A practice-led assessment of above-ground biomass restoration potential in a biodiversity hotspot

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Abstract

Restoring natural ecosystems, including through restoring AGB in tropical woody vegetation types, can be an effective means to mitigate biodiversity loss and climate change. However, increasing human demand for land and resources means that achieving this at scale will not be a straightforward task. I developed a framework to facilitate decision-making with regards to where and how to restore AGB, testing this in a 5.3M ha biodiversity hotspot in East Africa. Firstly, I used remotely-sensed spatial reflectance and climate data to up-scale plot-based AGB measurements across the region to estimate current and former AGB and therein AGB deficit. I then determined: (1) appropriate methods to restore AGB in areas with deficit; (2) the costs of their implementation; (3) likely AGB gain following restoration intervention; and, (4) the relative cost-effectiveness of restoration interventions within the landscape, including pessimistic, realistic and optimistic scenarios over five- and fifty-year investment timeframes. This assessment identified 3.94M ha with AGB deficit, an estimated 46% of which was expected to recover naturally, while 2.13M ha would require intervention through assisted-natural regeneration (46 – 98%) and tree planting (2 – 53%), with potential to restore up to 1.28Mg ha^{-1} $year^{-1}$ (an aggregate 64.16 $\pm$ 18.14Mg ha^{-1} after 50 years) at a cost of USD$8,316 ha^{-1} $year^{-1}$ over five years, reducing to USD$1,568 ha^{-1} $year^{-1}$ with 50 years investment. A higher proportion of cost-effective options for ABG restoration overlapped with areas of logistical feasibility under optimistic assumptions for the involvement of local people in project activities. This underscores the need for long-term investments that actively seek to create incentives for community involvement in order to generate cost-effective solutions for AGB restoration that are sustainable in the long-term.

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Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

This research has resulted in the peer-reviewed publication (in development):

Wills et al. (2020) A practice-led assessment of above-ground biomass restoration potential in a biodiversity hotspot. Phil Trans B.

This draft publication also forms the main body of the thesis presented in Chapter 2.

1. Introduction and Literature Review

1.1 Introduction

Approximately 13 million hectares of land is converted to alternative uses each year (FAO 2010). Sixty percent of contemporary land use changes can be attributed to direct human activities (Song et al. 2018), primarily conversion to agriculture, forestry and human-induced wildfires (Curtis et al. 2018). In the tropics, forests, woodlands and other native vegetation types are the primary sources of new agricultural land (Gibbs et al. 2010; Pendrill et al. 2019). The annual rate of deforestation in these areas is estimated at 5.8M ha (Achard et al. 2002). The conversion of natural habitats in the tropics is leading to unprecedented losses of biodiversity (Giam 2017) and, second to the burning of fossil fuels, deforestation is a key driver of greenhouse gas emissions and climate change (IPCC 2007).

Global carbon budgets are regulated by vegetation, which sequesters carbon dioxide in the air, converting carbon into biomass and emitting oxygen back into the atmosphere. In the tropics, forests are typically more productive than those at higher latitudes (Pugh et al. 2019), making them a more effective carbon sink. However, when these forests become degraded, their carbon storage capabilities are reduced (Martin et al. 2017; Pugh et al. 2019) and carbon dioxide is released back into the atmosphere (Houghton 2005). From 2000 to 2010, deforestation resulted in 1.5–2 billion tons of carbon dioxide (20% of the global total) being emitted into the atmosphere annually (FAO 2010). An increase in climate change-induced droughts and cloud cover, due to rising temperatures and thus increasing water carrying capacity of the air (IPCC 2007), is expected in tropical regions (IPCC 2007). This is further expected to reduce primary productivity and carbon sequestration capacity of tropical vegetation (Alvarez-Davila et al. 2017).

Tropical forests harbour more than half of the species worldwide (Wright 2005). However, recent estimates suggest that 10% of remaining tropical forests comprise fragments less than 10,000ha in size (Taubert et al. 2018). The combined effects of climate change and habitat fragmentation, which limits the dispersal abilities of species (Beaudrot et al. 2016), have a profound effect on species extinction trajectories (Urban

2015). It has been estimated that a sustained rate of 6.2-10.7% habitat loss per decade over the next 50 years (assuming no restoration and limited dispersal) would result in 8.76% of amphibians, birds and mammals (1,700 of 19,400 species tested) becoming at risk of extinction by 2070 (Powers and Jetz 2019).

In addition to affecting biodiversity, ecosystem degradation and climate change have negative impacts on human health and wellbeing. Warming temperatures increase the risk of extreme weather events such as floods, droughts and storms (IPCC 2007). Changes in vegetation cover have been shown to affect water availability by up to 30.7% (Wei et al. 2017). Furthermore, the disruption of vegetation-climate feedbacks as a result of deforestation and the effect that this has on local weather, e.g. by causing reductions in cloud cover and rainfall, particularly in the tropics and subtropics (IPCC 2007), is likely to lead to declining crop yields (Camill 2010). Thus, these processes also pose a threat to global food security.

The pressing need to address deforestation, biodiversity loss and climate change in order to ensure human health and wellbeing is gaining increasing priority in the international development agenda. The United Nations Sustainable Development Goals (UN-SDGs) call upon member states to *"Take urgent action to combat climate change and its impacts"* and to *"Protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss"* (UN 2015; Baumgartner 2019). In addition to promoting the sustainable management of remaining forests, the restoration of previously degraded systems is also gaining increasing traction as a strategy to combat climate change and biodiversity loss. The Aichi Targets adopted by the UN Convention on Biological Diversity commit to slowing biodiversity loss not only through reducing deforestation but also through restoration of natural ecosystems (UN 2011; Aronson et al. 2017). Similarly, biomass restoration is being employed by many countries as a means to meet their Intended Nationally Determined Contributions (INDCs) to global CO_2 emissions reductions (Rudel et al. 2019). These have given rise to quantitative targets along with a set of institutional mechanisms to finance and support these. For example, signatories of the Bonn Challenge committed to restore 150 million hectares of degraded forests by 2020 (Pendrill et al. 2019; Rudel et al. 2019). Schemes such as Reducing Emissions from Deforestation and Degradation (REDD), whereby industrial companies and nations are able to pay landowners for the carbon sequestration (and other) environmental services provided by woody vegetation on their lands, present one means of financing forest conservation and restoration efforts (Sunderlin et al. 2014).

A credit to these commitments and their achievements, global tree cover increased by 2.24 million km^2 (7.1%) from 1982 to 2016 (Song et al. 2018). However, this was driven primarily by a net gain in tree cover (including restored native vegetation as well as monoculture plantations) in subtropical, temperate and boreal zones in the northern hemisphere (Song et al. 2018). Meanwhile, the tropics are experiencing a continued net loss of tree canopy cover (Song et al. 2018; Pendrill et al. 2019). The African Forest Landscape Restoration Initiative (AFRI100) and Initiative 20x20 are demonstrations of the commitment of nations in the tropics to restoring their forests. Yet, given that the displacement of forests, woodlands and other woody vegetation is the primary means of obtaining land for agricultural expansion in the tropics (Gibbs et al. 2010), restoring these native habitats at scale in these areas will not be a straightforward task.

In order for ambitious aspirations for restoration to be met in tropical regions, important decisions will need to be made with regards to where best to rehabilitate natural habitats versus other land uses. In this thesis, I set out to explore some of the issues around this. Firstly, I undertake a review of the literature and data needs to support decision making with regards to spatial priority-setting for restoration. The second part of this literature review explores the different methods for restoring native vegetation, including the various merits of these methods in different social and ecological contexts. Finally, at the end of the literature review, I introduce my own research aims, which seek to address some of the existing data shortfalls for restoration planning, with a focus on restoring native above-ground biomass (AGB). The second chapter comprises a draft publication which has come out of this research and forms the main body of the thesis. In the third and final chapter, I summarise the key findings, suggest directions for further research and reflect on the importance of this study in the context of my own experience working in support of nature conservation and restoration in the study region.

1.2 Literature Review

Accurate spatial and temporal information on current verses historical plant biomass is needed to identify and inform restoration planning in areas where degradation has occurred. However, the intensive, costly and time consuming nature of inventories limits their applicability over large areas (Rosa et al. 2018). This has necessitated the development of methods for deduction and spatial up-scaling of biomass and canopy cover estimates from field data along with environmental predictors to generate estimates of historical cover (Bastin et al. 2019). Remote sensing data have great potential of monitoring biomass recovery trends where repeated measurements on the ground are not feasible (Pickell et al. 2016) and are also increasingly been used to upscale biomass measurement from the ground to high spatial resolution landscape-scale maps (Pfeifer et al. 2012; Adhikari et al. 2017). The expansion of global (e.g. Mitchard et al. 2011; Ploton et al. 2017; Bastin et al. 2019) and regional (e.g. Pfeifer et al. 2016; Alvarez-Davila et al. 2017) plot networks set up to monitor the structure and composition of vegetation over time in response to climate change has enabled improved testing and calibration of these datasets (Pfeifer et al. 2016). This has further improved the capacity for earth observation data to produce high-quality maps that be used to inform conservation and restoration planning and decision-making (Bustamante et al. 2014).

While biomass maps constitute valuable tools that help to identify where vegetation has been degraded and thus to inform restoration planning, more information is needed in order determine the appropriate approaches to restoration. Various social, ecological and economic factors affect the likelihood of success of restoration initiatives. For instance, the degree of fragmentation within a landscape together with the distance of restoration sites to intact reference systems and former land use can affect restoration outcomes (Crouzeilles et al. 2016). These variables affect the availability of seed stock and dispersal of seed rain from nearby intact ecosystems within a landscape (Barbosa and Asner 2017). The longevity of restoration interventions is also important, with research showing that timescales ranging from 15 to 50 years necessary to approach pre disturbance canopy closure and biomass (Shoo et al. 2017), while up to 80 years may be necessary to regain species richness (Martin et al 2017). Even longer timeframes than this are likely to be necessary if the goal is to restore habitats with species assemblages that reflect reference systems (Catterall et al. 2012). Careful consideration of factors that affect the long-term sustainability of restoration, including local governance and land uses (Reid et al. 2017) as well as appropriate methods and availability of financing (Sayer et al. 2015), is therefore necessary in order to ensure that restoration objectives are sustained in the long-term.

Three key methods for restoring natural habitats include: (1) passive natural regeneration, i.e. simply leaving an area to regenerate in the absence of any intervention; (2) assisted (or accelerated) natural regeneration (ANR), i.e. supporting natural regrowth through removal of competing vegetation and other disturbances (such as grazing livestock and fire); and, (3) active restoration, i.e. through planting native vegetation (Elliott et al. 2013). In some instances, degraded natural habitats may be capable of recovering in the absence of intensive human intervention (Shoo et al. 2015). ANR activities, such as clearing grasses and other vegetation which compete with trees for light and resources and/or installing firebreaks to protect new regrowth in these areas, can serve to speed up the restoration process for forests and other woody vegetation types (Elliott et al. 2013). However, passive restoration and ANR are only generally effective in areas that have sufficient remaining seed stock and/or are located nearby intact habitats that can serve as sources of seeds for regrowth (Elliott et al. 2013; Barbosa and Asner 2017). These methods are therefore not as effective at restoring highly degraded landscapes (Reid et al. 2018). Furthermore, even in areas with natural regeneration potential, inter-specific differences in dispersal ability often result in secondary regrowth following ANR that is dominated by a few pioneer species (Shoo et al. 2015; Ssali et al. 2017) and thus characterised by low diversity when compared to primary habitats (Gatti et al. 2014; Martin et al 2017; Sams et al. 2017).

