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Biomass storage in Swedish forests: A case of land use

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Master thesis, 30 credits, in *Physical Geography and Ecosystem Science*

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Abstract

Forests are mitigating climate change by absorbing carbon dioxide from the atmosphere and storing it in the biosphere. Primary forests in particular have the potential to store large amounts of carbon and many are still accumulating carbon. Carbon storage in primary forests is also of interest as it may serve as a baseline against which to evaluate the effects of land use and land use change on carbon storage. However, uncertainties in terms of both historic and current carbon stocks are limiting our understanding of terrestrial carbon cycling and how it is affected by land use and land use change. Hence, the aim of this study was to estimate and compare the storage of living biomass in Swedish primary forests with the storage of living biomass in surrounding secondary forests. The estimates were made using a raster of remotely sensed vegetation biomass. Swedish primary forests stored more biomass than surrounding secondary forests, both on average and in the majority of cases. The carbon storage in Swedish primary forests was similar to estimates for Europe in general and to that found in primary forests in the Nordics and the Baltics. In addition, this study confirms previous findings of a biomass storage gradient along temperature, altitude, and latitude gradients. The results show that land use has a large impact on forest carbon storage and that there is large potential to store carbon in primary forests.

Keywords: Physical Geography, Ecosystem analysis, Forest biomass, Biomass storage, Forest carbon, Carbon storage, Carbon cycling, Land use, Primary forest

Sammanfattning

Skogar mildrar klimatförändringarna genom att absorbera koldioxid från atmosfären och lagra den i biosfären. Primärskogar i synnerhet har potential att lagra stora mängder kol och många primärskogar ackumulerar fortfarande kol. Kolförråd i primärskogar är även av intresse då de kan användas som referenspunkter gentemot vilka effekter av markanvändning och förändrad markanvändning kan utvärderas. Trots detta återstår osäkerheter relaterade till historiska och nuvarande kolförråd i olika skogstyper vilket i sin tur begränsar förståelsen för den terrestra kolcykeln samt hur denna påverkas av markanvändning och förändrad markanvändning. Syftet med denna studie var således att uppskatta och jämföra mängden levande biomassa i svenska primärskogar med mängden levande biomassa i omgivande sekundärskogar. Skattningarna genomfördes genom att använda ett raster för levande biomassa vilket framställts genom fjärranalys. Primärskogarna lagrade mer biomassa än omgivande sekundärskogar både i majoriteten av fall och i genomsnitt. Kolförråden i de svenska primärskogarna var jämförbara med kolförråd i primärskogar i Europa generellt liksom i Norden och Baltikum. Denna studie bekräftar även tidigare forskning som funnit att lagring av kol i skogar förändras längs temperatur-, altitud- och latitudgradienter. I sin helhet visar resultaten att markanvändning har stora effekter på skogliga kolförråd samt att det finns stor potential att lagra kol i primärskogar.

CONTENTS

1. Introduction

The expected continuation of greenhouse gas (GHG) emissions (Meinshausen et al. 2011) is projected to reinforce climate change, which has already impacted both human and natural systems across the globe (IPCC 2014). The terrestrial biosphere is mitigating climate change by absorbing, or sequestering, carbon (C) from the atmosphere and storing it in the biosphere (Harmon, Ferrell & Franklin, 1990; Houghton, Hall & Goetz 2009; Bloom et al. 2016; Friedlingstein et al. 2019; Pugh et al. 2019). Forests in particular are important storages of C due to their high C densities (Houghton 2007). Additionally, the terrestrial biosphere has been estimated to have sequestered ~30% of emissions from fossil fuel consumption and land use change (LUC) since 1850 (Friedlingstein et al. 2019), and forests are believed to be responsible for the majority of this sequestration (Pan et al. 2011). However, while understanding C cycling in both managed and unmanaged forests underpins climate change mitigation efforts (Pan et al. 2011; Seedre et al. 2015), a knowledge gap in terms of both historic and current vegetation and soil C stocks is limiting our understanding of terrestrial C cycling and the effects of land use (LU) and LUC (Harmon, Ferrell and Franklin 1990; Han and Zhou 2020; Bradshaw and Warkentin 2015; Friedlingstein et al. 2019).

