al. 1998, Florinsky et al. 2002). Here we demonstrate the effect that even a simple a metric for landscape position (e.g. slope) can have on reforestation success. Across the entire study site (Figure 1) additional processes (e.g. up-slope catchment, proximity to forest, and historical land-management) likely affect both edaphic and microclimatic conditions critical for tree growth, thereby contributing to the large variation in growth rates observed between

experimental plots (Figure 4). The use of topographic position index (TPI, Jenness 2006) or landform classification (Pennock et al. 1987), which both take into account the relationship of a specific plot with its surrounding landscape (e.g. convex or concave slope position) may have helped explain this within plot variation. However, proximity of remnant forest and isolated trees close to our plots precluded the use of our available DEM for these purposes. Heterogeneity of P availability in tropical landscapes is a fundamental driver of forest species richness (Xu et al. 2016) and has been associated with species distributions at the landscape (Condit et al. 2013) and plot level (John et al. 2007). Our study, albeit in a degraded landscape, suggests that differential species growth at the seedling stage across the landscape may translate into altered climax forest composition.

At the landscape scale, the success of *F. brayleyana* in commercial forestry plots across the Australian wet tropics has previously been correlated with basic soil properties (Manson et al. 2013), although differential success was ascribed to soil texture and differences in soil water holding capacity and not P availability. However, Manson et al (2013) only measured total soil-[P] and not plant available [P] – an important distinction in soils with high levels of occluded (typically unavailable) P (Cross and Schlesinger 1995, Tiessen 1998). Indeed, it appears that P acquisition in tropical trees, without proteoid roots, is often regulated by the dynamic and rapid cycling of organically bound P compounds (Turner and Engelbrecht 2011). Consequently, the fertility of many tropical systems is maintained by high inputs of organic matter (Tiessen et al. 1994b), and it is the formation of a surface-soil high in organic matter in close proximity to a dense fine-root mat, that maintains the highly efficient cycling of nutrients in tropical forests (Cuevas and Medina 1986, 1988). Disruption to this tight nutrient cycle by land-clearing and protracted agriculture without additional fertilizer, such as occurred in this study, can therefore result in P-limitation during landscape recovery (Imai et al. 2012). As ecosystem (and edaphic) conditions recover with the

increasing age of reforested stands, the relevance of microtopography (i.e. slope) on organic matter concentration may be reduced. However, the initial establishment of seedlings represents a critical phase for determining reforestation success, and therefore species selection and reforestation strategies must be guided by these initial differences in seedling establishment rates.

Bulk leaf-tissue isotopic composition (Figure 7, Table 3) showed distinct differences between the two studied species, and in the case of $\delta^{13}\text{C}$, across the change in landscape position. In our study, observed changes in $\delta^{13}\text{C}$ of bulk *C. sublimis* leaf tissue (Figure 7a) may have been related to increased water availability (Cernusak et al. 2009) in rows with lower slope and higher organic matter concentrations. However, *F. brayleyana* showed a pattern counter to this, indicating that the influence of water availability on $\delta^{13}\text{C}$ may be considered secondary to nutrient deficiency altering photosynthetic capacity of *F. brayleyana* on steep slopes. In contrast to $\delta^{13}\text{C}$ values, $\delta^{15}\text{N}$ of leaf tissue showed a similar relationship for the two species in relation to slope (Figure 7b), despite a substantial (~5 ‰) offset. In addition to the well-known role that cluster roots play in P acquisition (Lambers et al. 2015), they have been implicated in the modification of N cycling. Organic acids, such as those exuded by cluster roots, are known to increase the solubility of organic-N in the soil (Matsumoto et al. 2005) which in concert with altering the pH of the rhizosphere and modification to microbial activity (Delgado et al. 2015) likely alters organic-N cycling in proximity to cluster roots. This could account for the elevated [N] (Figure 6b) and enriched leaf $\delta^{15}\text{N}$ (Figure 7b) in *C. sublimis* compared with *F. brayleyana*.

Reforestation methods vary between countries and among land managers and are dependent upon the ecological circumstances and stated goals of the reforestation program (Lamb et al. 2005). However, it is apparent that successful reforestation requires a detailed knowledge of the history of site degradation and the implications for the edaphic properties at

a site (Griscom and Ashton 2011). In this study we have demonstrated that site edaphic characteristics can vary within tens of metres due to topographic relief and that species and families may respond differently to these conditions.