Active restoration through planting can help to facilitate the recovery of biomass in severely degraded sites while also overcoming dispersal constraints for some species (Elliot et al. 2013). However, the high cost associated with planting trees often impedes its application over large areas (Lamb et al. 2005). This has spurred a growing body of research into cost-effective planting methods that facilitate rapid accumulation of biomass in secondary forests while also maximising species functional diversity. One strategy that has gained popularity in tropical restoration science is the Framework Species Approach (FSA; Goosem and Tucker 1995). This involves planting a purposefully selected combination of between 20 and 30 indigenous species at relatively high density (Elliot et al. 2013). The species selected should include a combination of fast growing pioneers (making up approximately 30% of the species mix), which serve to rapidly shade out weeds, alongside a combination of: large-seeded and climax (old growth) plants, to overcome dispersal constraints for these species (Shoo et al. 2015); animal-dispersed species, to attract seed dispersers which in turn may bring additional seeds from nearby intact habitats (Elliott and Kuaraksa 2008); and, legumes, to fix soil nitrogen (Elliott et al. 2013). The FSA, developed in Australia, has been tested extensively to restore tropical forests in Thailand, where it has been successful at enhancing both tree and bird species diversity in restored sites (Elliott and Kuaraksa 2008).

In practice, methodological decisions with regards to where and how to restore natural habitats are not only likely to be made on the basis of the relative ecological merit of each method but on the available expertise and resources (Sayer et al. 2016). Limited human and financial resources are among the most important constraints to restoration projects (Sayer et al 2016). Achieving effective restoration at scale necessitates sound understanding of the costs of the different options available (Shoo et al. 2015) since interventions that are planned to maximise cost-effectiveness are likely to be the most successful (Brancalion and van Melis 2017). There are different ways to manage the direct financial costs of restoration activities, e.g. by making use of ANR in areas with sufficient seed sources (Brancalion and van Melis 2017). Despite this, there remains little systematic research on the 'bottom up' costs of restoration, such as training, labour and transport (Polglase et al. 2013; Shoo et al. 2015, but see Shoo et al. 2016), which are often the most expensive components of restoration interventions (Elliot et al. 2013).

1.2.1 Research justification

Natural resources management practitioners are faced with an amalgam of complex decisions that need to be navigated in order to achieve effective restoration at scale. Despite advances in restoration science and the development of improved tools to support restoration planning, these remain somewhat detached from decision making and actions being implemented on the ground (Brancalion and van Melis 2017). A lack of clarity with regards to where and how to restore natural habitats compromises the legitimacy and effectiveness of restoration activities, targets and investments (Sayer et al. 2015). This is reflected in the findings of a recent global study (Bastin et al. 2019) which ascertained that 10% of the 41 commitments made under The Bonn Challenge exceeded nations' available land area for restoration, while 43% of countries committed just half of their suitable land. These findings suggest that there is either a lack of useful data to inform national planning for restoration (Sayer et al. 2015) and/or that the available data is not being utilised effectively (Knight et al. 2009; Brancalion and Melis 2017).

I set out to address this by developing a systematic approach to support strategic decision making in regards to where and how to allocate resources for tropical restoration, with a focus on recovering AGB in a biodiverse region in East Africa. To do this, I used a combination of vegetation plots and earth observations data to estimate and compare current verses historical AGB. From this, I identified areas with potential for AGB recovery, those that warrant restoration intervention, along with the appropriate methods, costs of implementation and likely AGB gains as a result of restoration. This enabled me to answer the following research questions:

1. What is the potential for AGB restoration in the study region?
2. What will it cost to implement activities to restore AGB in these areas?
3. Where should AGB restoration be prioritised in order to maximise cost-effectiveness?

2. Peer Reviewed Publication

2.1 Title and Publishing Journal

Title: A practice-led assessment of above-ground biomass restoration potential in a biodiversity hotspot. Target journal: The Royal Society Publishing, Philosophical Transactions B.

2.2 Publication Body

2.2.1 Introduction

Restoring degraded habitats can enhance their species diversity and capacity to store carbon. Species richness is often higher in secondary forests when compared to degraded sites (Catterall et al. 2012; Shoo et al. 2015; Martin at al. 2017) and approaches levels that are commensurate with primary forests within 15 to 50 years (Martin et al. 2013; Ryan et al. 2015; Meli et al. 2017). By contrast, full species assemblages that are characteristic of primary forests take much longer and may never fully recover (Catterall et al. 2012; Catterall et al. 2015; Martin et al 2017). Similarly, it can take anywhere from 15 to over 1,000 years for woody biomass (and thus carbon stored) in secondary forests to reach reference levels (Shoo et al. 2016; Martin et al. 2017; Pugh et al. 2019). However, faster growth rates exhibited by early-succession secondary forests (including those undergoing restoration) mean that their carbon sequestration potential is higher (Poorter et al. 2016). Thus, restoration – used in conjunction with protecting existing intact vegetation (Veldman et al. 2019) and a reduction in anthropogenic emissions (Friedlingstein et al. 2019; Lewis et al. 2019; Veldman et al. 2019) – can be an effective strategy to mitigate biodiversity loss and climate change (Griscom et al. 2017).

The recognition of these potential benefits has led to ambitious commitments by nations across the globe to restore native vegetation. At the time of writing, 63 signatories of the Bonn Challenge have committed to restore 173 million hectares of degraded forests (against a target to restore 350 million by 2030; Bonn Challenge 2020). However, given that continued demand for land for agriculture and other land uses is resulting in net forest loss (Gibbs et al. 2010), it is unclear where the land needed to realise these ambitious restoration targets will come from. Global assessments of restoration potential have yielded estimates that between two and eight billion hectares worldwide could be allocated to restore forests (Minnemeyer et al. 2011; Bastin et al. 2019). The findings from these studies point towards restoration in the tropics, where forests are typically more bio-diverse (Wright 2005) and store more carbon (Pugh et al. 2019) than those at higher latitudes, as having the greatest potential to bring about win-win solutions for biodiversity conservation mitigation (Brancalion et al. 2019; Soto-Navarro et al. 2019).

While useful for directing attention to biogeographical regions with the greatest opportunity for and higher potential benefits to gain from restoration, the coarse resolution of data used in these global-scale assessments means that they are limited in their utility to inform restoration decision-making on the ground (Minnemeyer et al. 2011; Brancalion et al. 2019). One recent global analysis of restoration potential (Bastin et al. 2019) received widespread criticism on the basis of: (a) incorrect carbon accounting (Friedlingstein et al. 2019; Lewis et al. 2019), including overlooking existing biomass and carbon stocks in habitats earmarked for restoration (Veldman et al. 2019); and, (b) due to overlooking biologically important habitats, such as tropical grasslands and savannas, that are naturally low in above-ground biomass (AGB; Veldman et al. 2019). These oversights run the risk of these habitats being displaced if attempts are made to restore forests in areas where they would not naturally occur (Bond et al. 2019; Veldman et al. 2019). Thus, in order for aspirations for restoration to be met, important decisions will need to be made with regards to where best to rehabilitate native vegetation verses other land uses. Fine-scale habitat maps and historical knowledge of landscape ecology and habitat dynamics are needed in order to properly address these issues and to inform effective restoration planning on the ground (Minnemeyer et al. 2011; Chazdon and Brancalion 2019).

In addition to prioritising where to restore native habitats, conservation practitioners are faced with an amalgam of complex methodological decisions that need to be made. Plot-based restoration trials have revealed that the appropriateness of different approaches (i.e. assisted natural regeneration verses active restoration through planting) varies geographically in relation to local ecological (e.g. previous land use; Suganuma et al. 2016) and landscape (e.g. distance from nearby intact ecosystems; Crouzeilles et al. 2020) features. These affect soil seed stock and dispersal (Wijedasa et al. 2020), and thus the potential for a site to regenerate naturally (Elliot et al. 2013), as well as the rate of biomass accumulation and type and diversity of species likely to become re-established (Shoo et al. 2015). Different restoration methods also vary in the level of manpower and resources required and hence also their cost (Lamb et al. 2005; Elliott et al. 2013). Thus, practical management decisions are likely to be governed not only by the relative ecological merit of each technique but also with regards to available expertise and financing (Sayer et al. 2016). As such, restoration interventions that implemented in locations and use methods that serve to maximise cost-effectiveness are likely to be the most successful (Brancalion and van Melis 2017).

While there have been some regional assessments aiming to assess the cost-effectiveness of different restoration interventions, these have tended to focus on identifying priority areas for restoration where biodiversity conservation and ecosystem services provision outcomes overlap (Gourevitch et al. 2016; refs). Fewer have sought to address the more practical aspects surrounding methodological decisions and their relative cost. Studies that have incorporated costs either report only labour costs for specific activities such as vegetation management and planting (Wheeler et al. 2016) or use ball park figures to estimate the costs of restoring a given area (Verdone and Seidi 2017; Polglase et al. 2013). It is not clear within these assessments that costs of transport logistics, capacity building, project staff and administration have been fully accounted for and detailed published data that breaks down the full-costs of implementing restoration interventions is limited (Polglase et al. 2013; Shoo et al. 2015). Thus, more information is needed in order to inform practical restoration planning that serves to maximise ecological outcomes while minimising costs (Brancalion and van Melis 2017).

Here, we present a systematic approach to support strategic decision-making regarding where and how to allocate resources for restoration, using a strategically important region in East Africa as a case study. We used remote sensing methods alongside data from a series of permanent sample plots to estimate and compare current versus historical AGB and therein AGB deficit across the region. From this, we identified areas with potential for AGB restoration and developed a framework (based on published literature and our own pilot studies in the region) for deciding which methods are appropriate to implement in which locations. Finally, we assessed the costs of employing these methods over five- and 50-year project timeframes. These costs are compared with expected returns in terms of AGB gain and carbon storage to identify key priority areas for restoration investments and to retrospectively evaluate the landscape features that lead to cost-effective restoration.

2.2.2 Methods

2.2.2.1 Study region

Our study region comprised the Udzungwa and Mahenge Mountains and Greater Kilombero Valley, hereafter "Udzungwa-Kilombero Landscape" (52,971km^2; Figure 1), of Tanzania. The Udzungwa-Kilombero Landscape forms a significant part of the Eastern Afromontane biodiversity hotspot and miombo-mopane wilderness area. It overlaps with a RAMSAR wetland, Game Reserve (the largest in Africa), three National Parks, two Nature Reserves, 31 National Forest Reserves, an Important Primate Area, two Important Bird Areas and the Eastern Arc Mountains proposed World Heritage Site (IUCN 2019). Land cover in the region comprised a combination of human-dominated and wilderness areas, including primary, secondary and degraded forests, savanna woodlands and grassland (Table S1).