When a forest is converted into another land use type, the initial loss of C depends on the amount of C stored in the forest prior to conversion (Searchinger et al. 2008; Houghton, Hall and Goetz 2009; Pan et al. 2011). However, estimates of LU and LUC effects on C storage depend on baseline conditions (Ghazoul et al. 2015; Ford and Keeton 2017; Liu et al. 2018; Vance 2018; Zhou et al. 2019), causing debate on C neutrality assumptions of biofuel production (Searchinger et al. 2008; Helin et al. 2013; Nabuurs, Arets and Schelhaas 2017). Primary forests may act as baselines from which to evaluate the effects of LU and LUC on C storage (Harmon, Ferrell and Franklin 1990; Han and Zhou 2020), but uncertainties remain in terms of amount of C transferred to the atmosphere during conversion of primary forests – partly due to limited knowledge on biomass and soil C stocks in different forest types (Achard et al. 2004; Norden et al. 2015; Han and Zhou 2020).

Of the total global terrestrial biomass 70-90% can be found in forests (Houghton, Hall & Goetz 2009) but it is asymmetrically spread over biogeographical regions: more than half is stored in tropical forests, ~1/3 in boreal forests and ~14% in temperate forests (Pan et al. 2011). In contrast to total storage, the density of total C is similar in tropical and boreal forests, yet the proportion of C stored in biomass and soil pools differ markedly: tropical forests store more than 50% in biomass and about 20% in soils while boreal forests store approximately 20% in biomass and 60% in soils (Pan et al. 2011). Forest C storage is also heterogenous on smaller scales, co-varying with multiple factors including stand age and land use history (e.g. Keith, Mackey and Lindenmayer 2009; Pan et al. 2011; Zanchi et al. 2014; Lundmark et al. 2018), both being of primary concern when separating primary forests from secondary forests (Bråkenhielm 1982; Hedefalk et al. 1999; FAO 2010; Duvemo et al. 2014).

The interest in primary forest C storage is growing (Badalamenti et al. 2019) and research on primary forests in different ecoregions have shown that they can store large amounts of C and that many are still accumulating C (Luyssaert et al. 2008; Keith, Mackey and Lindenmayer 2009; Pan et al. 2011; Brienen et al. 2015; Pugh et al. 2019). Large C storages have also been found in primary forests in countries surrounding Sweden (Finér et al. 2003; Kenina et al. 2018; Kenina et al. 2019; Nord-

Larsen et al. 2019) but no studies have, to my knowledge, examined Swedish primary forest C storages. Moreover, most studies examining primary forest C storage are based on field inventories (e.g. Keith, Mackey and Lindenmayer 2009; Kenina et al. 2019; Nord-Larsen et al. 2019), limiting large scale estimates and country-wide assessments of C storage potentials.

The potential of primary forests to store large amounts of C (Luyssaert et al. 2008; Pan et al. 2011; Brienen et al. 2015; Kenina et al. 2019) combined with the incomplete understanding of terrestrial C cycling and how it is affected by LU and LUC (Harmon, Ferrell and Franklin 1990; Friedlingstein et al. 2019; Han and Zhou 2020) call for scientific efforts directed towards these forests. Thus, the purpose of this study is to add to the knowledge of primary forest C storage potential and the effect of LU and LUC on forest C. This will be done by estimating the storage of living biomass in Swedish primary forests and compare it to the storage of living biomass in surrounding secondary forests. Such estimates are made possible by the coordinated use of a raster for aboveground tree biomass covering almost all of Sweden (Nilsson et al. 2017; Swedish Forest Agency 2020) and biomass data from the Swedish National Forest Inventory (NFI) (Fridman et al. 2014; SLU 2017a).

The biomass raster was produced by the Swedish Forest Agency and the Swedish Agricultural University (SLU) by relating airborne laser scanning data to field inventoried forest biomass using different linear regression models for different parts of Sweden (Nilsson et al. 2017; Swedish Forest Agency 2020). However, the biomass raster has not been validated on stand level (only on plot level) and it is not clear what linear regression models or parameter values were used when producing it (Nilsson et al. 2017). Consequently, it is necessary to evaluate the biomass raster, and perhaps also to apply adjustments, to ensure that it is viable for country-wide estimates of biomass in Swedish forests.

In short, the study is aimed at answering the following questions:

1. Is the relationship between biomass raster values and field inventory biomass of 1:1 character? If not, can a 1:1 relationship be attained by adjusting the raster?
2. Are primary forests in Sweden storing more or less C in living biomass than surrounding secondary forests, and how large is the difference?

