Regulating services of successional forest types in tropical montane cloud forests in the Cordillera de Talamanca, Costa Rica

Arran S. Redman

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Declaration

I declare that this is the result of my own investigation and that it has not been submitted or accepted in whole or part for any degree, nor is it being submitted for any other degree.

Candidate: **Arran S. Redman**

Signature:

Abstract

Characterised by their unique climate and hydrological function, tropical montane cloud forests (TMCFs) are recognised for their water provisioning services. However, their role in carbon sequestration and storage is poorly understood. Historically TMCFs in the Cordillera de Talamanca of Costa Rica, were subjected to significant amounts of human disturbance and nearly half of the tropical forest biome is made up of secondary forests. Reforestation of abandoned agricultural lands has now been proposed as a means of climate regulation for human induced carbon emissions to the atmosphere. This study reports the recovery of climate regulating and water provisioning services in different succession types of secondary TMCFs. Succession types included active (plantation) and passive (natural regeneration) reforestation methods, using undisturbed primary forests and grazed mountain pastures as comparisons. Climate regulation services were assessed by measuring the carbon stocks of above and below-ground biomass, particularly through soil and stand characteristics. Litterfall, littler standing crop and root biomass were measured to facilitate total carbon stock estimates and forest recovery. Infiltration rates were measured and compared between succession types to understand their ability to regulate water provisioning services and deal with high water inputs. The results were associated with published data from similar TMCF habitats and compared to carbon stock data from varying tropical primary and secondary forests. The recovery of both climate regulating services and water provisioning services increased with time since agricultural abandonment. Carbon stocks and soil organic matter content were high in older natural regeneration, greater than primary forests. Both climate regulating services and water provisioning services were heavily reduced in pasture lands, with slight recovery in the young planted and naturally regenerated secondary forests. The results indicate that full recovery of measured services takes approximately 50 years in natural regenerated TMCF habitats, with greater climate regulating services in late successional forests than original primary forests. Primary forests remained chief provider of water provisioning services in TMCF habitats. This study fortifies the idea that the regeneration of tropical forests could play a vital role in the mitigation of human induced carbon emissions, especially in TMCF systems.

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Lastly but not least, I dedicate this project to Amity Allen, being in the field beside me from the moment this project initiated, to being my rock and stability at the end.

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1.0 **Introduction**

Tropical montane cloud forests (TMCFs) are becoming increasingly recognised for their regional and global importance. This is because they provide vital ecosystem services in flood mitigation, water quality, soil conservation and their major influence on carbon storage and climate regulation (Fehse *et al*., 2002; Cayuela, Benayas and Echeverria, 2006; Martinez *et al*., 2009; Spracklen and Righelato, 2014, 2015). They are characterised by distinct climatic patterns where prevailing-wind driven orographic clouds envelope mountain ranges and create persistent cloud cover (Loope and Giambelluca, 1998; Hafkenscheid, 2000). The morphology, stand characteristics and soil properties are directly or indirectly distinguished through cloud formation (Bruijnzeel and Proctor, 1995). A saturated environment is created by convective rainfall and the interception of cloud droplets on soil and vegetative surfaces through cloud-stripping. Horizontal precipitation provides sustained water inputs throughout all tropical seasons, having a greater input than vertical rainfall in the verano (dry) season (Schneider *et al.*, 1999). TMCFs are important at a local, regional and global scale, delivering ecosystem services in water provisions, flood mitigation and climate regulation. Slow release mechanisms of water through the soil infiltration and throughflow, are vital to reduce flooding and stabilise fresh water resources.

The diversity of ecosystem services in TMCFs are matched by their biological diversity, although less rich in species than tropical lowland forests, levels of endemism are high. Covering only 2% of the earth's surface, TMCFs are dominantly classified as biodiversity hot spots, globally important for ecological functions and services (Ray *et al.*, 2006; Beck *et al.*, 2008). However, these ecosystems are under considerable threat, with 53% of the Earth's forests concentrated in the tropics, they experience the highest rates of deforestation and land use change globally (Silver *et al.*, 2000). Tropical deforestation and land conversion significantly impacts the global carbon cycle. Annual carbon losses from above and below ground biomass in tropical regions accounts to 1.7 ($\pm$0.5) Pg yr^{-1} (Brown *et al.*, 1993; Lal, 2004, 2005; Baccini A. *et al.*, 2015), driven by deforestation and land use change of predominantly primary forest systems. Annual carbon sequestration of tropical forests is approximately 3.2 ($\pm$1.3) Pg yr^{-1}, rendering tropical forests as net carbon sinks, although this is a highly debated topic (Machida *et al.*, 2007; Schimel *et al.*, 2014; Fatichi *et al.*, 2018).

Considerable research has been directed toward the role in which tropical forests play in the global carbon cycle (Silver *et al.*, 2000; Fehse *et al.*, 2002; Canadell and Raupach, 2008).

However, much less is known about the considerably smaller but more concentrated biome of tropical montane forests (Silver *et al.*, 2004; Leuschner *et al.*, 2013; Spracklen and Righelato, 2014). Approximately 2.78% of the total original tropical forest area, is montane cloud forests (Myers, 1992; Bubb *et al.*, 2004). It is well understood that tropical forests hold the majority of the carbon stock in above-ground biomass (Brown and Lugo, 1992; Chave *et al.*, 2005; Pan *et al.*, 2011). With climatic and altitudinal stress, TMCFs have reduced stand structure, especially in upper montane systems. However, the reduced biomass of stand volume is made up by the high concentration of canopy soil, root and epiphytical mass, accounting for up to a third of above-ground biomass (Vance and Nadkarni, 1990; Köhler *et al.*, 2007; Gradstein, 2008; Hertel and Köhler, 2010; Bohlman *et al.*, 2010). Due to climatic factors discussed, TMCF distribute carbon and energy reserves into fine root systems, increasing soil organic matter and total carbon stocks (Hertel *et al.*, 2006; Hertel and Leuschner, 2010; Karspu and Palmira, 2011). Soil carbon reserves and below-ground biomass of TMCF are thought to match and in cases exceed those of above-ground biomass.

The clearing of pre-montane forests for agricultural conversion in Costa Rica began at least 1400 years before present (B.P.) (Anchukaitis and Horn, 2005). Land-use change and deforestation of TMCFs causes a significant modification to the functionality and service provisions of that land area. The leading cause of deforestation in the Neotropics is cattle grazing and the creation of pastures (Holl *et al.*, 2000). This land-use change significantly alters the provisioning services of that land area, causing degradation to climatic regulation and water provisions. Martinez et al., (2009) found that the social and economic cost of land use change of TMCFs to water provisioning services alone, were significantly greater than the economic gains to land owners from land conversion. Water quality of streams running through converted land was significantly reduced through nutrient (particularly nitrate), cation and suspended solid pollution. Areas that have had deforestation or land conversion practices typically have reduced soil stability overtime. Compaction from grazing animals causes an observed reduction of infiltration and throughfall of water, causing increased flood risks and a higher probability of landslides (Bruijnzeel, 2005; Sidle *et al.*, 2006). The total value of climate regulating services of TMCFs is comparatively understudied yet thought to be significant (Spracklen and Righelato, 2014). Agricultural conversion of TMCFs causes a significant disturbance to carbon stocks. Total above-ground biomass is nearly completely reduced from the replacement of dense primary tree and canopy species biomass by perennial grasses and light ground vegetation (Bruijnzeel, 2005; Martínez *et al.*, 2009; FAO, 2018). Soil carbon stocks become

reduced initially after deforestation because of enhanced decomposition rates, reduced inputs and inputs of a lesser quality (Lugo and Brown, 1993). Land use change and soil cultivation are thought to have contributed 136 ±55 Pg of carbon emissions into the atmosphere since the industrial revolution, 78 ±12 Pg of this is from degrading soil organic carbon pools (Brown *et al.*, 1993; Rudel, 2001; Lal, 2004). Soil carbon loss is directly influenced by increased ratio of temperature and precipitation through the removal of canopy protection and climatic mitigation created by the original forested habitat (Brown and Lugo, 1982).

Over half of the tropical forest biome is in some stage of recovery from human disturbance, especially in isolated mountainous regions (Lugo and Brown, 1993; Silver *et al.*, 2000). Recovering tropical forests are likely to sequester carbon at a rapid rate and serve as net sinks for CO_2. The patterns of carbon accumulation during secondary succession offer valuable clues about the success of reforestation (Silver *et al.*, 2000). Above-ground biomass and carbon stock has a rapid initial growth following tropical reforestation and afforestation, with rates beginning to slow after approximately fifty years. Below-ground carbon pools accumulate at a slower rate but have a reduced turnover time and thus have a potential for longer term storage (Lugo and Brown, 1992; Hertel *et al.*, 2006). Observed passive (natural regeneration) and active (plantation) methods have shown divergent directions of carbon allocation and biomass development in the tropics. Plantations allocate a high proportion of carbon into above-ground biomass and natural regenerated forests allocate a higher proportion into root systems (Cuevas *et al.*, 1991; Lugo, 1992). However, it is unclear whether management methods of habitat regeneration have a significant influence on provisioning ecosystem services.

This paper investigates the successional development of TMCF in the Cordillera de Talamanca, Costa Rica, in terms of ecosystem services, including climate regulation and water provisions. This study focuses on soil and stand characteristics of multiple succession types including:

- Pasture

- Plantation

- Natural regeneration with under thirty years since disturbance (NR <30 yr)

- Natural regeneration with over thirty years since disturbance (NR >30 yr)

- Primary, old growth forests

The objectives were to firstly establish the extent to which successional forests have rejuvenated soil and stand characteristics of primary forest levels; secondly, to determine what type of reforestation management is optimal, in terms of time and progression, especially between NR <30 yr and plantations; thirdly, further the understanding of the significance of ecosystem services within TMCF habitats, with focus on their ability to sequester and sore carbon. This study specifically examines the TMCFs of the pacific slopes of the Cordillera de Talamanca, including an altitudinal observation of climate regulating services.

2.0 Literature review

2.1 *Tropical mountain forests*

Accounting for just 2.5% of tropical rainforest cover, tropical montane cloud forests (TMCFs) are unique terrestrial ecosystems, located in sporadic mountainous landscapes defined by regular cycles of cloud formation (Bubb, 2004). The typical tropical TMCF is composed of forests with distinctive floristic and structured form. They occur within an altitudinal belt between 500-3,500 m, across the montane and sub-montane floristic zones, predominantly existing between 1,500-2,500 m above sea level (Doumenge *et al.*, 1995; Aldrich *et al.*, 1997). The atmospheric environment is characterised by persistent, frequent or seasonal cloud cover at the vegetation level (Ray *et al.*, 2006). Enveloping cloud cover and wind driven orographic clouds, influence atmospheric conditions through reduced solar radiation and vapor deficit, canopy wetting and the suppression of evapotranspiration (Schneider *et al.*, 1999). Consequently, net precipitation is significantly enhanced, throughfall beyond rainfall contribution, influenced by canopy interception and cloud stripping (Fig. 1) (Hamilton *et al.*, 1995; Hamilton, 2018). Cloud stripping, also known as horizontal precipitation, typical of TMCFs, is the condensation of cloud droplets on vegetative and soil surfaces (Schneider *et al.*, 1999).