The Udzungwa-Kilombero Landscape was selected not only on the basis of its high international significance for biodiversity and ecosystem services but also due to natural habitat degradation in recent decades as a result of population growth, logging and increased demand for land for crop production (Wilcock et al. 2016). Furthermore, a proposed agricultural growth corridor in the region presented a significant impending threat to habitat connectivity (Laurence et al. 2015). Thus, the Udzungwa-Kilombero Landscape is a region that would benefit greatly from a strategy to inform restoration planning against other competing land uses, in a developing nation with commitment to restore 5.2Mha of native vegetation by 2030 (AUDA 2020). Finally, the Udzungwa-Kilombero Landscape had high variation in climate (rainfall 494 – 1938 mm yr^{-1}; Fick and Hijmans 2017), topography (elevation 108-2,555m; SRTM 2000), human disturbance (Ahrends et al. in review) and habitat fragmentation (Marshall et al. 2010) along with an established network of vegetation monitoring plots (Figure 1). It therefore provided an ideal case study in which to trial landscape-level restoration planning methods against challenging variation in environmental conditions, with good reference data.

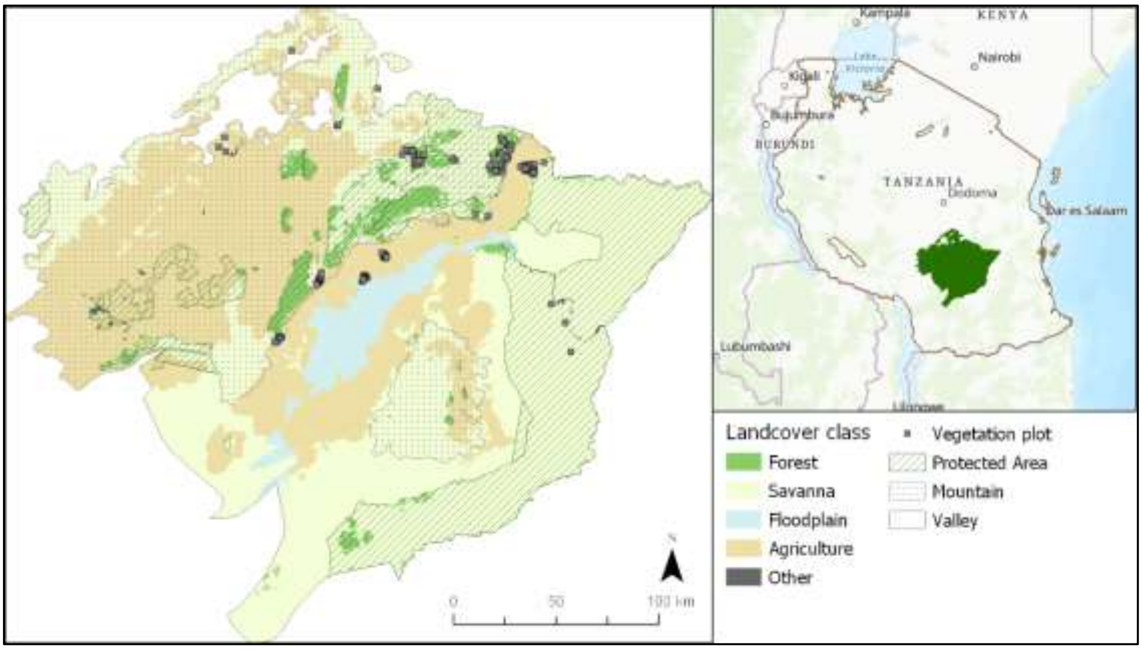

Figure 1. Location of the Udzungwa-Kilombero Landscape in Tanzania, including boundaries for the Udzungwa (22,788km^2) and Mahenge (2,606km^2) Mountains (Platts et al. 2011), the Kilombero Valley (27,577km^2; defined by the Udzungwa Mountains to the northwest, by major rivers to the north and east and by the Morogoro region political boundary to the south) and the locations of vegetation plots used to estimate above-ground biomass for the region.

2.2.2.2 Restoration planning approach

Our restoration planning approach (Figure 2) involved four steps to determine: (1) the amount of AGB (and carbon) that could potentially be restored across the region ("restoration potential"); (2) the most likely appropriate methods for restoring AGB in areas with restoration potential; (3) the relative costs of these methods, accounting for all logistical, human and administrative costs; and, (4) the expected AGB gain and thus cost-effectiveness of the planned interventions. We generated pessimistic, realistic and optimistic estimates for appropriate methods, cost and AGB gain over 5-year and 50-

year scenarios to reflect timeframes for realistic donor investment (from personal experience) and time for AGB recovery (Martin et al. 2013; Cole et al. 2014; Poorter et al. 2016; Shoo et al. 2016), respectively. This culminated in six potential scenarios for cost-effective restoration intervention.

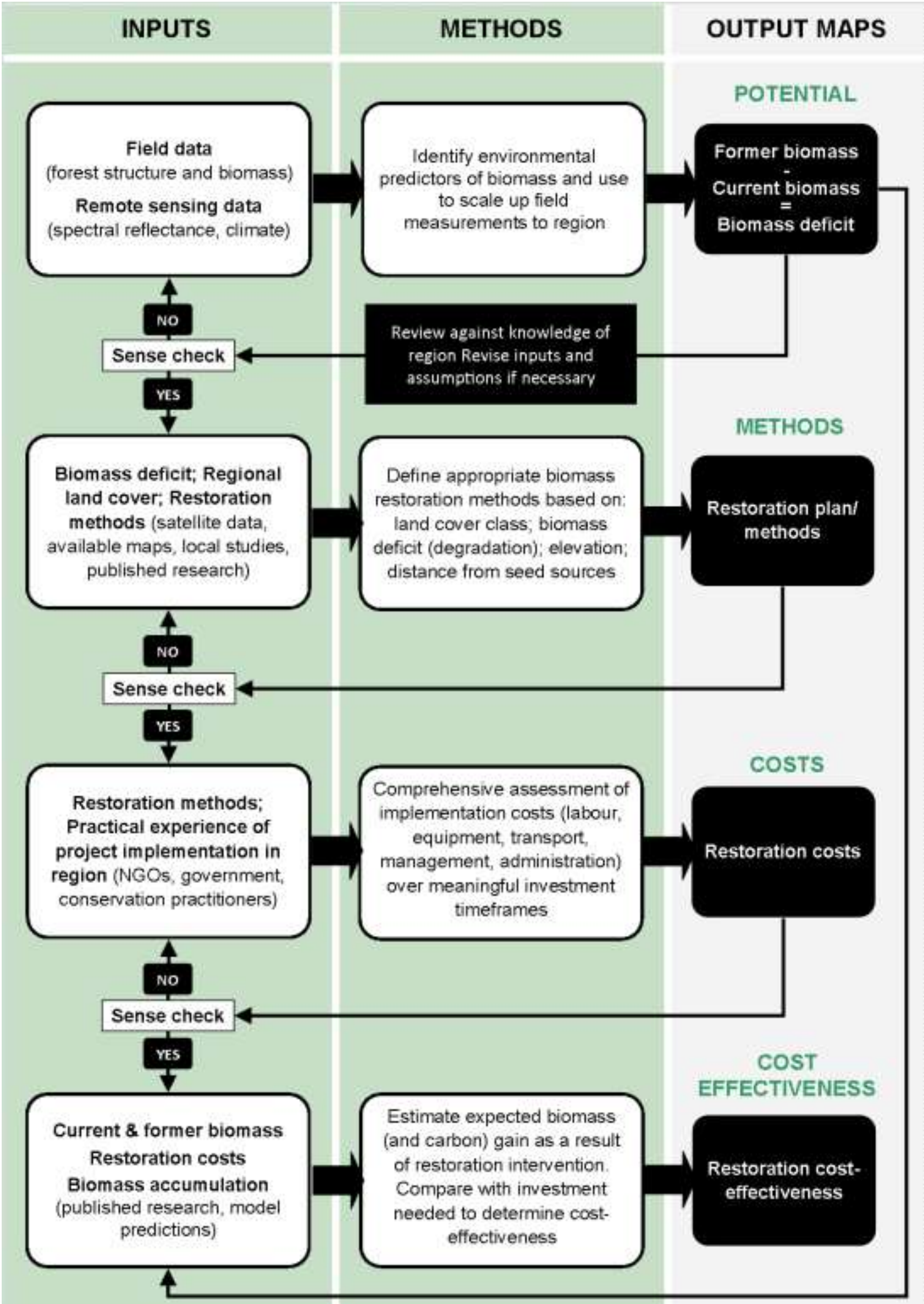

Figure 2. A stepwise restoration planning approach to support strategic decision-making with regards to where and how to allocate resources for restoring native above-ground biomass, first trialled in the Udzungwa-Kilombero Landscape, Tanzania.

2.2.2.2.1 Step 1. Restoration potential

In order to determine restoration potential, we estimated landscape AGB cover: (a) at the time of the most recent available quantitative vegetation assessments, hereafter "current AGB"; and, (b) prior to disturbance and deforestation within 100-200 years of this study, hereafter "former AGB", based on historic maps (Rodgers 1992; Willcock et al. 2016). Vegetation data were compiled from 195 plots (mean size = 0.34 ha, range = 0.08 - 1.00 ha) that captured the full range of regional tree canopy cover (0-100%) and elevation (222-2,300m; Figure 1). These plots included 17,983 woody plant stems (trees, lianas, palms and stranglers) measured between 2007 and 2017 following adapted RAINFOR protocols (Marshall and Pfeifer 2019). AGB for each tree stem was estimated from diameter at breast height (130cm; dbh), and where available, stem height and wood density, using allometric equations (woodland: Chave et al. 2014 dry forest equation; moist forest: mean values from Chave et al. 2014, Mugasha et al. 2013 and Ngomanda et al. 2014). Liana AGB was estimated from dbh using a standard equation (Schnitzer et al. 2006). From this, we calculated mean AGB and stem density per square metre, plus 95% confidence intervals based on 10,000 bootstrapped iterations.

We mapped current AGB across the region from plot-based estimates of AGB, using Landsat sensor data and derived metrics. The 2015 Google Earth Engine Landsat tile used was at 30m x 30m pixel resolution, covered the entire landscape and encompassed Red, Near-Infrared, and the two Short wave infrared (SWIR) spectral bands, from which we computed texture indices (dissimilarity and average) for each band (Hansen et al. 2013). We excluded predictors that were highly inter-correlated (Pearson's $R^2 \geq 0.6$), keeping only those that correlated more highly with AGB. From this, the final predictive model linking AGB to sensor data encompassed SWIR band 1, Near-Infrared, Red dissimilarity, Near Infrared dissimilarity and SWIR band 1 Dissimilarity. We subsequently used random forest models with 10-fold cross-validation and three repeats to model AGB as function of the remotely sensed variables in the final dataset. To calibrate the model, we split the AGB dataset into training and test data at 80:20%

ratio. We thus used 156 plots for model calibration and the remaining 39 plots for validation. The final model used for prediction yielded 49% explained variability in AGB data.