The primary forests investigated in this study are expected to store more biomass than surrounding secondary forests as land use is expected to have negative effects on biomass storage (indicated in for example Harmon, Ferrell and Franklin 1990 and Keith, Mackey and Lindenmayer 2009).

2. Background

2.1. Primary and secondary forests – briefly on how they are different

An exhaustive description of primary and secondary forest definitions and their limitations is out of the scope of this study. Therefore, this section will give only an overview of what generally sets the two forest types apart.

Several different terms are used to describe similar types of forest: old-growth, late-successional, natural, over-mature, pristine, virgin, and primary to name a few (Wirth et al. 2009). These terms are often used interchangeably, but they can be separated into two main categories, one referring to forests that have not been disturbed by human activities (e.g. primary) and one referring to forests with stands that are, relatively speaking, old (e.g. old-growth) (With et al. 2009; Bernier et al. 2017). This study is focused on the former category and the term primary forest will be used when referring to forests belonging to it.

While there is great variation and ongoing discussion on definitions of both primary and secondary forests (Chokkalingam and de Jong 2001; Wirth et al. 2009; Bernier et al. 2017), the main difference between the two is that secondary forests are managed to yield products for human consumption whereas primary forests are undisturbed by human activities (Bråkenhielm 1982; Marks 1995; FAO 2010; Bernier et al. 2017). In other words, the main factor separating the two forest types is the presence or absence of human activities. Indeed, the central role of humans is emphasised in the current global standard primary forest definition (Bernier et al. 2017) from the FAO: "Naturally regenerated forest of native tree species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed" (FAO 2016). Furthermore, in Sweden, primary forests are normally richer in dead wood than secondary forests, they are normally more species diverse and are experiencing natural rather than anthropogenic disturbances whereas secondary forests are prone to both (Bråkenhielm 1982).

For a description on the definition of primary forest applied in this study, see the methodology section *Applied definition of primary forest*.

2.2. Primary forest extent

The area covered by primary forests has decreased on a global scale but the extent in both the temperate and the boreal region has increased (Morales-Hidalgo, Oswalt & Somanathan 2015). The Swedish Forest Agency together with SLU reports on Swedish forest resources for the FAO report Global Forest Resource Assessment (FRA) (latest report: FAO 2016). In the latest report from Sweden, the extent of primary forests in Sweden was reported as unchanged between 1990 and 2015 (Duvemo et al. 2014). But rather than being an actual measure of the evolution of primary forest extent, the reported no-change was said to be the result of clashing interpretations and definitions (Duvemo et al. 2014). In a more recent attempt to map European primary forests, the boreal region was found to host the largest total area of primary forests in Europe (Sabatini et al. 2018). Interestingly, it was found that the widest continuous stretches of such forests, although to a large extent unidentified, may reside in Sweden (Sabatini et al. 2018). In other words, the full extent of Swedish primary forests has not been documented (or disseminated).

2.3. Primary forests as biomass storages

There is an increasing amount of studies concerning C storage and storage capacity in primary forests (Badalamenti et al. 2019), and studies that have included direct measurements of C suggests that stored C increases along a successional gradient, that it is greater in late-successional and primary forests than in secondary forests (Luyssaert et al. 2008; Keith, Mackey, and Lindenmayer 2009; Jacob et al. 2013; Badalamenti et al. 2019; Nord-Larsen et al. 2019; Seedre et al. 2020) and inventories in primary forests in the Pacific Northwest of USA (Luyssaert et al. 2008) and in Australia (Keith, Mackey & Lindenmayer 2009) have revealed vast C storages. In fact, the world's highest discovered mean C density (1 867 tC/ha) was found in an Australian primary forest (1 053 tC/ha in above ground living biomass (AGB)) (Keith, Mackey and Lindenmayer 2009). Within the boreal domain, mean carbon density in primary forest living biomass has been estimated to 84 tC/ha in dry forests and 97 tC/ha in moist forests (59 tC/ha and 64 tC/ha when only considering AGB) (Keith, Mackey and Lindenmayer 2009).