When characterising wet tropical mountains, transparency is often needed when describing the transition of habitats considered in the term TMCF. Grubb and Whitmore (1966) initially divided tropical forests into 'lowland rain forest' (LRF), 'lower montane rain forest' (LMRF) and 'upper montane rain forests' (UMRF). Each habitat is distinguished by altitude limits,
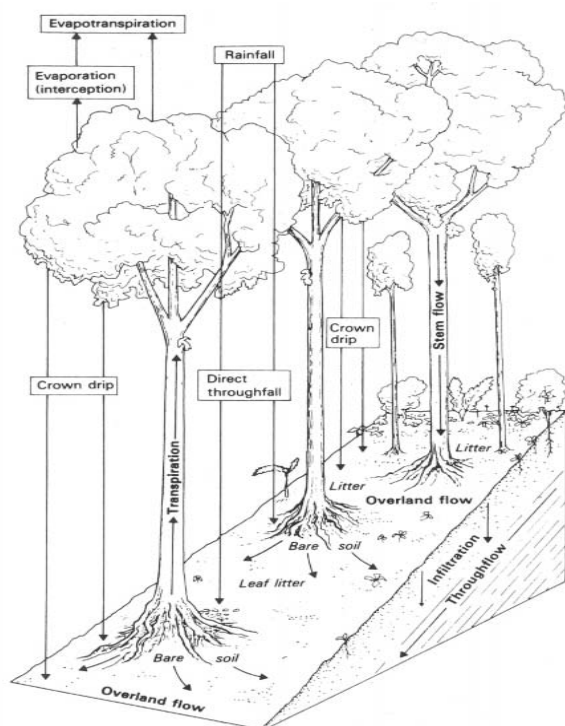
Fig. 1.

Hillslope forest hydrological cycle (Bruijnzeel, 1990).

cloud cover persistence and frequency, as well as characteristic differences and floral zonation. Although the typical names and definitions for TMCF used today resemble Grubb and Whitmore's (1966) original definition and description, further separated and adapted modern terms are now frequently used. In this paper the terms lower montane cloud forest (LMCF) and upper montane cloud forest (UMCF) are used, since they are most representative to the studied habitat type. (Bruijnzeel and Hamilton, 2000; Hafkenscheid, 2000; Mulligan *et al.*, 2011).

2.2 *Stand Characteristics*

The morphology and stand characteristics of TMCFs are different to other tropical forests.

Tree constitution is reduced as tree growth is commonly stunted because of climatic stress, saturated soils and reduced oxygen levels (Schneider *et al.,* 1999; Bruijnzeel *et al.,* 2011). Although forest canopy heights, accompanied with temperature, are commonly observed to decrease with heightened elevations (Coomes and Allen, 2007), the relationship is heightened in TMCFs due to their unique climate system. Compared with LRFs, stem density and canopy density tends to be greater in TMCFs, combined with a development of smaller, thicker and harder sclerophyll leaves (Hamilton *et al.*, 1995; Aldrich *et al.*, 1997). Canopies of a TMCF can have a heightened biomass with the contribution of epiphytes, such as bromeliads, bryophytes, orchids and ferns due to their ability to intercept moisture from the unique climate of a TMCF (Loope and Giambelluca, 1998; Schneider *et al.*, 1999). Due to the climatic factors discussed, canopy soil, roots and epiphytical mass can make up to a third of total above-ground biomass within this biome (Grandstein, 2008). Abiotic contributions cause changes to the appearance, characteristics and structure of TMCF habitats. Altitudinal increase and aspect to prevailing winds primarily affect biotic factors and create TMCF variation (Bruijnzeel and Hamilton, 2000). At higher altitudes cloud submersion tends to be more frequent and consistent, trees are further stunted and there is an even greater density of epiphytes (Bubb *et al.*, 2004; Mulligan *et al.*, 2011).

2.3 *Habitat variation*

LMCF and UMCF are two hydraulically and chemically distinct habitats within TMCFs. The transition from LRF to LMCF is predominantly controlled by temperature, usually at elevations where the average minimum temperatures are <18°C. At this threshold there is a transition where many lowland species are displaced by a floristically different range of montane species (Bruijnzeel, 2005). The altitudinal elevation in which this transition occurs changes with continentality, proximity to equator and in outlying islands and archipelagos. On large equatorial inland mountains such as the Andes, the transitional ecotone usually occurs at an altitude of 1200-1500 m (Grubb and Whitmore, 1966; Bruijnzeel and Hamilton, 2000; Bruijnzeel, 2005). This has been found to be the same in the Cordillera de Talamanca, Costa Rica (Kappelle *et al.*, 1995; Ray *et al.*, 2006; Kappelle, 2016).

LMCF characteristically have relatively tall stands (15-35m) with a modest bryophytic cover on stems (25-50%) (Bruijnzeel *et al.,* 2011). With an altitudinal increase, cloud submersion becomes increasingly consistent and prolonged, with intermittent cloud formation observed from above 1200 m. The transition from LMCF to UMCF has been found to coincide with cloud condensation persistency, usually occurring between 2000-3000 m (Grubb and Whitmore, 1966; Bruijnzeel and Hamilton, 2000; Bruijnzeel, 2005). Trees become distinctively shorter in stature (2-20m) and have a high bryophytic cover on stems (70-80%) (Bruijnzeel *et al.*, 2011). On the upper scale of these montane ecosystems, there is a transition into the highest altitudinal cloud forest type, subalpine forest. This transitional zone is defined where maximum average temperatures remain at <10°C. Small-statured trees and shrubs dominate this species-poor landscape, characterised by gnarled features and tinier leaves. Mosses remain abundant, yet there is a comparative absence of epiphytes. Subalpine forests (Fig. 2.) are encountered solely on the highest reaches of tropical mountains, transitioning from UMCF at 2800-3200 m on large equatorial mountains and as high as 3900 m in Papa New Guinea and Latin America (Grubb and Stevens, 1985; Bruijnzeel, 2005).

Fig. 2.

Upper montane to subalpine, elfin forest transition zone in the Cordillera de Talamanca at 3100 meters in elevation above sea level.

2.4 *Ecological importance*

As both biologically rich and diverse, many TMCF habitats reside within global biodiversity hotspots (Ray *et al.*, 2006). Covering just 1.4% of Earths land surface these 'hotspots' contain 44% and 35% of all species of vascular plants and vertebrate species respectively (Myers *et al.*, 2000). The number of species threatened with extinction overrules current conservation efforts and resources and is expected to increase over time (Myers, 1988). Having heightened values in biodiversity and endemism, whilst being depleted faster than any other biome, there are set opinions (Mittermeier *et al.*, 1998; Myers *et al.*, 2000) to place attention on identifying protection priorities on areas such as biodiversity hotspots.

2.5 *Threats of deforestation*

Global primary vegetated habitats cover 12% of their original extent and 52% of the world's forests are concentrated in the tropics, with the highest rates of deforestation and land conversion globally (Myers *et al.*, 2000; Silver *et al.*, 2000). Carr (2004) found that population growth and deforestation are significantly associated at a global and regional scale, yet

evidence that the link is direct is scant. These same results were found in an array of studies (Repetto, 1990; Heuman and Buchanan, 2005; Defries *et al.*, 2010), expanding that the loss of tropical forests has been driven by international agricultural demand, political and economic pressure and a global necessity for cheap resources.

2.6 *Tropical montane soils*

The soils of a TMCF exhibit a wide range of chemical and physical properties since the geological setting is not distinctive and there are variations between TMCF altitudinal belts (Bruijnzeel and Hamilton, 2000). TMCFs exist in a diverse range of geological landscape types, many have volcanic histories or are ancient alpine slopes comprised of granite bedrock and present post glacial scaring. However, certain below-ground features appear representative. Roman *et al.* (2011) found that TMCF soils contained a high organic matter content and had a lower overall pH than LRFs. Although greater site variation exists in TMCFs, on average total soil nitrogen and the level of extractible prosperous is greater and soils are rich in exchangeable cations. Deep organic horizons have been identified in TMCF habitats, developed over a mineral soil (Bruijnzeel and Hamilton, 2000). Surface horizons may consist of histosols; with peat developing in the typically wet and regularly close to saturated state of TMCF soils, or of mor-humus developing in low pH conditions and where phenolics may occur (metabolites with a slow decomposition nature) (Hamilton *et al.*, 1995; Min *et al.*, 2015; Fahey *et al.*, 2016). It is well considered that TMCF soils have reducing conditions due to high saturation caused from a high hydrological input, combined with the low evaporative demand from the cool and humid climate conditions. The slow nutrient recycling from dead organic matter and reducing conditions, collectively contribute to chronic nutrient limitations (especially N) to plant production, leading to the stunted form of many TMCF trees (Hafkenscheid, 2000). However, many publications fail to confirm habitat variations and site-specific definitions within TMCF sites (Bruijnzeel and Proctor, 1995; Hamilton *et al.*, 1995; Aldrich *et al.*, 1997; Tanner *et al.*, 1998; Fahey *et al.*, 2016).

Combining reports and new data, Roman *et al.* (2011) found there was significant variation between LMCF and UMCF, and that not all TMCF trends were representative. TMCF sites containing peaty soils were non-representative nor were they all inherently toxic or limiting to plant productivity. It was found that the size of organic horizons between TMCF sites were hugely variable yet better developed in UMCFs. The absolute size of nutrient pools did not seem to alter between habitat types and that the nutrient limitations in UMCF are derived from

the plants ability to access nutrients from soil reserves. Furthermore, UMCF had a higher frequency of waterlogging, lower pH, greater soil organic matter content and higher total nitrogen, total phosphorous and base cations than LMCF soils. Global comparison or TMCF soils is severely limited by the paucity of sound comparable soil data derived from these habitats. A greater consistency in sampling, analysis and reporting is needed, as well as a standardised soil classification (Sollins, 2015). Detailed descriptions of geological substrate and local site conditions should be a standard element of research, with comparable distinct measurements between organic and mineral horizons (Bruijnzeel and Proctor, 1995; Roman *et al*, 2011).

2.7 *Regulating services*

2.7.1 *Water provisioning services*

TMCFs have vital ecosystem services through their unique hydrological processes and distinct chemical and biological niches. Freshwater provisions derived from TMCFs are essential to industry and civilisations located in the lowlands and valleys of tropic regions (Bruijnzeel and Proctor, 1995). Accentuated levels of freshwater sources are located in TMCFs due the regular enveloping orographic cloud formations and mist causing condensation on earth and vegetative surfaces (Aldrich *et al.*, 1997; Schneider *et al.*, 1999; Ray *et al.*, 2006). Upper catchment areas containing TMCF provide a stable, high-quality supply of water resources, indispensable for irrigation, hydroelectric power generation and drinking water (Bruijnzeel *et al.,* 2011). The large organic layers in LMCF and UMCF have heightened water absorbing and infiltration potential, providing a slow release, dry weather stream flow (Foster, 2001). In dry seasons rainfall in severely reduced in tropical montane environments, yet cloud cover prevails. Horizontal precipitation allows for water capture, a mechanism that accounts for 5-20% of annual rainfall (Hamilton, 1995; Bruijnzeel *et al.*, 2011). On the other hand, the absorption ability of soils, with thick root matter and dense vegetative canopies, provide able flood mitigation and erosion services, especially in times of prolonged rainfall and cyclone activity (Sidle *et al.*, 2006).