To estimate former AGB, we up-scaled plot-based estimates of AGB for vegetation plots with closed canopy using climatic predictor variables. This assumed that climate was the key constringing parameter for the maximum amount of woody AGB that could be achieved through restoration at a given location. Former AGB was then estimated by determining the relationship between AGB and climate for a closed canopy subset of plots (n = 59; mean size = 0.43ha, range = 0.08 – 1.00ha). Plot data were supplemented by 33 randomly selected remotely-sensed AGB estimates (taken from our current AGB map) in closed-canopy savanna spectrum areas and 10 estimates from known, unlogged, closed vegetation in lowland sites (<800m above sea level), since these were not adequately represented by the field data. Climate data included a standard set of variables measuring temperature, rainfall, and moisture and seasonality derived from these and were derived from Worldclim version 2 (Fick and Hijmans 2017) at 30 arc second resolution and interpolated to 3 arc second (~100m) resolution. We used random forest models equivalent to those used for spectral band modelling, with identical cross-validation and calibration, to upscale former AGB. The final six predictor variables used in the upscaling were: mean diurnal range (the mean difference in minimum and maximum monthly temperature); isothermality (the mean diurnal range proportionate to the annual temperature range); mean temperature of the driest quarter; seasonality in temperature (the standard deviation of monthly temperatures multiplied by 100); precipitation of the warmest quarter; and, mwd. The resulting model yielded 75% of explained variability in AGB.

In order to map current AGB per ha, the resulting surfaces were re-projected from 30 m pixel rasters to UTM 36S at 25 x 25m pixel resolution and then aggregated by summing AGB values across four neighbouring pixels. For former AGB, we first re-projected 1 km resolution climate rasters to scales of 1 ha resolution and used the resulting climate layers to upscale and map former AGB. We calculated the expected AGB loss due to disturbance across the landscape, hereafter “AGB deficit”, by subtracting current AGB from former AGB. This enabled us to identify areas with potential for AGB recovery (i.e. with AGB deficit greater than or equal to zero) and subsequently to determine appropriate methods of AGB restoration in these areas under step 2. Additional details on the methodology used to perform AGB calculations under step 1 is provided in the Supplementary Information.

2.2.2.2.2 Step 2. Restoration methods

For each pixel with AGB deficit, we determined: (1) whether intervention would be needed in order to restore AGB; and, (2) for pixels with restoration potential, the most likely appropriate approach to woody AGB restoration, basing this on: land cover type, AGB deficit, elevation and distance from nearby intact habitat (Table 1). This was guided by author experiences of habitat management in the region and on published guidance (Elliot et al. 2013). See Supplementary Information (Table S2) for detailed description of the methods employed to determine appropriate restoration methods under step 2.

2.2.2.2.3 Step 3. Restoration costs

We estimated the cost per treatment of restoration intervention for each 1 ha landscape pixel and subsequently scaled this over five and 50-year investment timeframes based on our assumptions regarding: (a) the number of repeats per annum; and, (b) the number of years for which each method would need to be employed in order to regain sufficient woody AGB after which vegetation would be expected to recover without further assistance/active intervention. Estimates for the number of treatments per method were generated based on our experience from pilot studies in the region and on published literature. Pricing estimates were based on our own experience in donor grant budgeting for four regional organisations, and included costs for: (a) land procurement for restoration and tree nursery establishment; (b) labour, equipment and transport for restoration activities and subsequent monitoring and management; (c) community engagement in areas close to human settlement; and, (d) project management. All costs were calculated in the local currency (Tanzanian Shillings; TZS) and subsequently converted to United States Dollars (US$) at a rate of 1:0.00043, accounting for inflation at 2.2%yr^{-1} (https://data.oecd.org). See Supplementary Information (Table S3) for detailed description of the costs included and how these were calculated.

Table 1. A framework to determine appropriate tropical restoration methods. *In forest land cover class, distance refers to the Euclidean distance of a pixel from the most proximal road and forest edge; in savanna / agriculture mosaic, this refers to the Euclidean distance to the most proximal savanna / forest pixel.

Landcover class	**Landcover feature**	**Passive**	**Vine cutting**	**Herb/shrub cutting**	**Lantana cutting**	**Firebreak cutting**	**Grass cutting**	**Enrichment planting**	**Framework planting**	**Nurse trees**	**Soil**
					PESSIMISTIC SCENARIO						
Forest	AGB deficit (%)	<40	≥40	≥40	≥40	-	-	≥90	-	-	-
	Elevation (m)	Any	<1,000	≥1,000	<1,400	-	-	Any	-	-	-
	Distance (m)*	NA	NA	NA	≤200	NA	NA	NA	NA	NA	NA
Savanna / Agriculture mosaic	AGB deficit (%)	-	-	-	-	≥30	≥30	≥50	≥50 and <90	≥90	≥90
	Distance (m)*	-	-	-	-	Any	Any	Any	≥100	Any	Any
					REALISTIC SCENARIO						
Forest	AGB deficit (%)	<50	≥50	≥50	≥50	-	-	-	-	-	-
	Elevation (m)	Any	<1,000	≥1,000	<1,400	-	-	-	-	-	-
	Distance (m)*	NA	NA	NA	≤100	NA	NA	-	NA	NA	NA
Savanna / Agriculture mosaic	AGB deficit (%)	-	-	-	-	≥40	≥40	-	≥65 and <95	≥95	≥95
	Distance (m)*	-	-	-	-	Any	Any	-	≥200	Any	Any
					OPTIMISTIC SCENARIO						
Forest	AGB deficit (%)	<80	≥80	≥80	-	-	-	-	-	-	-
	Elevation (m)	Any	<1,000	≥1,000	-	-	-	-	-	-	-
	Distance (m)*	NA	NA	NA	-	NA	NA	-	NA	NA	NA
Savanna / Agriculture mosaic	AGB deficit (%)	-	-	-	-	≥50	≥50	-	≥80 and <100	100	100
	Distance (m)*	-	-	-	-	Any	Any	-	≥300	Any	Any

2.2.2.2.4 Step 4. Cost-effectiveness

For each 1 ha pixel, we estimated the likely AGB gain (and carbon sequestration; i.e. 45.6±0.2% AGB; Martin et al. 2018) that could be achieved over 5 and 50 years and its variability across the region. We then determined expected cost-effectiveness for each landscape pixel using the following equation (modified from Firn et al. 2015):

$$\mathrm{AGB\$}_\mathrm{i} = \Delta\mathrm{AGB}_i \,/\, \$_i \qquad \text{Equation 1}$$

Where for time period *i*, AGB$ was the cost-effectiveness, i.e. expected carbon sequestration per US$ ($\mathrm{kg.US\$^{-1}}$), ΔAGB was the expected change in AGB and $ was the expected cost in US$.

Our projections of AGB gain with time were made using modelled estimates of AGB accumulation for our region. These were extracted from a global dataset (Pugh et al. 2019) and comprised 18 pixels at 0.5 degree resolution, each with 300 annual estimates from zero in year 1 to maximum AGB. We computed the mean, minimum and maximum AGB value for each year across these 18 pixels and then computed each value as a percentage of the maximum AGB achieved for each across the 300 years. Next, we computed our own estimates of current AGB for the region as a percentage of former AGB and compared these with the modelled data to determine at which point in the time series each landscape pixel was located. We then determined what percentage of former AGB would be expected to be reached after five and fifty years of intervention from the time-series data, using minimum, mean and maximum estimates of AGB accumulation rates as the basis of predictions for our pessimistic, realistic and optimistic scenarios, respectively. This enabled us to deduce the percentage of former AGB that would likely be realised following intervention under the various scenarios and to convert this into actual estimates of AGB accumulation per hectare per annum and overall within the landscape.

2.2.2.3 Statistical analyses

Spatial analyses were conducted using R version 3.6.3 (CRAN 2017). The packages caret package (Kuhn 2008) was used for modelling and the raster package (Hijmans and van Etten 2012) for spatial up-scaling of current and former AGB, restoration methods and implementation costs estimates across the region. Distance matrices were computed in ArcGIS Pro version 2.3.0 (Esri Inc. 2018), including the Euclidean Distance tool (for calculating distance from intact habitat) and Path Distance tool (for calculating the ground distance travelled using a Digital Elevation Model).

All statistical analyses were completed using the R version 3.6.3 (CRAN 2017) base package. Means with standard deviations are used to summarise estimates of current AGB and former AGB as well as AGB deficit and expected AGB gain following restoration intervention, since these datasets follow a broadly normal distribution. In the case of datasets that are not normally distributed, including estimates of cost and cost-effectiveness per hectare, the median and inter-quartile range is used. In addition to summarising overall tendencies, we interpreted these spatial datasets in terms of pre-defined units of use for landscape managers, namely: (a) governance type (protected areas versus outside); (b) land cover class (defined in Table S1); and, (c) logistical accessibility, with areas within 3km of the agriculture mosaic or roads considered logistically more accessible relative to more remote locations which would necessitate multi-day trips to access and restore (see Table S3). When reporting frequencies and averages under our different scenarios, unless stated otherwise, we provide the value under our realistic (R) scenario in the main text with values under our pessimistic (P) and optimistic (O) scenarios given in parenthesis.

2.2.3 Results

2.2.3.1 Step 1. Restoration potential

Our model predicting AGB in vegetation plots from spectral bands explained 49% of the AGB variation (R_2 = 0.49; RMSE = 8.86; MAE = 6.49; Figure S1a) and yielded a map of current AGB that accurately matched author familiarity with the region (Figure 3a). Our climate model explained 75% of AGB variability in primary vegetation (R_2 = 0.75; RMSE = 73.98; MAE = 57.56; Figure S1b). Surprisingly, this yielded a former AGB map with similar AGB in forest fragments and surrounding savanna land cover classes to the current AGB map (Figure 3b; Table S4), suggesting that to some degree the moist-evergreen and dry-deciduous forest mosaic within the study region is naturally maintained. By comparing these two maps, we were able to produce a third map of AGB deficit for the region (Figure 3c). We identified 74.13% (3.94 M ha) of the landscape as having potential for AGB recovery (i.e. current AGB less than former AGB) and a mean deficit of 41.80±20.46% in these areas (Table S4).