No studies on C or biomass storage in Swedish primary forests have, to my knowledge, been published. However, studies on C storage in forests >100 years without visible signs of management in the Baltics, Denmark and Finland (where environmental conditions are comparable to those in Sweden) have shown a total ecosystem C storage range between 79 tons per ha (t/ha) and 395 t/ha – the higher figure originating from an inventory in a Danish semi-natural beech forest and the lower from an inventory in a northern Finnish pine forest (Vucetich et al. 2000; Finér et al. 2003; Kenina et al. 2018; Kenina et al. 2019; Nord-Larsen et al. 2019). C content in only living biomass in these inventories ranged between 28 t/ha and 229 t/ha (Vucetich et al. 2000; Finér et al. 2003; Kenina et al. 2018; Kenina et al. 2019; Nord-Larsen et al. 2019).

In addition to the substantial C storages in primary forests, continuous accumulation of C has been observed in tropical, temperate and boreal primary forests and in both below- and aboveground pools (Knohl et al. 2003; Zhou et al. 2006; Luyssaert et al. 2008; Keith, Mackey and Lindenmayer 2009; Pan et al. 2011; Brienen et al. 2015; Nord-Larsen et al. 2019). However, in a Czech spruce dominated forest between 116 and 145 years old and in Latvian needleleaf forests >160 years with no discernible management measures, no continuous accumulation could be discerned (Seedre et al. 2015; Kenina et al. 2018; Kenina et al. 2019).

2.4. Drivers of biomass storage and accumulation in primary forests

Stand age is one of the main factors influencing AGB storage in forests – AGB increasing with stand age (Bradford et al. 2008; Chatterjee, Vance and Tinker 2009). Biomass storage and accumulation in primary forests have also been related to environmental conditions – temperature and precipitation in particular – and land use history, with forests with little or no land use history storing most C (Vucetich et al. 2000; Keith, Mackey, and Lindenmayer 2009). The highest discovered biomass densities have been found in temperate forests with minimal land use history and where mean annual temperature is ~10°C and mean annual precipitation ranges between 1 000 mm and 2 500 mm (Keith, Mackey and Lindenmayer 2009). Furthermore, primary forest biomass storage, AGB storage especially, has been shown to decrease with increasing altitude and latitude (Vucetich et al. 2000; Jacob et al. 2013; Seedre et al. 2015).

Disturbance that leads to partial stand replacement has been shown to drive biomass accumulation in primary forests (Keith, Mackey and Lindenmayer 2009) and stand structure has been hypothesised to drive biomass accumulation (Luyssaert et al. 2008). Stand structure is thought to influence primary forest biomass storage due to two main factors: multi-layered canopies and C loss due to decomposition of dead wood being slower than accumulation due to growth of younger trees (Luyssaert et al. 2008). In other words, a disturbance generates dead wood and when it only partially replaces a stand, trees in a secondary layer are able to utilise freed resources and grow

– the growth resulting in an accumulation rate of C that is higher than the C emissions due to respiration from dead wood decomposition (Luyssaert et al. 2008; Keith, Mackey and Lindenmayer 2009). However, evidence on mechanisms behind primary forest C accumulation and storage is contrasting (Seedre et al. 2020).

2.5. The effect of management on forest biomass storage

About 57% of the Swedish land area is productive forestland – normally intensively managed – (Rytter et al. 2016) and the average total C density on Swedish productive forestland is 125 t/ha; ~45 t/ha stored in living biomass, ~75 t/ha in soils and ~5 t/ha in dead wood (SLU 2017b). However, biomass stored in secondary forests is a function of age due to the continuous accumulation of biomass in trees during their lifetime and due to the cyclic nature of secondary forests (Routa, Kellomaki and Strandman 2012; Seely, Welham and Kimmins 2002). Biomass stocks in secondary forests are also affected by land use history (Zanchi et al. 2014) and choices on management practices (Jandl et al. 2007; Chatterjee, Vance and Tinker 2009; Pan et al. 2011), for example soil preparation (Mjofors et al. 2017), crop choice (Torssonen et al. 2015), rotation length (Zanchi et al. 2014; Lundmark et al. 2018), thinning intensity (Zanchi et al. 2014) and harvesting method (Poudel et al. 2012; Lundmark et al. 2016).