2.7.2 *Climate regulating services*

Tropical deforestation has a significant impact on the global carbon cycle through the direct increase of carbon emissions into the atmosphere and the loss of above-ground, below-ground carbon accumulation and storage capacity (Silver *et al.*, 2000). Brown *et al.* (1993) estimates that the carbon flux from tropical land use change in the pre-industrial period accounted for

around 0.06 Pg yr^{-1}, by 1990 this had increased to 1.7 ± 0.5 Pg yr^{-1}. More recently tropical land-use and land-cover change is estimated to account for between 0.81-1.14 Pg yr^{-1} (Baccini A. *et al.*, 2015) and 1.6–1.7 Pg yr^{-1} (Lal, 2004, 2005) of carbon. Houghton *et al.* (1993), reviewed the potential carbon sequestration in terrestrial landscapes of the tropics. Using forestry statistics, the potential biomass accumulation in suitable areas yielded approximately 160-170 Pg of carbon. However, the estimates for both suitable areas and accumulation potential were unspecific, with a variation of $\pm 50\%$. Whereas Brown *et al.* (1993) estimated that total carbon stock in tropical forest biomass and soils (including litter layer) in 1990 was 159 Pg and 216 Pg respectively, having a total carbon stock of 375 Pg. The contribution of tropical forests to the balance of the carbon cycle is lacking agreement, with common acceptance that tropical forests are a major global carbon store. However, their annual carbon flux as a sink or a source is vague. Earlier studies estimated that between 1.5 and 3.2 Pg yr^{-1} of carbon is sequestered through tropical forests, this was primarily accounted for through biomass accumulation in recovering forests, soils and coarse woody debris 72%, 11-17%, 11-12% respectively (Lugo and Brown, 1992). Baccini A. *et al.* (2015) calculated that over a twelve-year period (2003-2014), tropical forests were a net carbon source of 0.425 Pg yr^{-1}. This data however, did not include key factors such as soil carbon and non-woody tissues. There has now been an interception, with more common acceptance that tropical forests are an increasingly important carbon sink ($+0.1 \pm 0.8$ Pg yr^{-1}) (Machida *et al.*, 2007; Schimel *et al.*, 2014; Fatichi *et al.*, 2018). With carbon flux values close to the boundary between net source and net sink, it seems that earlier studies were correct in thinking that the carbon sequestration from recovering forests in tropical lands was almost equal to the emissions from tropical deforestation (Lugo and Brown, 1992). Several large-scale biomass inventories and growth analysis forest plot networks as well as using an eddy covariance technique in tropical primary forests, measured ecosystem level CO_2 fluxes over two decades (Grace *et al.*, 1995; Slik *et al.*, 2010). The result was that in most years primary forests provided carbon sinks, yet in dryer years forests proved to be net sources (Leuschner *et al.*, 2013). There is clear overall agreement that the halt of deforestation and continual succession of reforestation is a key method to combat human induced climate change (Houghton *et al.*, 1993; Rudel, 2001; Chazdon *et al.*, 2016; Fatichi *et al.*, 2018; Nolan *et al.*, 2018).

Tropical forests store approximately twice as much carbon in soils as mid-latitude forests, yet less than half of that of boreal forests (Kolbe *et al.*, 2016). Geographically, 55% of global forest carbon stock is located in tropical regions, 56% of this is stored in biomass and 32% in soils

(Pan *et al.*, 2011). Therefore, tropical forests account for the largest phytomass (living organic matter) carbon stores globally (Scharlemann *et al.*, 2014). Characteristics of tropical forests are well studied and the biophysical factors of carbon sequestration and carbon storage in tropic regions are increasingly understood. However, transitioning into TMCFs, above and below-ground carbon stock and sequestration potential becomes less clear (Beck *et al.*, 2008).

Scharlemann *et al.* (2014) suggest that tropical montane forests have one of the lowest organic carbon stocks by climatic region. This is contradicted by Raich *et al.* (2006) and Leuschner *et al.* (2006, 2013) who found that the carbon stock of TMCFs were equally great if not greater than LRFs. The significant carbon stock in TMCFs, particularly in UMFs is due to an increasing carbon and nutrient allocation to roots with the cost of trees above ground biomass (AGB), with increasing elevation. There was an observed coarse root biomass at higher altitudes with increased carbon investment contributing to greater soil organic carbon (Moser *et al.*, 2008). There is no overriding soil chemical characteristic that defines TMCFs, geological and mineral soil composition changes with geographical location, so it is therefore difficult to assume soil formation and carbon stock characteristics over all TMCF sites (Bautista-Cruz and Castillo, 2005). The AGB of TMCFs are another important carbon store thought to be similar in magnitude to the carbon stored in soils (Spracklen and Righelato, 2014). Although found to have less biomass storage than LRFs, a significant store of 104 Mg ha^{-1} was found in UMCFs 158 Mg ha^{-1} in LMCFs, above-ground biomass decreasing moderately with both slope and elevation (Spracklen and Righelato, 2014, 2015).

2.8 *Restoration of TMCFs and their services*

Using soil pollen and charcoal samples taken from soils within pre-montane habitats in the Cordillera de Talamanca it is clear that human disturbance has occurred here for millennia. It is suggested that the long-term conversion of TMCFs and pre-montane forests to agricultural pastures began in the Cordillera de Talamanca in at least 1400 B.P. (Anchukaitis and Horn, 2005). Regenerating forest cover on lands that were recently deforested (reforestation) and on lands that have not supported forest growth in recent times (afforestation), is thought to have high rates of initial rehabilitation of ecosystem services (Marin-Spiotta *et al.*, 2008; Martínez *et al.*, 2009). Tropical reforestation has been proposed by the International Panel on Climate Change (IPCC), as an effective method of mitigating climate change (Lal, 2004; Silver *et al.*, 2004; Marin-Spiotta *et al.*, 2008). Active and passive habitat restoration methods have been reviewed for their efficiency in regenerating ecosystem services by Silver *et al.* (2000) and

Locatelli *et al.* (2015). It is thought that active methods of reforestation such as plantations, allocating high proportions of carbon into stem wood and above-ground biomass. Passive management including natural regeneration is thought to allocate proportionally more carbon into root systems (Cuevas *et al.*, 1991; Lugo, 1992). Silver *et al.* (2000) and Locatelli *et al.* (2015) agreed in the fact that in tropical systems, natural regeneration methods rehabilitated services towards a quality that is similar to their natural function in primary systems. A higher diversity of tree and under canopy species are found within passive regeneration methods, thought to cause an increased deep and fine root biomass. This is likely to cause greater soil stabilization and infiltration rates, combined with greater initial soil organic matter accumulation, thus increasing water provisioning services, soil conservation and reduced landslide risk (Lugo, 1992; Hertel *et al.*, 2006; Sidle *et al.*, 2006). Literature suggests that ecosystem services, with a focus towards climate regulation and water provisions, initially increase rapidly following reforestation and affectation, with rates slowly plateauing overtime (Lugo, 1992; Silver *et al.*, 2000; Lal, 2004; Beck *et al.*, 2008). However, most literature is focused on regeneration of LRFs, with significantly less information about TMCFs.

3.0 Methods

The approach taken to meet the objectives of this study was to (a) undertake detailed quantification of soil and stand characteristics using replicated and comparable plots; (b) build an altitudinal subsidiary transect to understand the relationship altitude has on measured variables; (c) utilise primary and pasture plots to build comparable controls in order to balance intermediate successions.

3.1 *Study area*

The Cordillera de Talamanca is the back-bone mountain range that runs from far west Panama into central Costa Rica, separating the Atlantic and Pacific oceans. Descending into the Rio Chirripó Pacifico catchment from 2600 m to 1550 m, is Cloudbridge Nature Reserve. It is characterised topographically by steep sided ridges, a dendritic drainage pattern, dissected fluvial landforms and deep V-shaped valleys (Kappelle, 2016). Stand composition and characteristics were used to certify the natural habitat type of the study area, by comparing with existing literature such as that of Grubb and Whitmore (1966) and Kapelle (2006, 2016). Although known to be TMCF habitat, it is expected to be within lower montane zonation. Significant research has occurred in the higher reaches of the Cordillera de Talamanca, within the upper montane forest (above 2000 m), where the canopy genus *Quercus* dominates (Fig.

3.) (Grubb and Whitmore, 1966; Kappelle *et al.*, 1995; Bruijnzeel and Hamilton, 2000). Studies of pollen and charcoal in sediments revealed a nearly continuous record of human forest disturbance in mountainous regions of Costa Rica since 200 A.D. (Anchukaitis and Horn, 2005). Talamancan montane forests have a history of disturbance and deforestation, in the 1900s settlers cleared oak forests in the Cordillera de Talamanca, for timber, at a rate of 10-15 ha yr^{-1}. Subsistence agriculture utilised clearances planting crops such as corn (*Zea mays*) and beans (*Phaseolus spp.*), later introducing dairy cattle, pigs and horses to more accessible slopes (Kappelle, 2016). More recently however, after agricultural abandonment, the area of secondary forests is increasing (Silver *et al.*, 2004; Derhé *et al.*, 2016).

Fig. 3.

Large primary oak (*Quercus copeyensis*) within the upper montane forests.

3.1.1 *Geology and soil*

The geology consists of intrusive and volcanic rocks, alternated with marine sediments formed as a result of rifting from the Cocos and Caribbean plates between 15 and 35 million years ago (Holz, 2003). Local geology dominates as tertiary intrusive rock as well as Oligocene-Miocene sediments, mudstones and conglomerates and granodiorite with the occasional porphyritic rhyolite also found onsite (Kappelle *et al.*, 1995; Schruben, 1996; Schembre, 2009; Kappelle, 2016). Mineralogy of parent material intermediate in felsic and mafic composition,

granodiorite suspected to be prime weathering parent material, containing; SiO_2 (66.95%), Al_2O_3 (15.80%), Fe_2O_3 (4.05%) (Kesel and Spicer, 1985; Schembre, 2009). Soils of the area are reported as Humic Acrisols (FAO, 1975) and the soil type was further confirmed as a Humic Acrisol at each site through observation and physical analysis. The Humic Acrisols within Cloudbridge sites had an unbric A horizon, with organic matter in B horizon in some areas. Typically soils had reduced stone content in the upper 20 cm at an average of 2.5% by mass. However, subsoil had a substantially higher stone content, with presence of considerable boulders and soil depths that averaging 150cm ±33% before reaching bedrock or significant colluvium. Soil texture stayed consistent between sites, ranging from sandy loam in higher regions to silt loam in lower regions with areas of light loam. Profiles in developed TMCF remained with a dominant A horizon, typically dark and rich in organic matter. While in areas of recent disturbance (within the last thirty years), the A horizon seemed reduced with a noticeable dish-brown hue.

3.1.2 *Climate and weather*

Characterised by persistent enveloping cloud formations, the evergreen TMCF of the Cordillera de Talamanca is typically moist and cool with few restrictions from water deficit (Kappelle *et al.*, 1995). Annual rainfall was measured over four years, between 2013 and 2017 at 1550 m above sea level was 2582.9 mm. However, this is annually variable with a range of 2357.6 to 3127.2 mm. The higher of these two ranges was recorded in 2017, including two days with the highest recoded rainfall from the 4 years of data collection. On the 4th and 5th of October 2017, 298.4 mm of precipitation fell in 48 hours, as a consequence of the tropical storm named 'Nate'. Nonetheless, discounting outlier's, the annual rainfall ranges from 2357.6 to 2828.8 mm, with a mean of 2508.3 mm, showing a lesser annual variability. Represented by the Köppen climate system, Talamancan cloud forests have a clear yet variable seasonality, with a prolonged wet (*invierno* "winter") season lasting seven to nine months. Intermediately occurs a much shorter dry (*verano* "summer") period, running from December to April. Between 2015 to 2018, 91% of annual precipitation occurred within the invierno season. Driven by prevailing winds from the Atlantic Ocean, orography and temperature inversion over the Cordillera de Talamanca, the persistence of mist and cloud cover occurs even in the verano season. Regular annual cloud cover causes interception, stripping and horizontal precipitation, accounting for approximately 30% of the total annual water input, often providing a greater input than vertical rainfall in the dry season (Bruijnzeel, 1990; Cavelier *et al.*, 1996; Schneider

et al., 1999; Schmid *et al.*, 2011). The Departamento de Hidrología del Instituto Costarricense de Acueductos y Alcantarillados (AYA) weather station located at Cloudbridge, did not account for interception and horizontal precipitation. Therefore, total precipitation inputs could be as high as 3260 mm, discounting outliers.