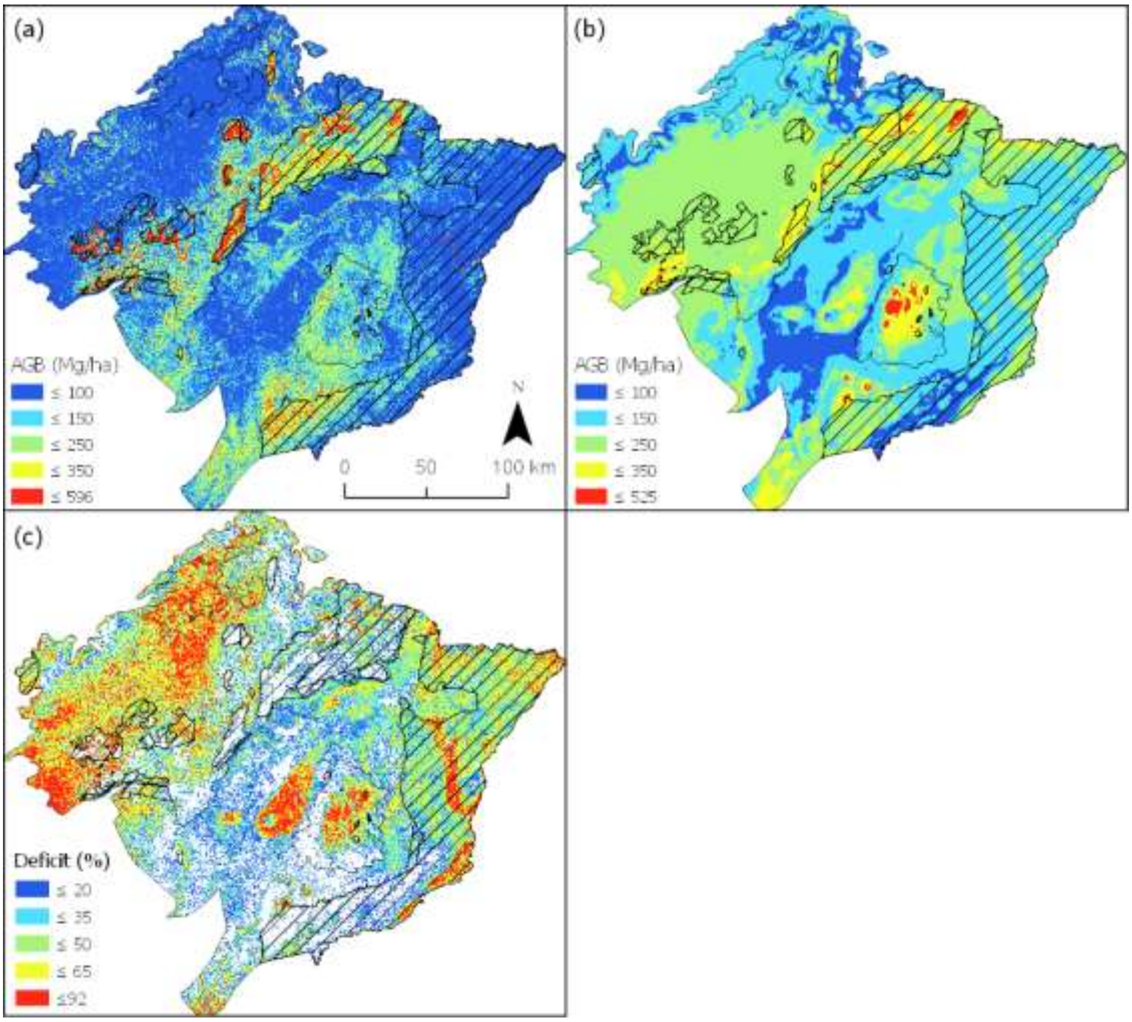

Figure 3. Above-ground biomass estimated from vegetation plots and up-scaled across the Udzungwa-Kilombero Landscape, including: (a) spectral reflectance data to estimate current AGB; (b) climate data to estimate maximum former AGB; (c) AGB deficit, from former minus current.

2.2.3.2 Step 2. Restoration methods

In areas with AGB recovery potential, we estimated that 45.86% (1.81M ha, under our realistic [R] scenario; range = 31.13%, 1.23M ha, under our pessimistic [P] scenario to 62.70%, 2.47M ha, under our optimistic [O] scenario) would most likely regenerate naturally in the absence of intervention, with the remaining 54.14% (R = 2.13M ha; P = 68.87%, 2.71M ha; O = 37.30%, 1.47M ha) requiring some form of intervention in order to restore former AGB (i.e. these areas would have restoration potential; Figure 4). Furthermore, we estimated that 75.54% (R = 1.61M ha; P = 45.84%, 1.24M ha; O = 97.72%, 1.44M ha) of the land requiring intervention to restore AGB could be restored through ANR while the remaining area would need to be actively restored through tree planting (Table 2).

Table 2. The relative area (ha) within the Udzungwa-Kilombero Landscape, landscape, that is restorable, disaggregated by restoration method.

Method	Area (pessimistic)	Area (realistic)	Area (optimistic)
No deficit	**1374045**	**1374045**	**1374045**
Recovery potential	3936766	3936766	3936766
Passive recovery	1225441	1805382	2468157
Any intervention	2711325	2131384	1468609
Assisted Natural Regeneration	1242742	1610040	1435177
Vines	3783	1505	6
Shrubs	8165	4492	20
Lantana	150	65	0
Firebreaks	2697066	2123893	1467749
Grass	2699377	2125387	1468583
Active restoration	1468583	521344	33432
Framework species planting	1468491	521344	33432
Nurse trees planting	92	0	0
Soil improvement	92	0	0
Community engagement	1506740	1230150	903775

2.2.3.3 Step 3. Restoration costs

We estimated that a median investment of USD \$8,316 ha^{-1} $year^{-1}$ (P = 8,307 ha^{-1} $year^{-1}$; O = 6,909 ha^{-1} $year^{-1}$) would be required to restore native vegetation to 5.04±1.45% of its former AGB over five years, while USD \$1,568 ha^{-1} $year^{-1}$ (P = 5,910 ha^{-1} $year^{-1}$; O = 1,205 ha^{-1} $year^{-1}$) over 50 years would permit recovery of 50.87±9.92% of the former

AGB (Table S5). The different approaches to restoring AGB differed in their relative costs (Table S5). Restoration through planting was substantially more expensive to implement than ANR in the short-term (USD$141 ha^{-1} year^{-1} over five years under our realistic scenario versus USD$8,159 ha^{-1} year^{-1} for planting methods). However, this was largely due to the high initial investment in labour needed to raise, transport and plant seedlings, meaning that costs for active methods only increased by 26% following a 10-fold increase in investment duration from five to fifty years, verses a 15-fold increase in costs for ANR (Table S5).

2.2.3.4 Step 4. Cost-effectiveness

We estimated that restoration interventions would enable 5.04±1.45% of the deficit (R = 4.81 Mg ha^{-1}) to be recovered after five years and 50.87±9.92% (R = 47.34 Mg ha^{-1}) following 50 years of intervention (Table S4). This translated to aggregate AGB gains of 5.00±1.44 Mg ha^{-1} over 5 years and 51.60±14.94 Mg ha^{-1} after 50 years. After accounting for the costs needed to restore AGB in these regions, this translated to AGB gains of 0.02 Mg ha^{-1} (median; IQR = 0.01 – 0.13) per USD$100 spent after 5 years, increasing to 0.05Mg ha^{-1} (IQR = 0.04 – 0.11) per USD$100 over 50 years (Figure 4).

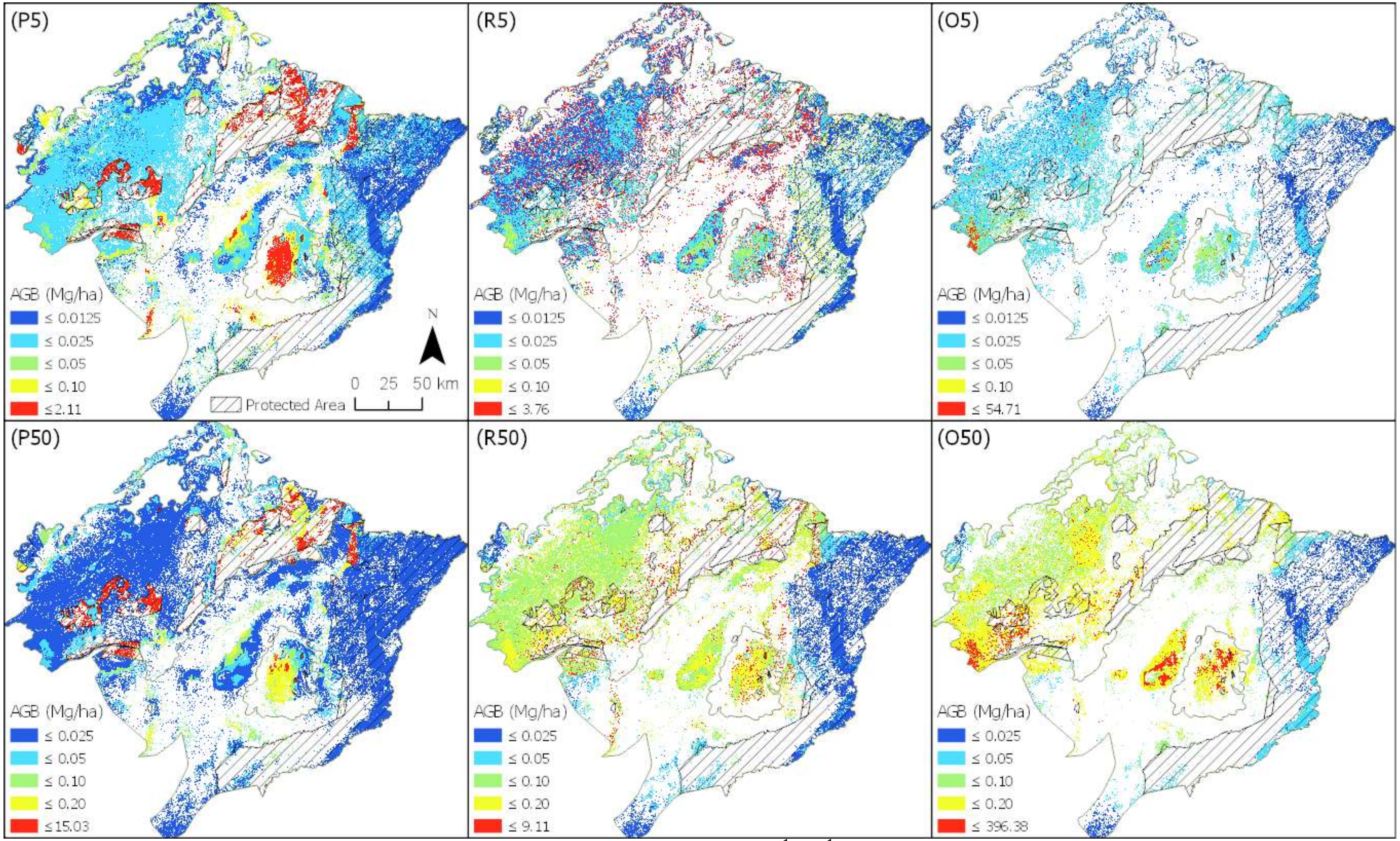

Figure 4. Estimated cost-effectiveness in terms of AGB gain (Mg $\$100^{-1}$ ha^{-1}) as a result of restoration interventions in the Udzungwa-Kilombero Landscape, Tanzania, including pessimistic (P), realistic (R) and optimistic (O) scenarios over five (5) and fifty (50) year investment timeframes.