In terms of LUC effects, the amount of C transferred from the biosphere to the atmosphere when an ecosystem is disturbed, anthropogenically or naturally, is dependent on the C density of that ecosystem (Houghton, Hall & Goetz 2009). This dependency explains the notion that much C stored in primary forests will be transferred to the atmosphere if they are disturbed (Luyssaert et al. 2008; Pan et al. 2011; Brienen et al. 2015). As an example, one study investigating the effect on C storage when converting a primary forest in the Pacific northwest in the US to a secondary forest suggests that more than 300 tC/ha may be lost due to such conversion (Harmon, Ferrell and Franklin 1990). In addition, estimates have suggested that if managed forests were to be restored to store 90% of their potential biomass storage, 7-12 years' worth of current fossil fuel emissions would be sequestered (Erb et al. 2018).

Stored forest C may change more or less instantly, e.g. through the removal of harvested wood, but is also a function of LU and management taking place decades to centuries ago (Foster et al. 2003). In Sweden for example, traces from historical low-intensity LU are still present in some of the most inaccessible forest areas commonly perceived as unaffected by anthropogenic activities (Josefsson, Östlund and Hörnberg 2009; Josefsson et al. 2010).

3. Methodology

3.1. Applied definition of primary forest

In their FRA, FAO defines primary forests as "Naturally regenerated forest of native tree species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed" (FAO 2016). The Swedish Forest Agency and SLU, when reporting to the FRA, define primary forests as productive forestland (land with environmental conditions allowing for an average production of at least 1 m^3 of stem per year and ha over 100 years) with stands older than 150 years, presence of dead wood with a diameter at breast height (dbh, 1.3 m) >25 cm and absence of forestry measures during the last 25 years (Duvemo 2014). In other words, definitions as to what constitutes a primary forest are diverging.

The locations and extents of Swedish primary forests accessible for this study are digitisations of a report produced in the 1980s (Bråkenhielm 1982). Hence, the definition of a primary forest used in this study is hinged on the definition used in the report by Bråkenhielm (1982). The definition in the Bråkenhielm (1982) report specifies that both primeval forests and older forests with primeval forest characteristics and little traces of anthropogenic activities may be considered primary (Bråkenhielm 1982). In addition, it is stated in the report that younger forests (e.g. forest regenerating from fire or other natural disturbance) were not included if there were no old stands present in the vicinity (Bråkenhielm 1982). In other words, this study does not claim to include all primary forests of Sweden. It should also be noted that, due to differences in land use history, the criteria for what was to be considered a primary forest were stricter when inventorying the north of Sweden as compared to when inventorying the south (Bråkenhielm 1982).

In short, the following parameters were determinants of whether a forest was to be classified as primary or not (Bråkenhielm 1982):

- Visible traces of absence or presence of anthropogenic activities including cut or sawed stubs, amount of dead wood and glades, tree demography, tree species diversity, presence of invasive species and remnants of charcoal kilns, culture cairns or roundpole fences. Areas with traces of for example extensive grazing and/or small-scale thinning, cleaning or firewood cutting within an area was accepted if that area otherwise fulfilled the requirements. Any traces of clear-cutting, soil preparation, drainage ditching or other intensive management led to the exclusion of such forests.
- The size of the area: areas south of Dalälven were to be at least 10 ha, areas on the coast of northern Sweden at least 25 ha and inland areas of northern Sweden at least 100 ha. These sizes were used as guidelines rather than absolute criteria: areas with natural borders and much of primary forest characteristics as well as several smaller areas close to each other were allowed to be smaller than the stated sizes.
- Whether or not areas bordering the forests were natural (e.g. lakes, wetlands, topographically rough terrain) or not. This parameter was especially important when regarding smaller areas as these were considered more prone to degradation than larger areas.
- Successional stage: in the south of Sweden in areas with high, medium and low site quality, tree stands had to have an age of 100, 120 and 140 years respectively to be included. In the north of Sweden, tree stands had to be 110, 140 and 170 years in areas with high, medium and low site quality respectively. The stated ages were based on coniferous forests – i.e. deciduous forests of lower ages were accepted.

For a full description on how these criteria were applied and for a more detailed description of the classification process, consult Bråkenhielm (1982).