3.1.3 *Sites, plot locations, forest types and dimensions*

Cloudbridge Nature Reserve spans over 288 ha, consisting of 255 ha of ex-agricultural land and 28 ha of primary TMCF. The surrounding land area was stratified and assessed using aerial photography and satellite imagery, while local knowledge was used to clarify history and certify time since forest disturbance. The study areas were located on three ridges within the Rio Chirripo Pacifico catchment, containing three sites (Fig. 4) of 13 plots (Fig. 5) of comparable successional land types (Table 1). The total are of forest that was covered in this study is expected to correspond to the habitat type 'TMCF', with two areas of upland grazing pasture at varying elevations. Elevation of study area remained between 1630 m and 1990 m, with a repeating trend of pasture at lower elevations (1630-1778 m) and primary forest at higher elevations (1942-1966 m). Of the three sites, two are on south-west facing slopes (206-252°) and one is on a north-east facing slope (28-62°). Degrees of slope averaged 28° between all sites, with consistency within sites (±6°) and constant within plots. All plots on the Gavilan and El Jilguero ridges were located on upper-mid slope positions, while all plots on the Los Quetzales ridge were located on the lower-mid slope position. Within all plots there was no occupation or inclusion of obvious convex zones of higher than average erosion, nor were there deposition zones of greater than net sedimentation. Areas of bulked debris, accumulated leaflitter or organic matter (example: under root area of fallen trees), were avoided within plots.

Table 1

Site information, considering plots (depicted in Fig. 4.) and succession types (depicted in Fig. 5), each site was located on a separate ridge within Cloudbridge Nature Reserve.

Site	Plot No.	Successional land type	Year of last disturbance	Altitude (m)
Jilguero	1	Pasture	2018	1630
	2	Plantation	1998	1656
	3	Natural regeneration under 30 years of age (NR <30 yr)	1998	1795
	4	Natural regeneration over 30 years of age (NR >30 yr)	1975	1911
	5	Primary	na	1966
Gavilan				
	1	Plantation	1998	1759
	2	Clearing (single comparison plot)	2017	1902
	3	Natural regeneration under 30 years of age (NR <30 yr)	1998	1922
	4	Primary	na	1942
Los Quetzales				
	1	Pasture	2018	1778
	2	Plantation	1998	1825
	3	Natural regeneration under 30 years of age (NR <30 yr)	1998	1838
	4	Natural regeneration over 30 years of age (NR >30 yr)	1975	1856

In November and December 2017, sites were stratified, assessed and established in the Rio Chirripo Pacifico Valley (Fig. a1). Each site encompassed a select variation of successional land types (Table 1), contained by a 100 m² plot with 10 × 10 m boundaries. All stems >2cm diameter at breast height (measured at 1.3 m) were identified and/or described, measured, with the location of all stems within each plot recorded (McDonald and Healey, 2000). Altitudinal variation within sites ranged between 1630-1966 m, 1759-1942 m and 1778-1856 m for El Jilguero, Gavilan and Los Quetzales sites respectively. Therefore, since altitude variation was considerable in February 2018, subsidiary plots were established over a 1000 m × 20 m transect on the mid to upper slopes of Skutch ridge. The altitudinal transect ranged from the foot of the ridge at 1680 m, to the peak at 2680 m (Fig. a2.). At every 50 m step of altitude, a 100 m² 10 × 10 m inner assessment plot was set, each with a constant aspect (100-120° east, south-east) and slope (26° ±5°). Forest type remained constant secondary forest, although there was differences in time since last disturbance. Above 2230 m, the succession type was NR >30 yr, whereas between 1680 to 2188 m the succession type was NR <30 yr. Higher elevations in the altitude transect historically had less disturbance (selective deforestation, rather than slash and burn farming) due to lesser accessibility. The disturbance histories of the forests concerned were determined using a combination of local knowledge and on-site observations of forest composition, structure and soil profiles. In some sites a layer of charcoal was observed suggesting that wildfire or slash and burn farming has occurred.

Fig. 4.

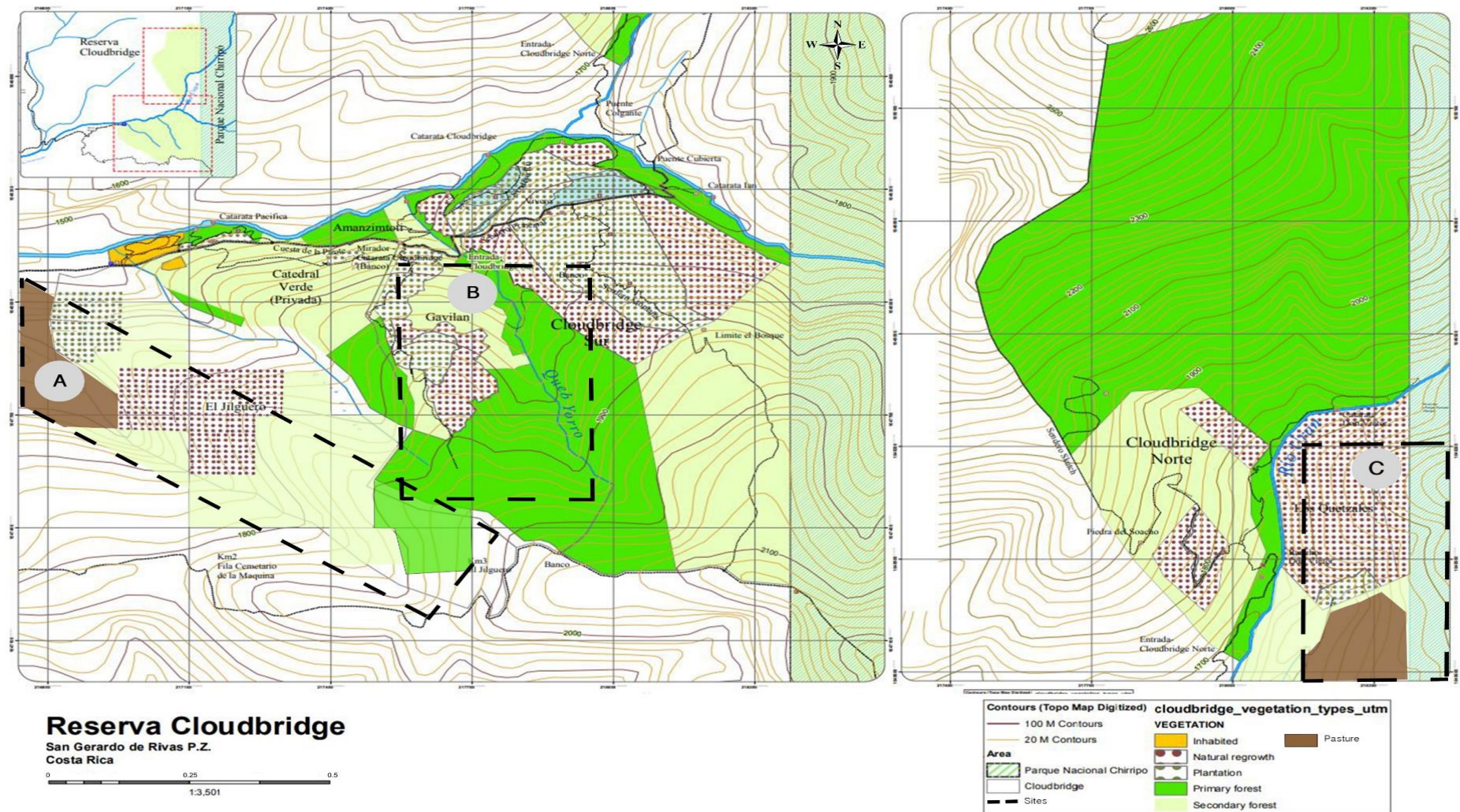Plot locations across Cloudbridge Nature Reserve and surrounding area.

Fig. 5.

Successional variation and land use with Cloudbridge Nature Reserve and surrounding area in 2017.

3.1.4 Successional land descriptions:

Historically this land was cleared in the 19th to mid-20th centuries, through government intervention to encourage agricultural development. However, in 1975 through the establishment of multiple national parks, much of the Cordillera de Talamanca was protected, for example in the Chirripo National Park that borders Cloudbridge Nature Reserve. Pasture lands typically occur in lower levels of the surrounding valleys and tributaries of Rio Chirripo Pacifico, most often below 1600 m. Some patches of remaining pasture land (~8 hectares) remained in isolation surrounded by regenerated forest at 1750 m. Typical agricultural practice in the Chirripo Valley meant that pastureland was grazed by a mix-herd of cows and horses. Livestock densities were low and pastures were dominated by weedy, hardy grasses (*Panicum spp.*) and wild flowers (*Side spp.* and *Rubus rosaefolia*), some shrubs occurred along fence lines, with few sporadic and dispersed remaining trees (Feinsinger *et al.*, 2019).

Plantations at Cloudbridge Nature Reserve have a constant management strategy, in which areas are biannually cut after a planting scheme to reduce the competition of vegetation against saplings. Since 2002, trees have been planted in most years, however, in this study, plantation plots contained trees from schemes of 2002-2006. Management strategies only occur for the first ten years, after which trees are beyond the suppression from dominating competitor plants. Tree species included in the planting schemes consisted mainly of primary forest species (*Ulmus mexicana, Quercus rapurahuensis, Cedrela tonduzi, Alnus acuminata* and *Inga oerstediana*).

On the Gavilan ridge, one plot was located in an area of clearing, previously a naturally regenerated area (<30 yr) that was dominated by the growth of ferns. Management for planting meant the ferns have been cleared biannually, in which the first clearance occurred in 2016. In consequence an area of clearing had been created surrounded by naturally regenerated forest. This site was designated for comparison reasons, to understand soil characteristics of fern dominated regeneration areas. The area had a large quantity of recently planted (2016-2017) saplings, yet due to their age, it is presumed that their effect on the land had been insignificant. Besides saplings, the clearing plot contained two shrub plants of *Viburnum costaricanum*, presumed to be left for protection reasons.

NR <30 yr plots consisted of ferns, annuals, perennial weeds, mixed growth herbaceous shrubs and pioneer trees (*Sapium pachystachys, Viburnum costaricanum, Cecropia polyphlebia, Citharexylum donnell-smithii* and *Billia hippocastanum*). These sites had been succumbed to

agricultural abandonment between 1995-2000, having no land management and regenerating naturally with no anthropogenic influence except for historic land use. They were dense in under canopy vegetation, with poor accessibility and few pioneering higher canopy species.

NR >30 yr plots were at higher altitudes (>1700 meters), in areas with reduced accessibility. Succumbed to agricultural abandonment before 1975, these sites were originally areas of deforestation for timber retrieval of predominantly oaks and other large primary species. Farmers utilised this land to gain a greater grazing area, using 'slash and burn' techniques and seeding hardy leguminous plants (*Phaseolus spp.*). Due to urbanisation, designation of the Chirripo National Park and the inaccessibility of these lands, natural regeneration of secondary forests occurred. Observation of this successional land type appeared similar to the primary TMCF. However, signs of anthropogenic activities remained, including large sawn tree stumps, old fence lines and the absence of fully mature primary species. These forests contained the tree species; *Ulmus mexicana, Cedrela tonduzi, Persea schiedeana, Inga oerstediana Ocotea spp., Alnus acuminata* and *Quercus rapurahuensis*. A significant amount of deadwood (standing and fallen) was observed, representing a transition from pioneer species (*Cecropia polyphlebia*) to old growth species (*Quercus copeyensis*).