2.2.4 Discussion

Our modelled AGB estimates of between 102.98 and 492.88 Mg ha^{-1} in closed forests in the Udzungwa-Kilombero Landscape were comparable to previous estimates from the region (Marshall et al. 2017) and East Africa more broadly (Wheeler et al. 2016; Adhikari et al. 2017). However, our mean estimated AGB of 246.65 Mg ha^{-1} in closed forests was less than the average for Africa as predicted in a pan tropical study (360 Mg ha^{-1}; Avitabali et al. 2016) and that based on field measurements from across Africa (438.1 in submontane and 445.1 in lowland evergreen forests; Mitchard et al. 2011). This is most likely an artefact of our models underestimating AGB at the high end of the spectrum, with inaccuracies becoming evident in observed versus predicted AGB above 350 Mg ha^{-1} (Figure S1b). The inadequate predictive ability of models such as those used in this study in areas of high AGB has been reported elsewhere (Mitchard et al. 2011; Avitabali et al. 2016; Putili et al. 2017) and is particularly a challenge in regions with variable elevation, which can impact AGB (Avitabali et al. 2016) and especially in regards to the Afromontane region, where few large trees contribute disproportionately to aggregate AGB (Marshall et al. 2012; Marshall et al. 2017). This tendency has also been observed, though to a lesser extent, in deciduous woodlands in East Africa (Ryan et al. 2011; McNicol et al. 2017) and constitutes a key challenge with regards to accurate modelling of extant and historical AGB, which is needed in order to inform restoration planning. In our case, the problem was exacerbated due to vegetation plots not being fully representative of the closed forests and open and closed deciduous woodlands across all elevations. As such, these were supplemented with our own modelled estimates of current AGB from spatial reflectance data in these areas, which in turn underestimated high AGB values (Figure S1a). This underscores the need for restoration planning to account for uncertainty in terms of ecological knowledge, since if vegetation plots used during calibration of models for up-scaling are not sufficiently representative of the variation in geographic features and habitat types that exist within a region, then these will result in inaccurate maps. This has been a key point which has attracted much criticism (Mitchard et al. 2011; Alvarez-Davila et al. 2017) for a number of pan-tropical mapping exercises (Baccini et al. 2008; Saatchi et al. 2011; Bastin et al. 2019). If these gaps in knowledge are correctly identified and acknowledged, then they can be used to help guide future surveys to improve second-stage planning (Mitchard et al. 2014).

As was expected, forests in the Udzungwa-Kilombero Landscape had higher AGB (246.65±67.4Mg ha^{-1}) than savanna spectrum habitats (157.91±59.04 Mg ha^{-1}). However, due to savanna spectrum being more extensive than forests (Table S1), these constituted the largest aggregate store of AGB in the region. This corroborates findings that African savanna habitats are an important global carbon store (Saatchi et al. 2011). Critically, we found that AGB in savanna habitats in our region: (a) exceeded those observed elsewhere at the high end of the spectrum, harbouring up to 471.00 Mg ha^{-1}, compared with estimated highs of 102 Mg ha^{-1} from previous estimates in the region (Willcock et al. 2014) and between 114.89 Mg ha^{-1} and 350 Mg ha^{-1} elsewhere in Tanzania (McNicol et al. 2017; Putili et al. 2017); (b) overlapped in AGB potential with forests; and, (c) remained relatively unchanged over the past 200 or so years, with mean values for current AGB (128.91±72.06 Mg ha^{-1}) being similar to that of former AGB (157.91±59.01 Mg ha^{-1}). This observation challenges the findings of previous mapping exercises (Willcock et al. 2014) and assumptions that historically the Eastern Arc Mountains were once covered by closed forest (Newmark 1998), which has since been degraded by anthropogenic disturbances resulting in isolated forest fragments (Marshall et al. 2010; Newmark et al 2017). Instead, our findings suggest that to some degree the mosaic of closed and open forest and savanna is naturally occurring and maintained by climate, with unclear distinctions between the two land cover classes in some areas. This has important implications for restoration planning since it underscores the need to go beyond traditional methods for evaluating forest cover change by using subjective canopy cover thresholds to distinguish between forest and non-forest habitats (Chazdon and Branchalion 2019).

Notwithstanding the large amount of extant AGB stored in both forests and savanna habitats in the Udzungwa-Kilombero Landscape, we identified 3.94M ha of as having potential for AGB recovery. The majority of this potential existed within the savanna spectrum and agriculture mosaic (the latter of which our modelled estimates of former AGB suggest was akin in AGB to savanna habitats 200 years previous). This corroborates findings from other studies in the region that loss of open and closed deciduous woodlands has been more extensive than in closed forest (Green et al. 2013) and underscores the importance of restoration efforts in these areas. Furthermore, our finding that the degree of AGB deficit and thus also the requirement for restoration was lower in protected areas aligns with findings that these are effective at preventing degradation (Hall et al. 2009; Green et al. 2013), but also reflects that their location is biased towards closed forests (Green et al. 2013).

We estimated that between 31% and 62% of the area with AGB deficit would recover naturally without intervention beyond the prevention of further degradation activities. This suggests that there is greater potential (under our realistic and optimistic scenarios) for AGB recovery through natural regeneration than is typically afforded to this approach in restoration plans (Lewis et al. 2019). Notwithstanding this significant potential for natural regeneration, we estimated that up to 2.71M ha of the land area with recovery potential would require intervention in order to restore AGB. Across all land cover types, we identified significant potential for ANR, which was considered to be the most likely appropriate approach to facilitate AGB recovery across a minimum of 46% and up to 98% of the area in need of restoration intervention. Similar to findings elsewhere (Strassburg et al. 2019; Crouzeilles et al. 2020), we found that ANR was not only extensively applicable but also incurred less overall cost when compared with tree planting methods. Our calculations, which included all cost associated with restoring a given area, including logistical transport as well as human and administrative costs, revealed that ANR was 58 to 109 times cheaper on average to employ than active tree planting. This suggests that even greater savings, above the existing range of 77% to 44-fold costs reductions reported elsewhere (Marshall et al 2016; Crouzeilles et al. 2020) can be made through employing ANR as a restoration strategy.

At least partially due to the divergent costs of ANR versus tree planting methods, there is huge variation in the estimated costs of restoring native vegetation in the literature, which range from USD$214 ha^{-1} to USD$35,500 ha^{-1} (Catterall and Harrison 2006; Verdone and Seidi 2017). At USD$7-8,000ha^{-1} year^{-1} on average, our estimated costs of implementing restoration interventions is higher than that reported by published studies elsewhere. For example, costs of our active methods averaged USD$8,196 ha^{-1} year^{-1} versus USD$1,200 ha^{-1} over five years for labour and equipment costs for site preparation, planting and management of planted seedlings in Uganda (Wheeler et al. 2016). More aligned with our estimates, Raquel et al. (2019) reported costs of up to

\$14,195 ha^{-1} after accounting for seedling mortality rates in restoration plantings (Raquel et al. 2019). This highlights how the added risks associated with planting trees, which we accounted by including procedures for post-planting management and enrichment planting under our pessimistic scenario, can necessitate higher investments in order to ensure ecological success. An additional contribution to our higher costs is that these were calculated on a per hectare basis. In reality it is unlikely that restoration interventions will be implemented at this scale and, certain costs, particularly project management/oversight and logistical transport costs needed to reach a site are relatively constant, and therefore result in reduced overall cost per unit area. Recent research into the effects of this have shown that 10-fold increase in project size from 1ha to 100ha translates to a 57% reduction in costs and, due also to faster AGB accumulation through reduction in edge effects, a 268% improvement in cost-effectiveness (Strassburg et al. 2019). Thus, in addition to proper cost accounting, this a potentially very valuable line of research that warrants further investigation in order to better understand the optimal size of restoration investments. Nonetheless, we believe that our assessment of the costs is valuable in order to (a) draw broader conclusions with regards to where AGB restoration can be prioritised to maximise cost-effectiveness; and, (b) to address the sparsity of accurate cost-accounting in the literature.

We estimated that, sufficient financial investment and application of appropriate methods to restore AGB would result in recovery of 50.87±9.92% of the AGB deficit following 50 years of intervention. Assuming that AGB accumulation were to continue on this trajectory, our findings support those elsewhere that investment timeframes of 90 years or more are required to restore AGB to reference levels (Wheeler et al. 2016). This said, at 1.12-1.28Mg ha^{-1} year^{-1}, our estimated rate of biomass gain is notably low when compared with estimates elsewhere, which range from 3.9 Mg ha^{-1} year^{-1} (in nearby Uganda, Wheeler et al. 2016) to over 14 Mg ha^{-1} year^{-1} (Cardarwine et al. 2015). This could be artefact of the method we used to estimate AGB gain, which relied on a low resolution (50 x 50 km) global dataset that was formed using climatic predictors and had had not previously been tested for our region. We were also unable to come up with a reliable method to account for potential varying rates of AGB gain in different land cover classes based on this data. As such, the modelled AGB estimates might not have accurately captured the effects of topography and other environmental factors (Kearsley et al. 2013) on allometries (Djomo et al. 2010; Mayanda et al. 2019) and growth strategies (Fayolle et al. 2016) specific to the Udzungwa-Kilombero Landscape. Nonetheless, in the absence of better data specific to our study region, and given that the maximum AGB values predicted by the model were similar to those produced by our former AGB map, we consider this an acceptable initial, conservative estimate of AGB recovery following restoration in the Udzungwa-Kilombero Landscape.

We were able to measure our estimates of AGB gain against the implementation costs associated with restoring native vegetation in each landscape pixel in order to identify the most cost-effective options for restoration intervention within the landscape. Promisingly, we found that there was a high degree of overlap (50% under our 5-year pessimistic scenario increasing to 90% under our 50-year optimistic scenario) between the most cost-effective options for restoration and those which are accessible logistically. This contrasts with findings by Brancalion et al. (2019) that areas of logistical feasibility do not align well with those of high strategic priority. Our positive findings can be largely attributed to our assumptions of proactive community involvement contributing to lower costs under our optimistic scenario, thus underscoring the need to engage with local people in order to improve the financial (as well as social and ecological) feasibility of restoration interventions in areas of habitation (Lamb et al. 2012; Mansourian et al. 2017).

Implicit in the methods used to predict the likely success (in terms of AGB gain) and thus the cost-effectiveness of restoration interventions was the assumption that the rate of AGB gain would be consistent across methods and in respect to landscape variables. However, research suggests that not only can this be affected by climate (Poorter et al. 2016), but also local site conditions (such as soils type, Suganuma et al. 2016; former land use and severity of degradation; Gourevitch et al. 2016), the presence of remnant trees within the landscape and relative isolation in relation to intact reference systems (Crouzeilles et al. 2016). Further research into exactly how these variables affect AGB accumulation in secondary vegetation that is restored using different methods and in respect to different climatic and landscape variables would greatly improve our ability to predict the success of restoration efforts with confidence. This would in turn improve estimates of where it is most cost effective to invest in these interventions.