3.2. Study area

The study area included the full extent of Sweden (approximately between 55°N and 69°N and between 10°E and 24°E) located within the boreal and temperate continental zones (Rytter et al. 2016). The climate varies widely with yearly mean temperatures (during reference period 1961-1990) ranging from -8°C in the north to 10°C in the south and yearly mean precipitation largely following an east to west gradient, ranging between 400 mm and 2100 mm (SMHI 2020). The primary forests (n = 388) were distributed across all parts of Sweden (Figure 1).

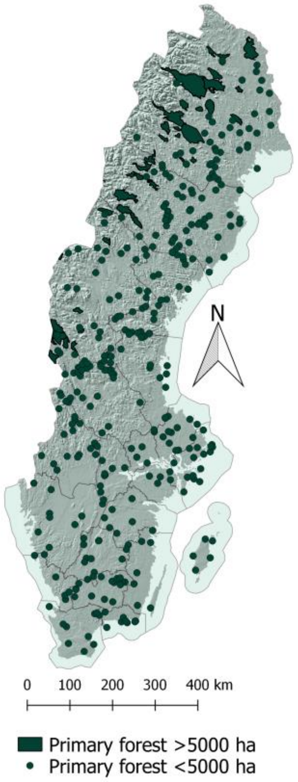

Figure 1. Study area with Swedish primary forests marked. Points are primary forests <5000 ha and polygons >5000 ha. Lines within Sweden are county borders.

3.3. Materials

Below follows a detailed description of the main data that were used in this study. For an overview of the main data, see Table 1.

The main data used in this analysis was a digital map (polygons) indicating where in Sweden primary forests are located (Ahlström et al. unpubl.), field inventory data from the National Forest Inventory (NFI) (SLU 2019a) and a raster layer representing living above ground tree dry weight biomass (i.e. excluding roots and stubs) (Nilsson et al. 2017; Swedish Forest Agency 2020). The NFI data includes coordinates for where field inventory has been undertaken, what year the field inventory was undertaken, biomass density measurements reported in dry weight (AGB and roots >2 cm thick, hereafter referred to as biomass), reported management measures, gross growth of forest stands and a land classification. The biomass raster is produced from airborne laser scanning data collected between 2009 and 2016 and covers all parts of Sweden except areas of montane birch forest in north-western Sweden (Nilsson et al. 2017; Swedish Forest Agency 2020). A shapefile containing data on when specific areas of Sweden were scanned for imagery used to produce the biomass raster (Swedish Forest Agency 2020) was used to track time differences between the year of NFI field inventory and the year of scanning for raster imagery.

The Swedish generalised national land cover raster, including the raster for productive forest land (Ahlkrona et al. 2019; Keskitalo et al. 2019), covers all of Sweden and was used to exclude non-forest areas and non-productive forest areas from the analyses. Forest areas in the Swedish national land cover raster are defined as tree-covered areas with a tree height of at least 5 m and a canopy cover of at least 10%, or areas where trees have the potential to reach such thresholds (Ahlkrona et al. 2019). Productive forest land is defined as land capable of supporting a production of at least 1 m^3 of timber per year and ha (SFS 1979:429; Keskitalo et al. 2019). The generalised version of the land cover raster was used to reduce the risk of including smaller forest patches, for example small stands in agricultural fields (Ahlkrona et al. 2019). The raster for productive forest land was used as a complement to the generalised land cover raster – reducing the risk of including non-secondary forest areas. In addition, it provided baseline conditions for the comparison of primary and secondary forests – i.e. increasing comparability. Several other GIS-layers were used for excluding unsuitable areas from the analyses, e.g. water bodies (see section *Areas of primary forests* and *Areas of secondary forests*).

When producing the biomass raster, cells were given a value of 0 if basal-area weighted tree height in that cell was <3 m (Nilsson et al. 2017; Swedish Forestry Agency 2020). Therefore, a raster for basal-area weighted tree height (Swedish Forest Agency 2020) was used in the process of data cleaning (see section *Data cleaning and handling* for specifics). The tree height raster covers all of Sweden except areas of montane birch forest in north-western Sweden (Nilsson et al. 2017).

A raster for stand age covering all areas in Sweden classified as forest in the Road Map from the Swedish Land Survey authority (SLU 2016a; Swedish Land Survey 2016) was used to investigate potential stand age differences between primary and secondary forests as well as to investigate mean stand ages in secondary forests. Rasters for mean annual temperature (covering all of Sweden) (Meineri and Hylander 2016) and soil wetness (covering all of Sweden except areas of montane birch forest) (Swedish Environmental Protection Agency 2019a) were used for testing potential effects on biomass storage. The wetness index is a unitless combination of the Depth to Water Index and the Soil Topographic Wetness Index called Metria index (Swedish

Table 1. Main data used in this study, description of content and reference to metadata/producer.