Primary forests in the Chirripo Pacifico Valley remained at the highest altitudes (>1900 meters), in inaccessible areas where timber was difficult to remove and cattle couldn't reach. This area made up 28 hectares of the Cloudbridge Nature Reserve, but also surrounded the reserve within the Chirripo National Park. The primary forests of the Cordillera de Talamanca are famous for the montane *Quercus* forests that typically reside above 1800 m. The primary forest plots set in this study contained *Quercus spp.*, although there was a large mix of woody shrubs, pioneer and primary species (*Manilkara zapota, Alnus acuminata, Ehretia latifolia, Sapium pachystachys, Ulmus mexicana, Persea schiedeana, Ficus crassiuscula* and *Inga spp.*). These plots had open under canopies, typically high in bryophytes and veins with a large proportion of deadwood.

3.2 *Stand characteristics*

A 10×10 m grid system was established at each plot, used to measure stem location and assist with random allocation of sampling. The same methodology was repeated over all plots of each site. The stem information (see section 3.1.3) was recorded with locality, reliable up to 1m. Canopy closure was measured using a convex spherical densitometer, at an angle over five

points of each plot (Korhonen *et al.*, 2006). Presence of climbing vines and epiphytes were recorded through observation and quantified through percentage of stem hosts.

3.2.1 *Litterfall and litter stock*

Three litter traps each of 0.25 m^2 were placed randomly in each plot over January and February 2018 (Fig. a1). These were emptied and randomly replaced in the plots on a monthly basis. The foliar, reproductive material and woody debris (<2 cm diameter) contents were separated, dried at 105 °C for 12 hours and weighed. Using contents from litter traps a monthly litterfall flux could be calculated over the two typically driest months of the Costa Rican climate. The standing crop of fine litter (litter stock) was determined in March and April 2019, by harvesting all above ground fine litter, reproductive material and woody debris (<2 cm in diameter) in three randomly positioned 0.25 m^2 quadrats in each plot. The content of the litter stock was dried at 105 °C for 12 hours and weighed after separating woody debris from foliar and reproductive material. The biomass of litterfall and standing crop was determined and carbon value calculated.

3.2.2 *Root biomass*

Three 0.008 m^3 earth fraction samples were removed from a random location in each plot in March 2018. Fine earth was removed from any root structure within the sample and remailing root biomass was washed and air dried. Root biomass was then oven dried at 105 °C for 12 h and repeatedly dried until equilibrium was reached. Dry root biomass was then weighed and recorded.

3.3 *Soil physical and chemical characteristics*

3.3.1 *Moisture content*

Five soil samples were collected from each plot in February 2018 (Fig. a1). Surface litter stock was removed before coring five randomly located bulked individual samples, taken to a depth of 15 cm with a core of 100 cm^3 in volume. Samples were dried at 105 °C for 12 h, weighed then dried for a further 2 h to ensure equilibrium was reached, recording moisture content for each sample.

3.3.2 *pH and electro conductivity (EC)*

Five composite soil samples were taken from each plot in March 2018, consisting of three randomly located individual bulked samples. Removing surface litter before coring to the depth

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of 15cm across the soil profile of horizons. Within laboratory conditions, each soil sample was air dried between 25 and 30 °C. A fine earth fraction was created using a 2 mm sieve, removing root and rock intrusions. From the fine earth fraction, suspensions were created from 10 g per 25 ml of deionised water. Each composite soil solution was hand shaken for 15 minutes. The suspension was stirred before inserting the pH glass electrode (Hanna, HI-991003) and the suspension was swirled over the electrodes, measuring the pH after >30 seconds, once the measurement had become stable. This procedure was repeated using an EC (Hanna, HI-8733) sensor.

3.3.3 *Infiltration rates*

During March 2018, infiltration rates were recorded in five random locations within each plot, to compare soil compaction, soil drainage potential and as an indication to water provisioning services. Removing the surface litter stock, a 100 cm^3 bulk density ring with a diameter of 510 mm was dug 5 mm into the soil surface. Filled with 100 ml of water, the time of infiltration was recorded, if infiltration was not completed, the percentage infiltration was recorded.

3.3.4 *Further laboratory analysis*

Translocation of soil samples was required from Costa Rica to Bangor University SNS Research facilities, Gwynedd, UK for the following analysis: i) bulk density, with soils cores of 100 cm^3 calculated from dry mass/volume; ii) total carbon and total nitrogen analysis was recorded using a Leco Truspec CNElemental analyser; iii) organic matter content – measured though loss on ignition, using a Carbolite CWF 1200 furnace at 450 °C for 16 hours.

3.4 *Carbon stocks*

Below ground carbon stocks (CS) were calculated from the carbon proportions (CP) of dry soil bulk density (BD), using the following calculation:

CS = BD x CP

Where bulk density was calculated using over 100 cm^3 and made equivalent to a hectare and the proportion carbon was calculated at 100th of the total carbon value. Bulked samples from a 20 cm profile were used for this calculation, therefore the carbon stock is representative of that depth.

Above-ground biomass was calculated using equations from Brown (1997), Chave *et al.* (2004) and Matthews and Mackie (2006) and specific gravity values acquired from Baker *et al.* (2004)

and Chave *et al.* (2005) . However, quantification of above-ground biomass was unreliably concluded, due to a means of scientific equipment and time constraints. Therefore, an approximate form factor, derived from tree volume and density, was measured and used in this study.

3.5 *Altitudinal transect*

Three composite samples were collected from each plot in February 2018. The samples were composites of five randomly located individual sites. Surface litter stock was removed before coring bulked samples over a depth of 15 cm. Analysis for moisture content (section 2.3.1) was tested on site at Cloudbridge laboratory unit. Dry samples were translocated to Bangor Research Unit and tested for total C+N, organic matter content, and the bulk density was calculated (section 2.3.4).

3.6 *Statistical analysis*

Three succession types; primary, pasture and NR >30 yr obtained an N value of 10, whereas plantations and NR <30 yr obtained an N value of 15. All data was assessed using the statistical package IBM SPSS statistics 25. All data was checked for normality and homogeneity of variances, using the Shapiro-Wilk test. Normally distributed data was tested using a one-way ANOVA and Tukey post hoc test, whereas data violating homogeneity of variances was subject to the Welch ANOVA and Games-Howell post hoc test (Draper and Smith, 1998). Significant difference was reported at the 95% level, unless otherwise noted and values reported in the text are means ±1 SE, unless noted otherwise. Pearson's correlation was used to highlight differences between all nominal, continuous independent variables, with significance reported at the 95% level.

The altitudinal transect was analysed for normality and homoscedasticity. After detection of heteroscedastic data, log transformation was used producing a normally distributed output. A linear regression was used to discover the relationship between altitude and organic matter content, total carbon and total nitrogen, proceeding with a Pearson's correlation to retrieve further evidence of relationship. Significance between correlations was derived using analysis of variance, differences were reported at the 95% level.

4.0 Results

4.1 *Forest characteristics*

All 11 forested plots corresponded to the TMCF habitat type, specifically allocated as lower montane cloud forest. This was indicated by species composition and stand characteristics, that were classified in having lower TMCF distributions discussed in section 3.1 of this paper. Species known to be dominant in upper montane forests (*Quercus copeyensis* and *Quercus costaricensis*), were found in the primary plots, with understory species (*Geonoma orbignyana, Anthurium concinnatum* and *Lauraceae spp.*) expected in lower montane forests. NR >30 yr had a mixed range of primary species (*Quercus spp. and Igna spp.*) and pioneering, light demanding species (*Chusquea, Lauracea, Geonoma and Cecropia spp.*) expected after disturbance. NR < 30 yr plots contained only understory and pioneering species, whereas plantations contained species similar to NR >30yr, but the trees were younger. Although observed differences were found between plots, overall species number and composition did not change significantly between forested succession types. Pasture plots corresponded to least productive upland pasture, dominated with hardy *Panicum* grasses and various annual and perennial wildflowers. Due to proximity, historic evidence and characteristics, it is presumed that if abandoned, pasture plots would regenerate into secondary forests of TMCF habitat type.

Stem density averaged 2033stems (>2 cm) ha^{-1}, across all succession types, excluding pasture. The highest stem density was recorded in primary forest plots, followed by NR >30 yr, NR <30 yr and plantation plots respectively. The basal area was greatest in the primary and NR >30 yr forest plots, significantly greater than NR <30 yr and plantation plots. Canopy closure was significantly different between nearly all succession types (Table 2). The highest canopy closure was recorded in primary and NR >30 yr plots, followed by plantations, with the lowest canopy closure in NR <30 yr plots after pasture (Table 2). Tree heights were not significantly different across successional types having an average of 8.25 m between all forested sites. Although primary and NR >30 yr, consistently contained the largest trees up to 29.67 m, averages were reduced due to the high concentrations of under canopy species. The above-ground biomass increased with time since agricultural abandonment, with primary forests containing the highest above-ground biomass at 37.74 Mg ha^{-1}, significantly higher than plantation and NR <30 yr plots. Between the two active and passive management methods of reforestation, plantation plots contained a higher above-ground biomass than NR <30 yr, but was not significant.

The altitude of succession types varied significantly, showing a positive correlation between time since disturbance and altitudinal gain. Primary plots at the highest altitudes, averaging 1954.00 m, NR <30, >30 yr at intermediate altitudes (1883.50, 1851.67 m respectively) and plantation and pasture plots recorded at the lowest altitudes at 1746.67 and 1704.00 m respectively.

Table 2
Soil and stand characteristics, succession type means and standard deviations, bold letters indicate significant differences between forest succession types at *p<0.05, **p<0.001 or ***p<0.0001*, ns = non-significant. Soil carbon stock is representative of the top 20 cm of soil profile.

	Pasture	Plantation	NR <30 yr	NR >30 yr	Primary	ANOVA
Soil characteristics						
pH	5.37 ± 0.37	5.05 ± 0.23	5.17 ± 0.30	5.04 ± 0.70	5.20 ± 0.30	ns
Electro conductivity (mS cm^{-1})	87.11 ± 16.32 **a**	100.39 ± 29.83 **a**	94.69 ± 26.18 **a**	160.62 ± 66.52 **b**	120.41 ± 37.15 **b**	*
Bulk density (g $^{cm-3}$)	0.71 ± 0.05 **a**	0.52 ± 0.08 **b**	0.51 ± 0.06 **b**	0.34 ± 0.09 **c**	0.39 ± 0.11 **c**	***
Soil moisture (%)	14.02 ± 2.26 **a**	24.09 ± 4.27 **b**	24.3 ± 3.21 **bc**	30.38 ± 5.95 **c**	33.44 ± 7.80 **cd**	***
Total nitrogen (%)	0.41 ± 0.09 **a**	0.59 ± 0.23 **a**	0.49 ± 0.14 **a**	1.38 ± 0.68 **b**	0.78 ± 0.43 **ab**	***
Ratio (C:N)	16:1	14:1	10:1	13:1	13:1	ns
Soil Carbon stock (Mg ha^{-1})	61.78 ± 21.34 **a**	61.59 ± 21.83 **a**	52.03 ± 12.35 **a**	113.16 ± 23.45 **b**	67.39 ± 20.00 **a**	***
Stand characteristics						
Stand density (stems ha$^{-1)}$)	na	1533.33 ± 513.16	1900 ± 300	2200 ± 565.68	2500 ± 282.84	ns
Tree height (m)	na	9.39 ± 4.36	6.52 ± 3.36	7.74 ± 4.92	9.05 ± 7.37	ns
Basal area (m^2 ha^{-1})	na	22.89 ± 11. 07	21.55 ± 3.87	64.99 ± 19.81	82.92 ± 16.00	ns
Canopy closure (%)	4.43 ± 1.34 **a**	77.72 ± 4.16 **b**	70.97 ± 6.39 **b**	87.67 ± 2.26 **c**	89.32 ± 2.07 **c**	***
Litterfall (kg ha^{-1})	18.15 ± 4.31 **a**	474.3 ± 256.24 **b**	465.81 ± 159.45 **b**	644.32 ± 256.06 **b**	511.27 ± 181.59 **b**	***
Litter stock (Mg ha^{-1})	0.14 ± 0.05 **a**	1.74 ± 1.21 **b**	1.08 ± 0.71 **b**	2.37 ± 1.45 **b**	1.14 ± 0.57 **b**	*
Root biomass (Mg ha^{-1})	0.46 ± 0.42 **a**	1.71 ± 1.12 **b**	1.77 ± 0.54 **bc**	4.02 ± 2.1 **d**	3.01 ± 1.15 **cd**	**
Land characteristics						
Altitude (m)	1704.00 ± 78.00 **a**	1746.00 ± 71.98 **a**	1852.67 ± 54.59 **b**	1883.50 ± 28.99 **bc**	1954.00 ± 12.65 **c**	***
Slope (º)	27.00 ± 2.58	28.40 ± 3.56	27.93 ± 2.79	28.60 ± 2.27	26.90 ± 2.18	ns