3. Discussion and Conclusions

The primary aim of this research was to develop and test a systematic approach to inform strategic decision making in regards to where and how to allocate resources for tropical restoration. This culminated in a series of six maps to inform cost-effective planning in order to restore native AGB in the study region. In addition to constituting a valuable decision making tool, these contribute to the limited available data to inform restoration planning in the African continent which, despite low opportunity costs when compared to other tropical regions (Brancalion et al. 2019) has been subject to limited assessments of restoration potential (Gatica-Saavedra et al. 2017).

The approach I used here conformed to the four principles of restoration planning (Brancalion and Chazdon 2017). Step 1: By explicitly incorporating community engagement into restoration planning, I ensured that any restoration intervention will jointly serve to restore natural habitats within the study region while also enhancing and diversifying local livelihoods. Step 2: By including a thresholds of AGB deficit in order to warrant restoration intervention and by focusing on restoring native vegetation in these areas, I ensured that restoration activities will not replace native grasslands or savannah ecosystems, but instead will promote landscape heterogeneity and biological diversity (Step 3). Step 4: Lastly, through my assessment of current AGB and carbon stocks underpinned by field measurements scaled up across the region, I set a baseline against which subsequent gains can be measured, thus enabling these to be distinguished (both quantitatively, through biomass measures, and qualitatively, though vegetation type and diversity) from residual stocks.

A number of important observations came out of this process, which can be used to guide the direction of future research. Firstly, I identified significant potential for restoring AGB in the region which have not previously been picked up on in global assessments of restoration potential (Bastin et al. 2019). Furthermore, the observation that savanna habitats are naturally maintained was a very important finding with implications for restoration planning and is something that would likely have been missed by courser resolution data and studies neglecting to consider non-human drivers of land cover change in restoration planning. This brings into question the usefulness of pan-tropical mapping exercises, which result in significant regional biases (Mitchard et al. 2014), for identifying restoration opportunities at the regional level.

Credible data and knowledge to support decision making is among the most important issues constraining restoration projects (Sayer et al. 2015). Examples exist where efforts are being made to bridge this gap through coordinating multiple different stakeholders and to combine capacity building efforts with development, testing, and dissemination of science- based, cost-effective restoration technology (Melo et al. 2013). Nonetheless, insufficient data to support decision making has resulted in some NGOs and government agencies developing their own prioritization approaches for use in restoration planning (Knight et al. 2009). Recent studies that serve to critically evaluate the academic discourse in the context of its usefulness for solving conservation problems and to guide management decisions have highlighted how big the research-practice gap has become (Maas et al. 2019) but also served to raise awareness of this issue among the academic community. Therefore, I hope that this research serves to contribute to a growing body of academic research that is designed to solve real conservation problems and thus is of greater utility to conservation practitioners, developed with them in mind.

Supplementary Information

Methods

Study region

Table S1. Definitions of land cover classes in the Udzungwa-Kilombero Landscape of Tanzania along with the threats to above-ground biomass restoration identified based on author experience in the region.

Land cover class	**Description**	**Threats to biomass restoration**
Forest (217,036 ha)	Evergreen understorey with evergreen or deciduous canopy trees.	Tree growth stalled/prevented by proliferation of vines (<1,000m elevation) or bracken, shrubs and/or bamboo (>1,000m elevation). Tree-cutting for local subsistence common.
Savanna spectrum (2.78M ha)	Grassy areas with/without shrubs and deciduous trees.	Tree growth stalled/prevented by fire-maintained grasses and dense bushland thickets. Localised grazing. Tree-cutting for local subsistence common.
Floodplain/ swamp (228,656 ha)	As savanna spectrum but with seasonal floods and gallery trees/palms.	Fire. Grazing. Flooding. Limited access. Tree-cutting for local subsistence common.
Agriculture mosaic	All forms of agriculture and non-urban settlements.	Land availability. High opportunity costs.

Land cover class	Description	Threats to biomass restoration
(2.08M ha)		
Other	Urban areas, water or bare rock.	Not applicable to restoration.

Restoration potential

AGB measurements from vegetation plots

Diameter at breast height (dbh; cm) was measured for all stems. Height (m) was measured for 38.69% of stems (n=6,958) with the remaining stem heights estimated from dbh using regional elevation-dbh-height models (Marshall et al. 2012). Based on previous research in the region, wood density was considered the least important measure for deriving AGB (Marshall et al. 2012), hence we included data from studies both with and without species information. For those stems with species information, wood density (wood specific gravity of dry AGB; give units) was either measured or derived from the global wood density database (Zanne et al. 2009) to species or genus level. For stems without firm species identification we estimated wood density based on mean values of other stems in the same plot, forest or canopy cover. The reliability of AGB estimates from incomplete information (height; estimated height/wood density) was verified by using Pearson’s correlation to compare these with complete estimates.

AGB upscaling

We did not account for the presence of exotic species in the existing AGB in the agriculture mosaic because: (a) we assumed that new restoration activities would not be attempted in areas of commercial plantation (with so much land available in total, and limited commercial options for native species at the time of writing, it made little sense to remove successful economic activity); and, (b) if exotic species needed removing, we assumed that local communities would engage in harvesting the trees for profit (perhaps after initial use as nurse trees for newly planted native species) and therefore this activity would incur no net cost.

Restoration methods

Table S2. A description and justification of the restoration methods used for restoration planning in the Udzungwa-Kilombero Landscape, Tanzania.

Restoration method	**Application and Justification**
Passive regrowth (no action)	We assumed that forests with <40% (pessimistic) to 80% (optimistic) AGB deficit and non-forest habitats (savanna-spectrum, floodplain and agriculture mosaic) with <30% (pessimistic) to 50% (optimistic) deficit had sufficient AGB remaining to recover naturally in absence of intervention (as per our justifications for ANR in these areas below). We therefore excluded these areas from all further restoration assessment, along with urban areas, bare rock and water.
Assisted natural regeneration	Research from our region (Marshall et al. 2020) and elsewhere in Africa (Ssali et al. 2017) shows that secondary vegetation holds back woody biomass recovery in forests, which our pilot observations suggest frequently occurs following only a 50% loss in AGB (ranging 40% to 80%). We therefore planned for ANR in areas with ≥40% (pessimistic) to ≥80% AGB deficit.
Vine and herb/shrub cutting	In forests, we allowed for biannual (pessimistic) to annual (optimistic) cutting of lianas, herbs and shrubs, which can otherwise restrict tree growth and survival (Marshall et al. 2016; Ssali et al. 2017), with cutting required over one (optimistic), two (realistic) and seven (pessimistic) years. Where correctly employed, this leads to greater tree recruitment, stem growth and net AGB accumulation (Marshall et al. 2016), along with a reduction in rhizome performance of shrubs such as bracken (Marrs et al. 1998).
Lantana	Lantana *(Lantana camara)* is an invasive species throughout much of

Restoration method	Application and Justification
removal	the tropics, including East Africa and our study region. Based on our knowledge of lantana growth in the region, we planned for their removal under our pessimistic and realistic scenarios by digging up the plants (Love et al. 2009) along disturbed forest edges located within 100m (realistic) to 200m (pessimistic) of roads.
Clearing grasses and firebreaks	Dense growth of grasses and thicket in degraded habitats can hinder the recruitment, growth and survival of native woody vegetation due to: (a) competition for light and other resources (Hooper et al 2005; Brancalion et al. 2016; Suganuma et al. 2016); and, (b) increasing the risk and incidence of wildfires as a result of heightened fuel load (Hoffmann et al. 2012; Berengeur et al. 2014; Wheeler et al. 2016). In sub-Saharan Africa, the area affected by wildfires is decreased dramatically where tree cover exceeds ~40% (Archibald et al. 2009). We therefore planned for regular (two to four times annually during the growing season) cutting of grasses and firebreaks over two (optimistic) to four (pessimistic) years in all savanna spectrum and agricultural areas with ≥40±10% AGB deficit. Firebreaks were assumed to be positioned either around (external) and/or within (internal) the area to be restored, with the latter intended to provide added security against wildfires where the external firebreak has been accidently breached (Lamb 2011). The extent of firebreak clearance (expressed as a percentage of the land area to be restored) was determined based on the size of expected area to be managed, governance system and land cover class.
Active restoration through tree	We initially assumed that areas in the savanna spectrum, floodplain and agriculture mosaic with >70% (pessimistic; Hanski 2011) to 90% (optimistic; Brancalion et al. 2019) AGB loss were likely to have significantly reduced ecosystem function and therefore would require

Restoration method	Application and Justification
planting	active restoration through planting in order to restore native vegetation. However, following interrogation of maps showing the distribution of tree planting based on these thresholds against our local knowledge of the region, we found that this did not accurately reflect the full extent of the area in need of active restoration. We therefore revised our thresholds based on AGB values of known areas in need to tree planting on our current AGB map. This resulted in revised thresholds of ≥50% (pessimistic) to ≥80% (optimistic) which resulted in maps which much more accurately depicted the likely distribution of locations where tree planting was needed to restore native vegetation assemblages.
Framework species planting	In more severely degraded areas where soil seed stocks are depleted or non-existent, and where intact habitats that could otherwise serve as a source for seed dispersal are absent, active management through planting is often necessary to restore forests (Elliott et al. 2013). Accordingly, we planned for planting using the Framework Species Approach (FSA; Goosem and Tucker 1995) in degraded areas located more than 100m (Euclidean distance; pessimistic scenario; Jang et al. 2019), 200m (realistic scenario, Crouzeilles et al. 2020) and 300m (optimistic scenario; Wijedasa et al 2020) from intact habitats, beyond which capacity for natural regeneration is dramatically decreased.
Enrichment planting	Generalist and fast-growing species tend to dominate natural regeneration in degraded habitats (Hooper et al. 2005; Gunter et al. 2007; Caughlin et al. 2016). This is likely to be compounded due to the likely important role that dispersal-limited species (e.g. threatened arboreal primates) play in seed dispersal in our study region (Caughlin et al. 2016; Marshall et al. 2010). Therefore, under our pessimistic scenario, we assumed that enrichment planting of climax species

Restoration method	Application and Justification
	would be needed to supplement FSA planting, including within 100m of forests.
Soil improvement and nurse tree planting	We assumed that areas with ≥90% (pessimistic) to 100% (optimistic) deficit would be severely degraded to the extent that they would require soil improvement in order to support woody vegetation (Breugal et al. 2010; Caughlin et al. 2016). We therefore planned for ploughing and application of plant mulches for up to three years (pessimistic scenario), followed by planting of nurse trees comprising fast growing pioneer species and those capable of improving soils, e.g. legumes. Finally, gradual replacement of nurse trees with native species was implemented over three to five years (Elliott et al. 2013).

Restoration costs

Table S3. A description of the costs factored into the restoration assessment for the Udzungwa-Kilombero Landscape.