Data description	Content used	Metadata/Producer
Map of locations and extents of Swedish primary forests	All	Ahlström et al. unpubl
NFI field inventory data	Coordinates for where field inventory has been undertaken What year the field inventory was undertaken Biomass density measurements reported in dry weight (AGB and roots >2 cm thick) Reported management measures Gross growth of forest stands Land classification	SLU 2019a
Raster with values of dry weight AGB density	Raster with biomass values (living above ground tree dry weight biomass) Metadata (shapefile) describing what year a specific area was scanned for imagery used to produce the raster	Nilsson et al. 2017; Swedish Forest Agency 2020
Swedish national land cover raster (generalised), including productivity raster	Areas of forest land (generalised) and productive forest land	Ahlkrona et al. 2019; Keskitalo et al. 2019
Basal-area weighted tree height raster	Basal-area weighted tree height values	Nilsson et al. 2017; Swedish Forest Agency 2020
Mean annual temperature raster	Mean annual temperature values	Meineri and Hylander 2016
Soil moisture raster	Soil moisture values	Swedish Environmental Protection Agency 2019
Digital elevation model (DEM)	Elevation values	European Environment Agency 2017

Environmental Protection Agency 2019a). A digital elevation model (DEM) from the European Environment Agency/Copernicus (European Environment Agency 2017) that covers all of Sweden was used to test the effect of elevation and slope on biomass storage.

GIS processing was done in ArcMap (v.10.5) and ArcGIS Pro (v.2.5) and all data cleaning, analysis and plotting was done in MATLAB (v.R2019b). ArcGIS Pro was used for extracting mean raster values across individual primary and secondary forests. ArcGIS Pro was used for this process as it contains tools that have undergone development for overcoming problems with data losses – developments that have not been applied to the tools available in ArcMap (ESRI n.d.a; ESRI n.d.b). For all other GIS processes, ArcMap was used.

3.4. Data preparation

3.4.1. Preparation of raster layers

Before resampling the raster layers, the generalised land cover raster (Ahlkrona et al. 2019) was reclassified to only contain classes of *forest* and *not forest*, and the raster layer for productive forest land (Keskitalo et al. 2019) was reclassified to only contain the classes *productive forest* and *not productive forest*. The class *forest* produced from the generalised raster was an aggregation of all forest classes, including areas classified as *temporarily not forest*. Areas classified as *temporarily not forest* in the national land cover raster include areas of windthrows, burnt areas as well as previously felled areas (Ahlkrona et al. 2019).

Except for the temperature raster layer, all raster layers were resampled to correspond to the grid and spatial resolution of the DEM (25 m x 25 m) – the raster with lowest resolution. The temperature raster was fitted to the grid of the DEM but was allowed to remain in its original resolution (50 m x 50 m) in order to not compromise the detail of the other raster layers (e.g. biomass raster with 12.5 m x 12.5 m spatial resolution) and due to its continuous character. The (reclassified) national land cover rasters were resampled using a majority technique (the most frequent class within a 3 x 3 cell window being assigned to the new cell). The rasters for biomass, basal-area weighted stand height and soil moisture were resampled with an applied bilinear interpolation. The stand age raster was resampled using a nearest neighbour technique due to its spatial resolution (24.99 x 24.99 m) being very similar to that of the DEM (25 m x 25 m).

For the investigation of potential effects of slope on biomass storage, a raster for slope (°) was produced from the DEM.

3.4.2. Areas of primary forests

The extents of primary forests in the original polygon GIS-layer available to this study (Ahlström et al. unpubl.) indicated within what areas the primary forests were located. However, within those polygons other land cover than forest was present (e.g. water bodies) and management measures may have been undertaken within the areas since they were pointed out as primary forests (Figure 2a). Hence, in a first step, any polygon areas of water bodies and any polygon areas covering areas where felling had been undertaken or planned were excluded (Figure 2b). In a second step, the produced polygons were superimposed on the national land cover raster (Ahlkrona et al. 2019) (Figure 2c) and areas falling within the polygons that were classified as forest or temporarily not forest were extracted (Figure 2d, areas of forest and temporarily not forest are in the figure aggregated into Forest). Raster cells with cell centres outside polygon boundaries were considered outside the polygon. Lastly, the raster for forest productivity was superimposed on the general forest raster produced in step two (Figure 2e), and only cells of these two rasters that overlapped were included – constituting what was finally classified as primary forest (Figure 2f). The layers used in the exclusion process are summarized in Table 2. From here on, primary forests refer to the areas remaining after making the exclusions described above (Figure 2f). The layers used in the exclusion process are summarized in Table 2.