4.2 *Above and below-ground interaction*

Litterfall, litter stock and root biomass were all significantly greater in forested plots compared with pasture plots (Table 2). Litterfall and litter stock resembled a similar trend to canopy closure, increasing with time since agricultural abandonment. However, primary forest litter stock was intermediate, lower than NR >30 yr and plantation plots. All forested plots had average monthly litter fall input of 523.92 kg ha^{-1}, whereas pasture plots received 18.15 kg ha$^-$

[1] of litter fall. Total root biomass (0-20 cm) dry weight was significantly different between all succession types. The largest root biomass occurred in NR >30 yr and primary plots (4022.92, 2903.33 kg ha^{-1} respectively) followed by plantation and NR <30 yr (1706.00, 1765.85 kg ha^{-1} respectively). Within the single comparison clearing site on Gavilan ridge, root biomass was slightly higher than the plantation and NR <30 yr plots, whereas litterfall lacked significance and canopy closure was similar to that of pasture.

4.3 *Soil characteristics*

The soil characteristics typically presented the same or similar trends between succession types. Soil organic matter content, total soil carbon, total soil nitrogen, electro conductivity and soil carbon stock were all greater in NR > 30 yr plots, slightly above that of primary forest plots, significantly higher than pasture, plantation and NR <30 yr plots. Pasture consistently had reduced soil conditions, with plantation and NR < 30 yr plots intermediate between pasture and primary (Table 2). Total soil carbon and nitrogen presented the same trend between succession types at an averaged 13:1 ratio (Fig. 6[a]), similar to that of organic matter content (Fig. 6[b]). There was 113.16 ± 23.45 Mg ha^{-1} of soil carbon in the top 20 cm profile of NR >30 yr plots, over double the carbon stock of NR <30 yr. The carbon stock of all other plots did not significantly differ, although, primary plots recorded the second highest soil carbon stock at 67.39 Mg ha^{-1}. Electro conductivity increased steadily from pasture to NR <30 yr and plantation with no significance, then increased further in primary and NR >30 yr plots which were significantly higher. On the Gavilan ridge the single comparison clearing plot site had the highest levels of total soil carbon, soil organic matter content and soil moisture content. A significant relationship was found between independent variables, where a strong positive relationship was found between organic matter content and total carbon, with litter fall, canopy closure, stem density and root biomass.
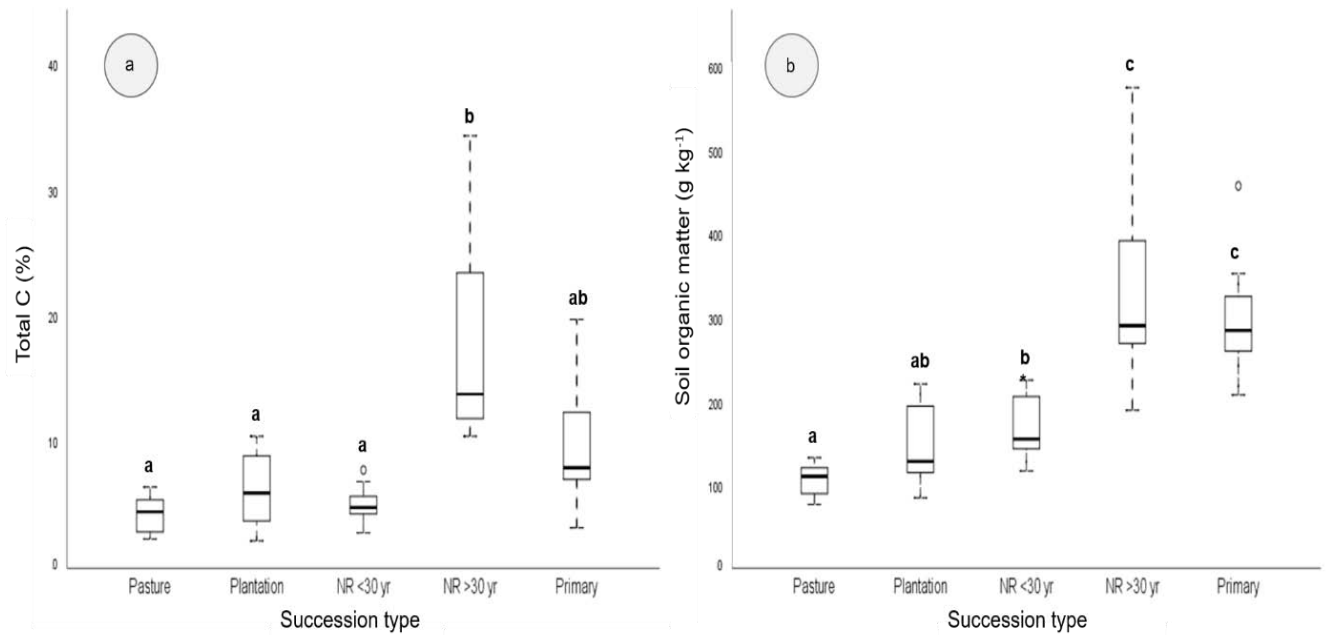
Fig. 6.
Total soil carbon (a) and soil organic matter content (b) of different succession types. Bold letters represent significant variance ($p<0.05$), between each succession type for both (a) and (b).

Soil pH showed no significant variation between succession type. Although all plots contained slight acidic soils, with increasing acidity with time since disturbance. Soil moisture was significantly lower in pasture plots, having greater soil moisture content with time since disturbance, yet forested plots lacked significant variation. Infiltration rates were significantly reduced within pasture plots, increasing rapidly with each successional type from plantation, NR <30 yr, Nr >30 yr and primary respectively (Fig. 7). The higher rates of infiltration were recorded in primary forest plots, however, with a larger range. Between the two young succession types, NR<30 yr had higher rates of infiltration at 2.31 ml s^{-1}.
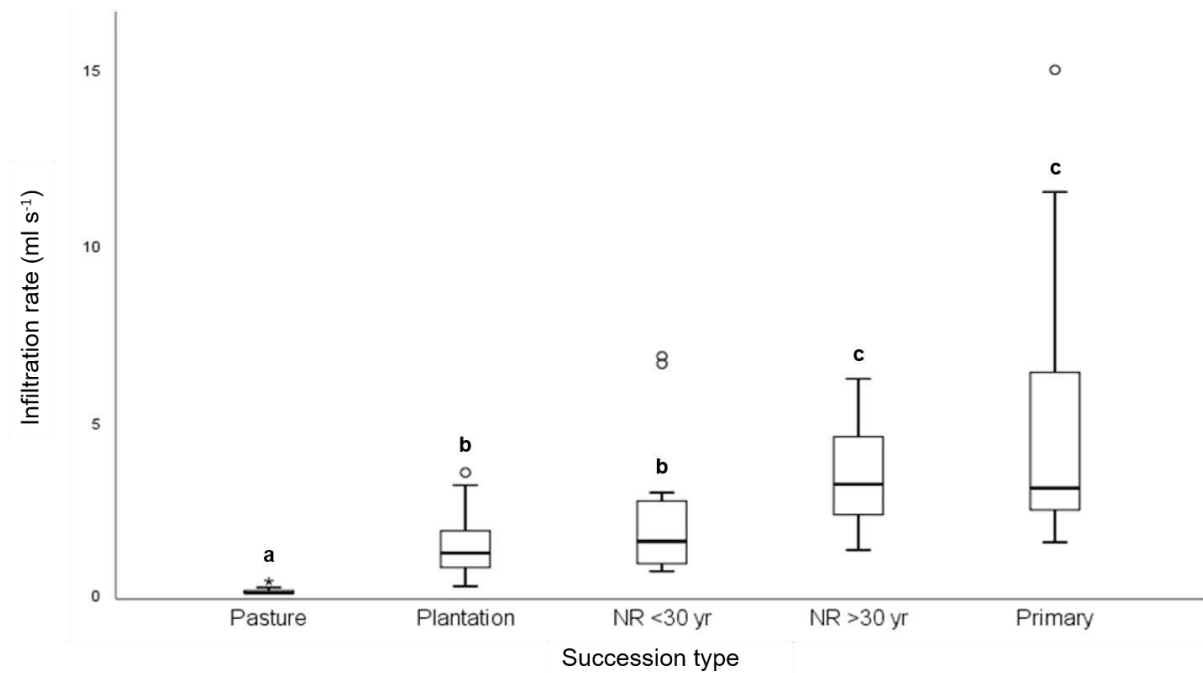
Fig. 7.
The variation of soil-water infiltration rates across different succession types, bold letters indicate significant differences between types ($p<0.05$).

4.4 *Altitude subsidiary transect*

As a combined altitudinal transect there was a positive relationship recorded between altitude and total soil carbon and soil organic matter content. Altitudinal accounted for 59% and 62% of carbon and organic matter content respectively ($P<0.0001$). Altitude had a lesser correlation with total nitrogen, although, still presented significant correlation ($p<0.05$). However, individually analysing the altitudinal subsidiary transect in their separate ages since disturbance, meant that different results were obtained. In the lower (1680-2188 m) section, altitude accounted for 32% and 39% of total carbon and organic matter collectively ($p<0.001$), and no variation in nitrogen was found. In the upper section (2230-2680 m), where there was no recent human disturbance, no significant correlation was found between altitude and total carbon and organic matter content, altitude accounting for <10% of the slight positive relationship. Nitrogen did have a significant correlation with altitude in the upper section of the altitudinal transect, with a slight positive correlation where 17% of the relationship was explained.