Type of cost	Calculation method
Land purchase	In areas of habitation, we assumed that land would need to be purchased in order to set it aside for restoration management (except in our optimistic scenario, where it was assumed that land owners would offer up land for free in exchange for ecosystem services and/or other economic benefits). We therefore produced an approximate map of land cost based on typical (realistic) land prices for 1ha of land, interpolating a smooth gradient of pricing between known areas. These

Type of cost	Calculation method
	estimated land prices were inflated by 25% in our pessimistic scenario.
Labour	We based our estimates of labour on local daily rates, which varied from US$2.15 (optimistic) to US$4.30 (pessimistic), and multiplied this by the number of workers and days necessary to complete each respective task. For methods involving tree planting, we also accounted for a two-day stipend of US$21.50day^{-1} (optimistic) to US$30.10day^{-1} (pessimistic) for the participation of a district government official, reflecting official rates for junior and senior government employees, respectively.
Equipment	Equipment costs were based on local market prices. Depreciation was factored into our cost calculations by assuming that equipment and tools would need to be repurchased after a number of years' usage.
Transport	We determined the appropriate transport method to reach each pixel on the basis of proximity to roads and areas of habitation. For this, we created a path-distance matrix combining Euclidean distance with a DEM base layer (SRTM 2000) to calculate the actual distance (m) travelled on the ground. We assumed that pixels located closer to habitation would be accessed by foot whereas those closer to roads would require motorised transport. All possible options for motorised transport (public bus, motorbike, private car and hired truck) were tested under all possible scenarios for distance travelled, carrying capacity (load) and thus the number of return trips required to perform each activity. This enabled us to determine the most cost effective transport option for each restoration method. For areas >3km from habitation or roads, we assumed that areas intended for restoration would require camping costs for one additional night spent per 7km travelled (based on our experience walking with heavily loaded field teams in the region). These included extra equipment, labourer

Type of cost	Calculation method
	stipends and consumables, plus porter salaries and a daily stipend for a district government official (tree planting methods only).
Community engagement	We assumed that restoration work in majority habitation areas (with the exception of large commercial farms), would require capacity-building and livelihood engagement. To plan for sustainable development of wood/fuel resources to balance the restoration work (and/or sustainable management of the restoration areas for these same resources), each village would also require: (a) development of a land-use/sustainability plan in year one; (b) sustainability start-up costs in years one and two (e.g. for tree nursery/fuel-efficient cook-stove training and materials development); and, (c) an annual progress workshop with village committees, including stipends and refreshments as well as participation of a district government official. Under our realistic and pessimistic scenarios we assumed that 50% and 100% of these costs in years one and two would be required again after five years, respectively. We also assumed that other land cover classes outside of protected areas within 3km of habitation (the typical distance travelled by one hour of walking to collect firewood, based on experience working in the region) would require 50% of these same livelihood engagement costs, because of their proximity to people and to allow for population expansion. Within protected areas we assumed that restoration work would incur no additional livelihood engagement costs beyond those routine livelihood engagement costs already established in existing protected area management.
Project management and administration	We budgeted for 10% of the salary of a Project Manager and for the full salary (including all government statutory costs) plus training and equipment costs of a: (a) Project Forester, to oversee all restoration activities; and, (b) Community Engagement Officer, to lead livelihood engagement activities. We also added 10% (optimistic) to 12%

Type of cost	Calculation method
	(pessimistic) to all costs to cover project direction and recruitment/finance administration, as is standard for the region.

<u>*Cost-effectiveness*</u>

Estimation of AGB gain

There is ambiguity in the literature regarding the relative growth rates of planted versus naturally regenerating trees (Omeja et al. 2009; Branchalion et al. 2016; Poorter et al. 2016; Shoo et al. 2016) as well as in relation to the degree to which different planting designs (Suganuma et al. 2017) and landscape characteristics (Crouzeilles et al. 2019) affect restoration success. Therefore, we assumed that, with sufficient management, planted versus naturally regenerating trees would be equally effective at recovering AGB deficit, so long as sufficient resources were invested (as outlined by our cost calculations). Our focus on AGB alone rather than AGB and biodiversity was justified by our focus on restoration methods that promote recovery of the natural ecosystems rather than biodiversity-poor monocultures (Elliot et al. 2013). Furthermore, markets for carbon offsets remain among the most promising mechanisms for financing restoration interventions (Brancalion and van Melis 2017) and carbon losses as a result of logging and fire – two key drivers of deforestation in the study region (Willcock et al. 2016) – are more pronounced in live AGB stocks than in soil and litter (Berengeur et al. 2014), thus justifying our focus on this pool.

Results

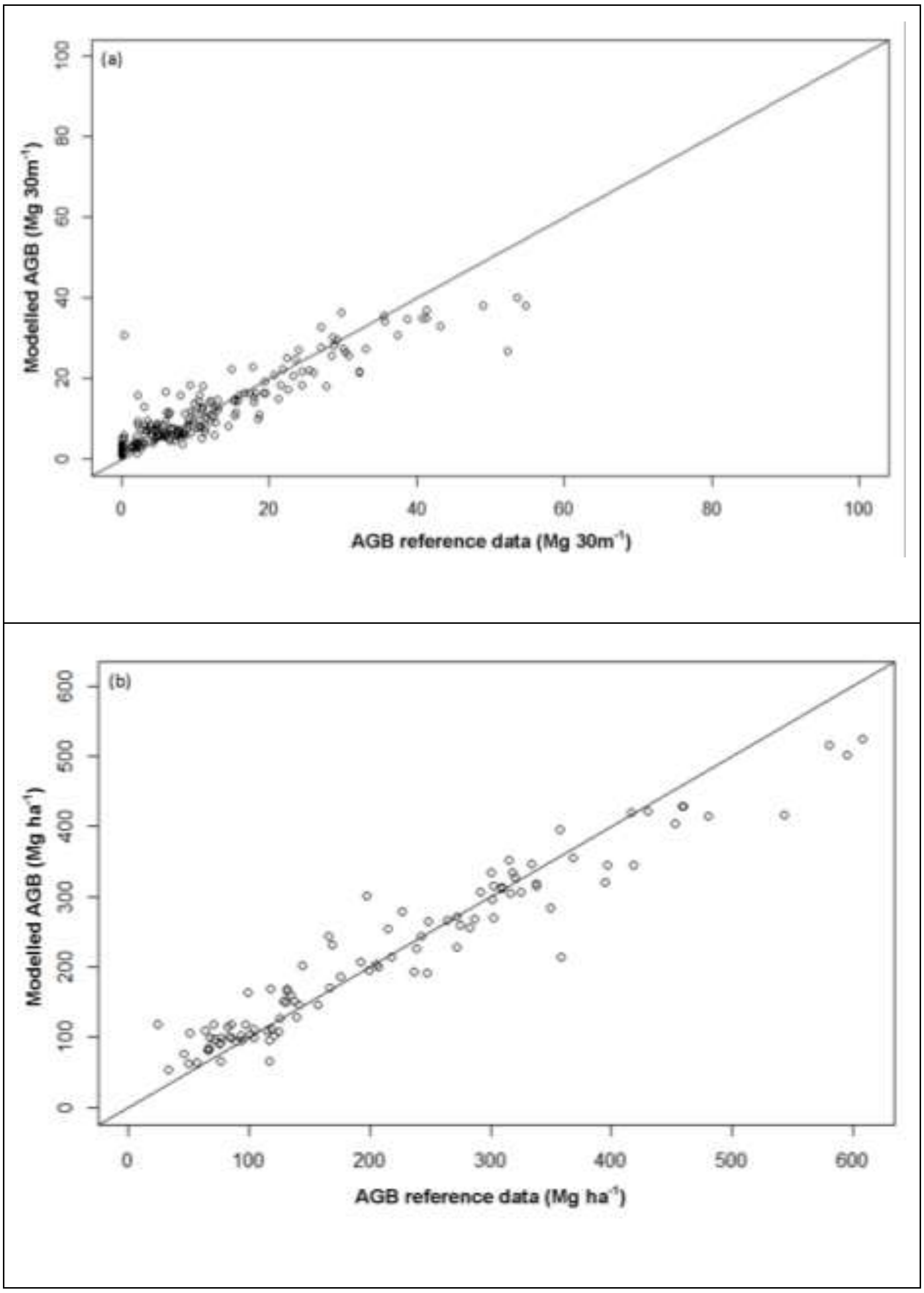

Figure S1. Observed against predicted values from models used to upscale plot-based AGB estimates across the Udzungwa-Kilombero Landscape, Tanzania, in order to estimate: (a) current AGB from spectral reflectance data; and, (b) former AGB from climatic predictors.

Table S4. Average current AGB, former AGB and AGB deficit in the Udzungwa-Kilombero Landscape, Tanzania, overall and disaggregated by land cover class.

Grouping	Min	Q1	Median	Q2	Max	Mean	StDev
Current AGB (Mg ha^{-1})							
Overall	19.56	74.35	95.72	145.96	564.54	124.71	82.98
Forest	55.47	220.22	297.47	401.81	559.46	308.16	112.27
Savanna	23.48	80.13	104.70	156.64	521.34	128.91	72.06
Floodplain	35.69	86.51	103.34	136.59	474.48	121.47	58.18
Agriculture	20.02	68.01	86.16	110.31	564.54	104.60	69.51
Former AGB (Mg ha^{-1})							
Overall	58.14	118.73	150.42	194.30	492.88	162.32	58.44
Forest	102.98	186.11	252.67	298.46	492.88	246.65	67.40
Savanna	58.14	117.18	141.93	185.56	471.00	157.91	59.04
Floodplain	81.01	103.28	112.57	131.10	304.46	124.18	35.52
Agriculture	66.68	125.68	165.53	197.62	420.57	166.03	51.38
AGB deficit (%)							
Overall	0.00%	25.86%	43.15%	58.17%	89.74%	41.80%	20.46%
Forest	0.04%	8.52%	18.53%	34.13%	81.81%	23.66%	17.22%
Savanna	0.00%	23.29%	38.97%	52.94%	87.01%	38.19%	19.27%
Floodplain	0.02%	12.25%	23.80%	38.59%	85.06%	28.26%	20.63%
Agriculture	0.03%	30.77%	48.69%	62.07%	89.74%	45.98%	20.31%

Table S5. Estimated costs (USD$ ha^{-1} year^{-1}, including all logistical transport, human and administrative expenses) of restoring native vegetation in the Udzungwa-Kilombero Landscape, Tanzania, including pessimistic (P), realistic (R) and optimistic (O) scenarios over five- and fifty-year investment timeframes.

Grouping	Min	Q1	Median	Q2	Max	Mean	StDev
5 years (P)	154	3744	6909	6967	41314	6877	4826
5 years (R)	79	2551	8316	8803	23918	6110	4029
5 years (O)	59	4026	8307	8308	19936	7413	2780

Grouping	Min	Q1	Median	Q2	Max	Mean	StDev
50 years (P)	30	1134	1568	3768	28624	2726	3324
50 years (R)	18	4654	5911	5999	57574	6862	5881
50 years (O)	6	841	1206	2764	20223	2234	2604
Realistic (5 years)							
ANR forests	14	97	141	191	544	148	156
ANR savanna	28	58	58	1662	12416	932	1698
Active	2670	3876	8196	8196	11437	6974	2002
Realistic (50 years)							
ANR forests	79	1577	2295	3104	8844	2390	2548
ANR savanna	537	1100	1100	31462	235059	17646	32154
Active	4631	5985	10327	10327	51176	10634	6236

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