For landscape restoration to be viable, the high costs of establishing self-maintaining and functionally biodiverse forests require that the most cost-effective methods are used, and that the survival and growth of each species planted are maximized (Summers et al. 2015, Ansell et al. 2016). A diagnostic protocol, similar to that used by Rodrigues et al. (2011), that identifies the barriers to successful forest restoration at a specific location, should be adopted which considers how microsite conditions, degradation history, and species-specific functional traits interact to influence species growth and performance and thus reforestation trajectories.

Authors' contributions

AWC, LC, NP and PvO conceived of the idea behind the paper and designed the additional sampling methodology for a project initiated by NP, PvO, maintained by NP and PvO; AWC, LC, NP, PvO and PDE collected the data; AWC and LC analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

Data available from the Dryad Digital Repository. DOI:
<http://dx.doi.org/10.5061/dryad.pr096> (Cheesman et al, 2017).

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Figures:

Figure 1: Landscape context of focal reforestation plot B8P4 on a valley side of a 6 year reforestation project in tropical north Queensland. a) Shows overview of the Thiaki project site and 16 ha of experimental reforestation plantings, b) a true colour image of experimental plot B8P4 before planting, and c) a digital elevation model showing the predominant slope

Figure 2: Kernel density plot of tree heights measured in July 2013 in 6 key species across the Thiaki reforestation project found within mixed-species plantings. Density plot of each species scaled to 1, to show relative probability across height. Only two species *Cardwellia sublimis* and *Syzygium cormiflorum* demonstrate a normal distribution (Shapiro-Wilk test $p > 0.01$) with all other species showing substantial variance and skewness in growth rates between individuals across the landscape, but no apparent impact of either planting density or initial weed treatment (Noel D. Preece, unpublished)

Figure 3: Photos of proteoid cluster roots of *Cardwellia sublimis* found in both (a) high slope and (b) low slope rows of plot B8P4

Figure 4: Relationship between average plot slope and average tree height (as of 2013) in two tropical tree species *Flindersia brayleyana* and *Cardwellia sublimis* grown in several mixed-species reforestation plots across a degraded pasture landscape. While *C. sublimis*

showed no significant trend, *F. brayleyana* showed a significant decline in tree height ($F_{1,22} = 11.1$, $p < 0.05$, $R^2 = 0.30$) with increasing plot slope.

Figure 5: Influence of slope on (a) the growth of two tree species and (b) surface soil organic matter concentration within a 0.25 ha reforestation plot.

Figure 6: Influence of soil organic matter on bulk leaf (a) phosphorus and (b) nitrogen concentration in two tropical trees, *Flindersia brayleyana* and *Cardwellia sublimis* grown in different soil catenas across a change in slope.

Figure 7: Influence of soil organic matter on bulk leaf (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ in two tropical trees, *Flindersia brayleyana* and *Cardwellia sublimis* grown in different soil catenas across a change in slope.

Table 1: Average tree height and estimated biomass in two tropical tree species grown within a single 0.25 ha plot in rows parallel to the major hill slope. D²h represents an estimate of biomass based upon (diameter at 30 cm)² x height

Row	Slope (°)	<i>Cardwellia sublimis</i>							<i>Flindersia brayleyana</i>						
		# of stems	height (m)			D ² h (dm ³)			# of stems	height (m)			D ² h (dm ³)		
1	25.0	6	3.4	±	0.2	17	±	6.3	10	1.4	±	0.6	0.7	±	0.6
2	25.9	11	3.2	±	0.5	14	±	6.1	7	2.2	±	1.0	3.4	±	3.2
3	21.9	7	3.5	±	0.5	23	±	11.1	5	1.6	±	1.0	1.7	±	2.8
4	22.6	6	3.3	±	0.2	16	±	0.9	5	1.6	±	0.8	1.8	±	2.0
5	21.8	5	3.5	±	0.5	21	±	9.8	3	1.5	±	0.9	1.2	±	1.2
6	20.7	5	3.4	±	0.8	16.	±	8.8	1	1.0	±	NA	0.2	±	NA
7	19.7	3	3.5	±	0.5	18	±	8.6	2	0.6	±	0.1	0.1	±	0.1
8	17.9	5	3.6	±	0.7	38	±	34.9	7	0.9	±	0.5	0.5	±	0.8
9	16.3	4	2.4	±	0.8	8	±	3.9	5	2.5	±	1.4	9.0	±	12.9
10	14.0	3	4.2	±	0.3	36	±	10.8	4	2.2	±	1.2	3.8	±	2.8
11	13.6	8	3.2	±	0.7	17	±	11.1	6	4.3	±	1.3	25.4	±	27.3
12	12.1	3	3.3	±	0.8	12	±	2.4	9	4.3	±	1.8	35.9	±	38.4
13	13.1	0							4	5.6	±	0.7	53.8	±	34.9
14	11.9	3	3.8	±	1.3	23	±	18.8	4	5.2	±	0.6	41.1	±	24.4