Exploring the variation of soil characteristics across the lower segment of the altitudinal transect, further separation was found between 1680-1880 m and 1927-2188 m (Fig. 8). Using one-way analysis of variance, significant differences in total carbon and organic matter content

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were found between the three segmented altitude groups (Fig. 8). Total nitrogen only differed with significance between the lower and uppermost altitude groups. Within each section altitude did not significantly account for variation in total soil carbon, nor soil organic matter content explaining <25% and <20% of the relationship respectively.
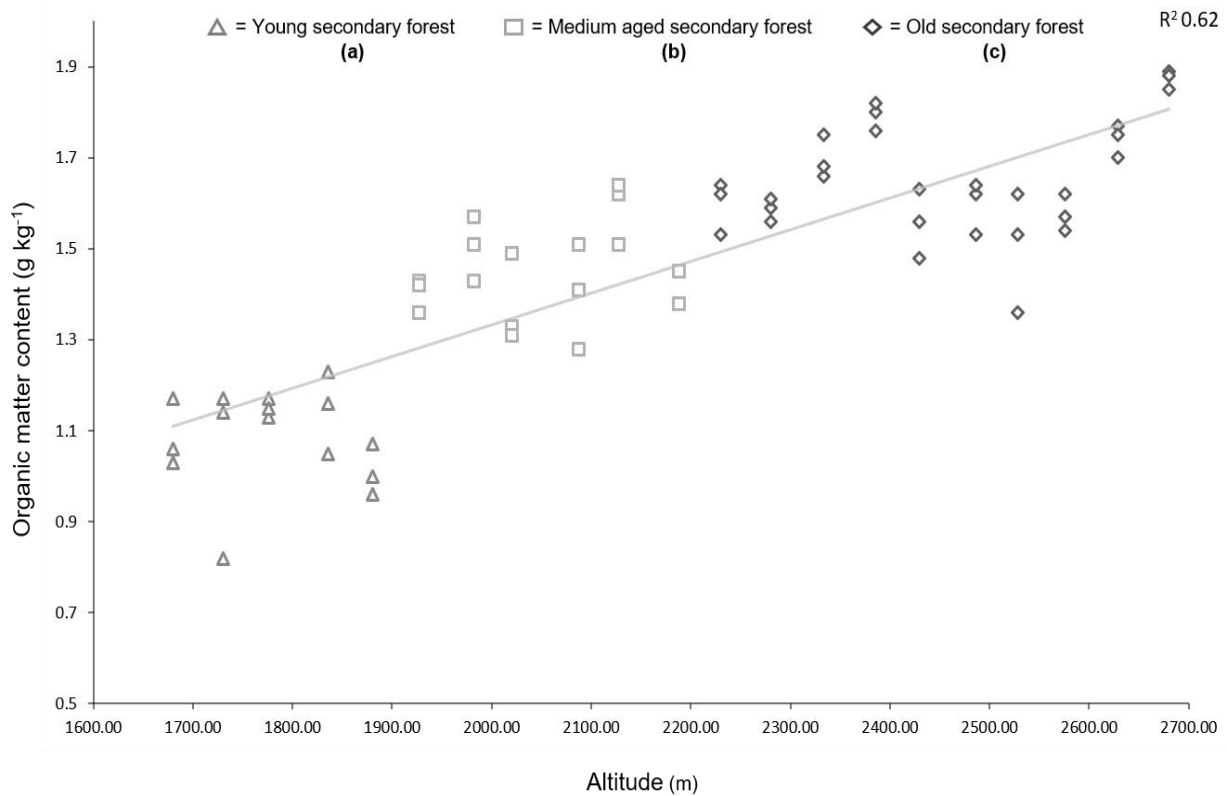

Fig. 8.
The relationship between altitude and organic matter content, each grouped scatter (a), (b) and (c) representing significant variation (*p*<0.001) between succession ages and the trend-line representing R^2 value of the total relationship.

5.0 Discussion

5.1 *Forest characteristics*

The forest composition and characteristics of planted and younger naturally regenerated plots suggest that after agricultural abandonment, forest stands in this area are progressing towards their natural state. Species composition of primary and NR >30 yr plots corresponds to TMCFs and LMCFs of the Cordillera de Talamanca (Delyser, 2010; Kappelle, 2016). However, under canopy upper montane species such as *Chusquea spp.* stated by Kappelle (2016), were found in confirmed lower montane forests of this site (Widmer, 1998; Tabarelli and Mantovani,

2000). The quantity of species across the plots in this study were far less that than other studies in the same system. Although, this is likely to be a consequence from difficulties of species identification, with a lesser focus towards species richness and diversity of vegetation, similar to that of Silver *et al.* (2000).

The positive correlation of stem density with time since disturbance was expected, with primary plots having the highest density. However, the restoration of 68% of primary stem densities within plantation and NR <30 yr plots is a significant success, being higher than other studies of reforestation at similar and greater ages (Silver *et al.*, 2004; Garcia *et al.*, 2016). Basal areas of primary and NR >30 yr was significantly large, greater than other studies of the same habitat type (Hafkenscheid, 2000; McDonald and Healey, 2000; Kappelle, 2006). The reason for noticeably large basal areas in this study is likely to be caused by an un-proportional amount of large individual primary trees within the study area. With a significant sized tree within a 100m^2 plot, it is unlikely to be representative of the entire hectare. Therefore it is recommended that if large trees are recorded within sampling areas, the plot size should be increased in benefit of proportional representation. Tree height didn't significantly differentiate between forested succession types, even though 10% of the largest trees were found in primary and NR >30 yr plots. The reason for reduced significance between succession type is because most NR <30 yr and plantation plots contained light demanding fast growing pioneer species (Quilici and Medina, 1998; Tabarelli and Mantovani, 2000), as well as reduced means from under-canopy trees. Comparing the rates of reforestation of TMCF within other studies, it seems that the recovery of forests after agricultural abandonment in Cloudbridge Nature Reserve is highly effective. Forest characteristics such as basal area, tree height and stem densities were all equal to or greater within Cloudbridge plantations compared to those of Lugo (1992) and natural regenerated forests at the same ages of McDonald and Healey (2000). Planted plots did have further developed stands than the younger naturally regenerated plots, having greater basal area, tree height, canopy closure and litter fall. This may represent a slightly quicker habitat restoration method, although significance was not found (Table 2).

Where many of the stand characteristics such as litterfall and root biomass increased with successional age, the content of soil organic matter also increased. This is to be expected, being a clear characteristic of a primary TMCF forest (Schneider *et al.*, 1999; Foster, 2001). Accumulations of organic matter represents attributes such as reduced microbial activity, combined with the unique cool and moist climate system (Grubb, 1977; Vance and Nadkarni,

1990). Therefore, the steady increase in soil organic matter content between forest succession types in this study shows the success of restoration.

5.2 *Altitudinal relationships*

Originally, this study aimed to design and coordinate one altitudinal subsidiary transect over 1000 m in vertical gain, to distinguish the relationship between altitude variation and soil carbon stocks as a control. However, as the experiment was initiated, it was clear that the transect was split into two different succession types. Soil analysis exposed a significant charcoal layer, and after local communication it was understood that the lower proportion (1680-2188 m) was anthropogenically disturbed within the last thirty years. Therefore creating two sections of the transect that are unreliably comparable. Analysing the transect over the total 1000 m in elevation gain, found a strong positive relationship between altitude and below-ground carbon stock. This study suspects that this relationship is actually picking up on the reduced soil organic matter contents from the lower areas that have had recent disturbances. Analysis of the transect as two separate sets of data justified this, presenting a slight correlation, yet largely reduced. Further analysis of the organic matter data identified an additional conglomerate group of data points at the lowest altitude (Fig. 8). It is thought that these three groups represent three successional stages along the altitudinal transect, with the most recent disturbance to lower and more accessible boundaries of the ridge. Although these findings have reduced the replication and reliability of the altitudinal control, it cements the hypothesis that disturbances reduce soil organic matter content and carbon stock. In this study altitude seems to have a positive, yet slight impact on below-ground carbon content. However, disturbance seems to be the greatest impact to total soil carbon and soil organic matter content. Additional analysis is needed, using reliable primary forests with no recent disturbance, which may well be difficult since reduced elevation attracts historic disturbance.

There are clear causal relationships driven by altitudinal factors within tropical forests. This is largely due to interdependent variables such as temperature, rainfall and the unique climatic systems found in mountain regions (Schneider *et al.*, 1999). As consequence net primary productivity and gross photosynthesis of trees decrease with altitude, causing the stunted effects in TMCFs. However, root densities and production increase with elevation with marked shifts of carbon investment in root metabolic activity to the production of root structures (Leuschner *et al.*, 2006, 2013). Altitude plays a key function in the characteristics of TMCFs,

although the exact significance of this function on specific characteristics and regulating services within TMCF systems needs to be expanded and identified with further research.

5.3 *Provisioning of ecosystem services*

Naturally rich in species, many TMCF habitats are considered biodiversity hotspots, high in ecocentric value, key for restoration and protection (Doumenge *et al.*, 1995; Aldrich *et al.*, 1997; Bubb *et al.*, 2004). However, these ecosystems are also anthropocentrically important though their provision of ecosystem services. In this study, infiltration rates increase with succession types. This significantly correlates with the organic matter content of soils, directly related to litter fall and particularly root biomass. The typically high root biomass from diverse and developed montane forests, provide not only stabilisation of the soil structure, but increased porosity, some studies finding key relationships with soil fauna (Leuschner *et al.*, 2006; Bauhus, 2009; Nottingham *et al.*, 2013).

 Infiltration is a particularly important component of water regulation within montane forests. Annual cyclonical events driven by Atlantic low-pressure systems, bring up to 3000 mm of precipitation within the invierno season. The conversion of TMCF into agriculture, seen in this study and others, causes reduced soil organic matter content, smaller A-O horizons, open canopies and soil compaction by grazing animals, with reduced litterfall and root biomass. These perturbations degrade the regulation of water provisioning services. Slow infiltration rates of water and high volumes of surface runoff, with a potentially reduced soil stability, increases the risk of landslides and soil erosion causing reduced water quality and diminished drought resistance (Bruijnzeel, 2005; Sidle *et al.*, 2006). After the tropical storm 'Nate' in October 2017, landslides removed vast amounts of agricultural land, disrupting infrastructure especially in and between mountain towns (Lopez, 2018; Smith, 2018). Intensified tropical precipitation in the invierno season annually removes huge soil reserves, diminishing carbon stocks and reducing land fertility. Disruption across down-steam areas results in a huge economic and environmental loss (OECD, 2018). This study, supported by literature, shows that within fifteen to twenty years of reforestation and afforestation of TMCFs, major rehabilitation of ecosystem services can occur. Infiltration rates are recovering to 40-50% of primary forest systems, causing slow release of water inputs, potentially reducing stream flow and river loads. Infiltration and natural filtration of water through soil profiles is also a key function towards the provision of drinking water, especially important in verano seasons and in times of drought. As seen by Schneider *et al.* (1999) and Schmid *et al.* (2011), cloud

interception in TMCF systems account for as much as 30% of total water input in dry seasons. A significant quantity in times of water shortage and stress.

5.4 *Carbon stocks and climate regulating services*

The ecosystem service of climate regulation was the key focused of this study, concentrating on soil organic carbon stocks in particular. The IPCC have regarded reforestation within tropical biomes as being essential in the mitigation of global climate change (Lal, 2004; Silver *et al.*, 2004; Marin-Spiotta *et al.*, 2008). Soils carbon stocks in this study were found to be intriguingly high in older naturally regenerated and primary forests. With carbon stocks twice as high as young naturally generated forests and significantly higher than lands of grazing pasture (Fig. 6). Even though carbon stock trends are affected by interrelated variables, it is likely that the compaction factor of soils within areas with reduced time since disturbance is an impounding factor. The surprisingly high carbon stock found within pasture soils, being above plantation and young naturally regenerated plots, is likely to be affected by soil compaction. Compaction is not accounted for within this stock calculation, however, soil samples were bulked rather than being cored directly. Therefore, compaction should have been less impacting as a factor of influence. Values of 113.16 ± 23.45 Mg ha^{-1}, lie within the expected carbon stock of tropical forests according to Lal (2005) and Scharlemann *et al.*, (2014), although their calculations were not depth specific. Lugo and Brown (1993), Hertel *et al.* (2006) and Spracklen and Righelato (2014) all state the potential carbon storage capacity of TMCFs is up to ten times greater in organic horizons of old growth montane forests, than LRFs and early successional montane forests. Most carbon stocks in old growth forests exist at around 200 Mg ha^{-1} in the top 30 cm soil profile, with significantly reduced carbon stock in mineral soils, around a tenth of the size (Roman *et al.*, 2011; Kappelle, 2016). However, the significantly high carbon stocks in late successional forests in this study are difficult to explain. Even though relatable in size to other similar studies, primary forests have been seen to typically have higher carbon stocks than late successional forests, usually due to the developed and mature organic horizons. It may be causal from similar relationships found in section 3.2 of this paper, with variables such as organic matter content and total carbon. A suggestion can only be made to further explore these results, with a study focused on carbon stocks, looking at specific interrelated variable such as total fine root content and rated of organic decomposition.