Table 2. Average soil biophysical characteristics across the 0.25 ha study plot. PSR = Phosphorus Saturation Ratio, molar ratio of Mehlich-3 extractable P to (Fe + Al)

Row	Slope (°)	Organic matter (%)	pH	Mehlich-3 Extractable				Elemental Total	
				Al mg g ⁻¹	Fe mg g ⁻¹	P μg g ⁻¹	PSR	Ca mg g ⁻¹	P mg g ⁻¹
1	25.0	22.1	4.8	1.5	0.16	8.3	0.005	0.6	1.6
2	25.9	21.8	4.7	1.6	0.16	7.7	0.004	0.48	1.6
3	21.9	21.8	4.7	1.5	0.17	8.5	0.005	1.1	1.5
4	22.6	22.6	4.8	1.4	0.18	12	0.007	0.65	1.7
5	21.8	20.3	4.7	1.3	0.17	8.7	0.005	0.58	1.8
6	20.7	22.7	5.0	1.3	0.17	9.7	0.006	1	1.9
7	19.7	21.6	4.8	1.4	0.15	9	0.005	0.66	1.9
8	17.9	22.5	4.7	1.4	0.16	13	0.008	0.55	2.1
9	16.3	24.2	5.0	1.3	0.16	15	0.009	0.87	2.5
10	14.0	25.7	5.2	1.1	0.17	19	0.014	1.5	2.8
11	13.6	23.8	5.1	1.2	0.21	18	0.012	1.2	2.9
12	12.1	24.4	5.1	1.1	0.2	18	0.013	1.3	3
13	13.1	26.6	5.4	0.99	0.27	34	0.026	1.7	3.7
14	11.9	24.9	5.5	0.94	0.24	31	0.026	1.9	3.7

Table 3: Average leaf nutrient concentrations in two tropical tree species grown within a single 0.25 ha plot in rows parallel to the major hill slope

Row	<i>Cardwellia sublimis</i>					<i>Flindersia brayleyana</i>				
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Molar N:P	Molar C:N	Molar C:P	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Molar N:P	Molar C:N	Molar C:P
	(‰)					(‰)				
1	-26.3	6.6	26.9	34.2	919.0	-30.4	1.5	15.1	63.4	957.4
2	-26.3	7.2	20.8	37.7	785.7	-29.7	1.4	11.5	58.0	668.9
3	-26.0	6.7	25.2	39.3	990.1	-30.2	1.5	9.7	63.6	618.2
4	-26.3	7.7	26.7	38.5	1026.1	-30.7	1.0	11.9	64.2	763.4
5	-26.0	7.4	18.9	45.2	855.5	-31.4	0.8	8.4	70.9	593.4
6	-25.9	7.8	19.9	40.1	799.7	-32.7	0.9	8.0	83.7	672.5
7	-27.1	8.3	18.7	42.0	788.3	-31.7	1.3	12.7	62.7	794.3
8	-26.8	7.5	16.8	45.0	756.9	-31.1	1.7	12.9	68.7	884.5
9	-26.2	8.4	24.8	36.7	910.0	-29.4	2.2	8.4	62.3	526.0
10	-26.9	7.6	17.3	37.7	652.3	-29.7	2.7	6.7	71.2	475.5
11	-26.7	8.3	17.6	39.1	687.0	-29.3	3.7	6.8	60.9	416.5
12	-27.0	8.0	16.1	48.9	787.4	-30.0	3.7	9.4	60.2	568.3
13			NA			-29.4	4.1	6.8	61.6	416.9
14	-27.1	8.7	25.2	40.9	1029.3	-29.2	4.5	7.1	53.8	383.5