The above-ground carbon stock of TMCFs is uncertain and infrequently discussed, with no apparent biomass expansion factors and rare expressions of specie specific wood densities. In

this study we used generic tropical expansion factors and dry weight densities. Therefore, results are likely to be unspecific to the species found within TMCF plots. However, the trends found should be representative and true. Being in that the above-ground biomass in primary plots were greatest of all succession types, followed by NR >30yr, plantation plots and NR <30 yr respectively. The results from above-ground biomass in this study were significantly lower than other tropical montane forests at 137, 287 and 183 Mg ha^{-1} in Puerto Rico, Jamaica and Ecuador respectively (Spracklen and Righelato, 2014). Spracklen and Righelato, (2015) found that in Ecuador tropical montane forests, above-ground biomass in secondary forests of twelve to fifteen years was 128.8 Mg ha^{-1} increasing to 134.1 Mg ha^{-1} in forests over 40 years of age. Quantification of above-ground carbon stocks were not quantified in this study, with reasoning explained in section 2.4 of this paper. However, Silver *et al.* (2000) found that after agricultural abandonment in tropical forests the fastest rates of above-ground biomass accumulation occurred within the first twenty years of regrowth (6.17 Mg ha^{-1}). The overall rate of accumulation over a 60-year period was 2.36 Mg ha^{-1}. Rates of above-ground carbon sequestration mirror this trend, having an exponential increase in the first 10 years, plateauing off between fifteen to twenty years. Marin-Spiotta *et al.*, (2008) found carbon sequestration rates of over 50 Mg ha^{-1} in the first twenty years of secondary tropical wet forests of the Neotropics. Literature suggests TMCF store significantly less above-ground carbon, than LRFs (Spracklen and Righelato, 2014, 2015). However, this study suggests more research is needed on the diluted understanding of carbon storage within TMCF and the balance between above and below-ground carbon stocks. There is potentially a significant amount of carbon potential within epiphytical mass and canopy soil within TMCFs, adding to the above-ground biomass which is matched by soil carbon stocks (Fehse *et al.*, 2002; Köhler *et al.*, 2007; Hertel and Köhler, 2010; Karspu and Palmira, 2011). It is clear, however, that regenerating TMCFs provide substantial climate regulating services within below-ground carbon stocks and above-ground biomass, including epiphytical mass.

5.5 *Associations and relationships*

TMCFs have an observed and measured reduced productivity, causing stunted stands and gnarled features especially in UMCFs. The reasons for this are low radiation inputs due to persistent cloud cover, low average temperatures and low nutrient availability caused by saturated soils, furthered by a low nutrient uptake capacity by roots with stunted respiration or transpiration (Edwards and Grubb, 1977; Bruijnzeel and Veneklaas, 1998). In this study total nitrogen was found to increase with time since agricultural abandonment, with an exception

that NR >30 yr had higher total nitrogen than primary. It is likely that the total nitrogen does not represent nitrogen availability to biota, since mineralisation and nutrient form are not accounted for. Carbon, nitrogen ratios were comparably low across all Cloudbridge plots, suggesting potentially rich nitrate soils, since carbon was also comparably high (Mcgroddy *et al.*, 2004; Soethe *et al.*, 2008). Edwards and Grubb (1977) also found TMCF sites with nitrogen rich soils, attributing their findings towards nutrient rich soil parent material.

A repetitive trend was found that considered multiple measured variables within this study. Soil characteristics of NR >30 yr, were greater than those of primary forests. This is likely to be associated with the fast development of stand structures, dominated by pioneering species, applying high energy inputs into root development and tree height (Tabarelli and Mantovani, 2000; Röderstein *et al.*, 2005). A transitioning phase from pioneer species to primary species begins in secondary forests after reaching peak productivity, usually after 30-60 years in these TMCFs. It is likely that the high organic matter content in NR >30 yr is derived from the turnover of fine roots, a key process in the carbon budget of montane habitats (Hertel and Leuschner, 2010). Increased diversity and mixed residual species commonly cause root biomass development, with a thick organic matter reserve often found atop of the mineral horizon, it is here where fine roots can reach very high densities (Hertel *et al.*, 2003). It is this association in which is likely to have caused such high recordings of organic matter content and total carbon within NR >30 yr soils. In primary forests however, with a prolonged climatic community, it is believed that the organic matter and carbon reserves become relieved and reach an equilibrium slightly lower than forests of late successional development.

6.0 Conclusion

The results presented in this study show a clear relationship between the successional development of LMCFs and the rehabilitation of water provisioning and climate regulating services. With further development in that late successional forests contain a potentially greater value in climate regulating services than the original primary forest. Habitat restoration of TMCF systems could provide low-cost, anthropocentric and ecocentric provisions, specifically in this study region regarding carbon sequestration and flood mitigation. Tropical montane forests have suffered a dramatic decline across the Neotropical Americas and have a huge potential for restoration. Agricultural abandonment of montane pastures has driven a growth of secondary forests with a TMCF habitat type. However, new enlightenment of the services that these restored habitats provide could help overcome barriers to dispersal and

establishment. Carbon reward schemes are a current incentive towards habitat restoration, likely to increase in coming years. Governmental and institutional recognition of TMCF services could be a significant driving force towards the future restoration and protection across the entirety of tropical montane systems.

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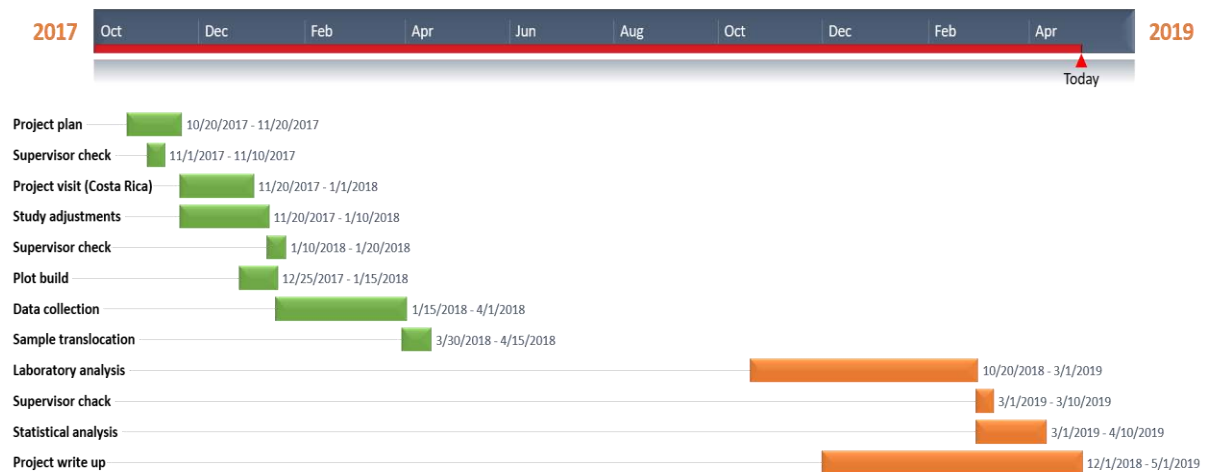
Appendices

Fig. a1.

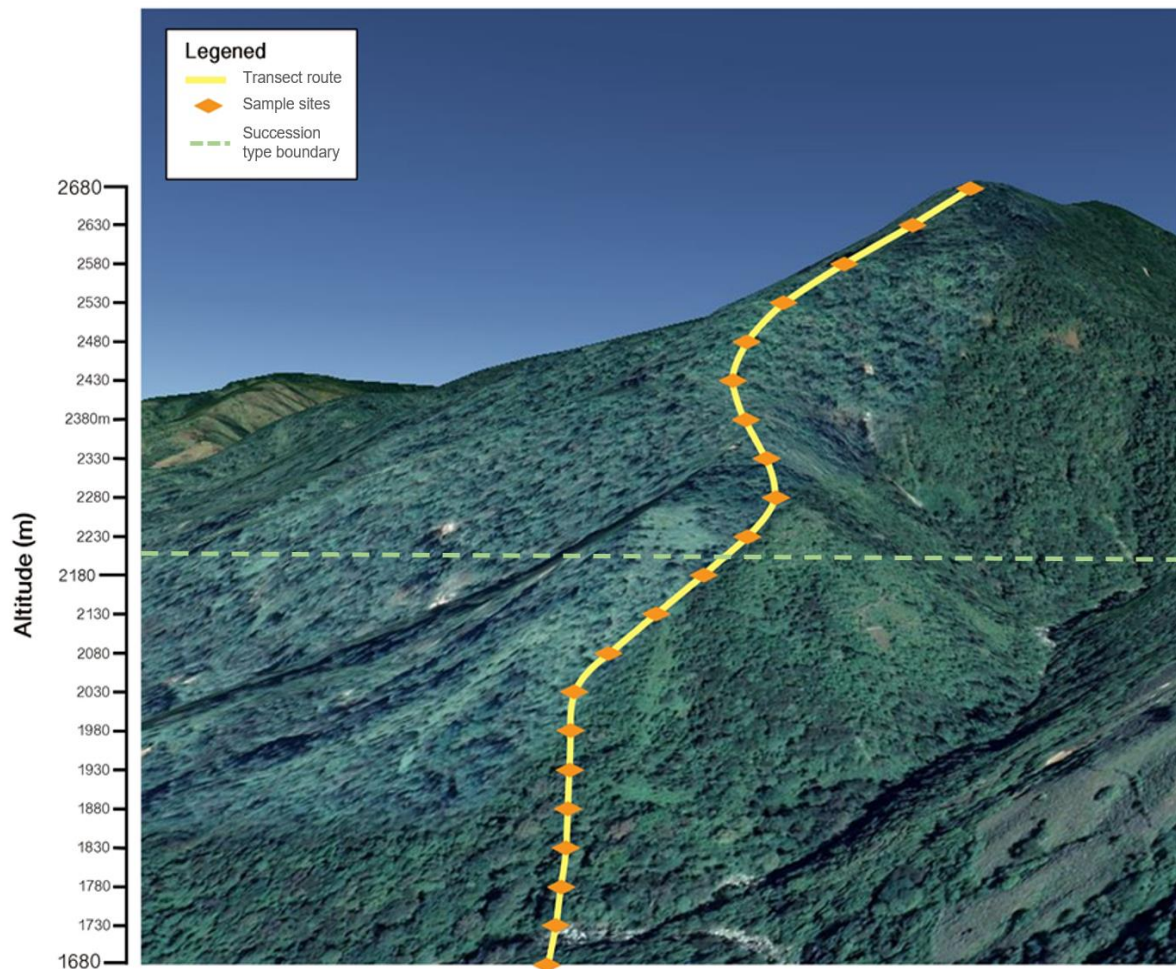Gantt chart of the project timeline.

Fig. a2.

Transect route and sample locations of the subsidiary altitude transect on Skutch ridge. Original image ©CNES, Google Earth.