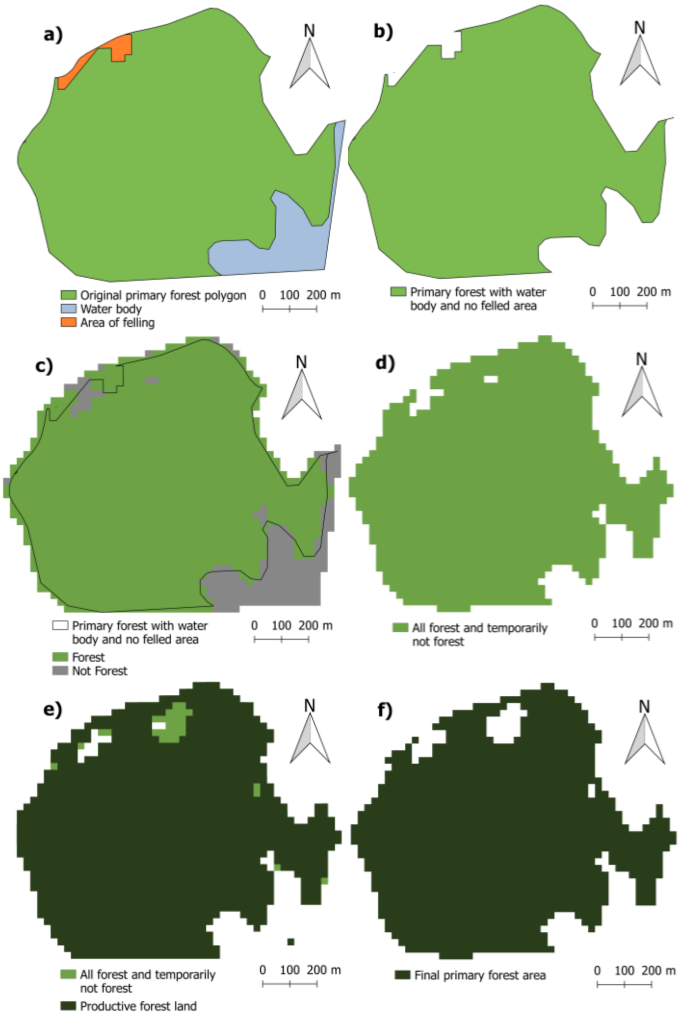

Figure 2. The process of delimiting primary forest areas. Any water bodies and areas where felling was planned or had been undertaken (a) were excluded (b). The polygons from (b) were superimposed on the generalized Swedish land cover raster (c) and areas not classified as *forest* or *temporarily not forest* were excluded (d). Lastly, the raster for productive forest land was superimpose on the general forest areas (e) and non-overlapping cells were excluded (f).

Table 2. GIS-layers of and use/land cover used for excluding areas within original primary forest areas (polygons). The areas remaining after exclusions were considered primary forests for the remainder of the study.

Excluded land use/land cover	Source	Metadata/Producer
Areas not classified as *forest* or *temporarily not forest* in the Swedish national land cover raster	https://gpt.vicmetria.nu/data/land/NMD/NMD2018_basskikt_generaliserad_Sverige_v1_0.zip	Ahlkrona et al. 2019
Areas not classified as *productive forest land* in the Swedish national land cover raster	http://gpt.vic-metria.nu/data/land/NMD/NMD_Produktivitet_v1_0.zip	Keskitalo et al. 2019
Undertaken and planned felling as reported by the Swedish Forest Agency	http://geodpags.skogsstyrelsen.se/geodataport/feeds/UtfordAvverk.xml http://geodpags.skogsstyrelsen.se/geodataport/feeds/AvverkAnm.xml	http://skogsdataportalen.skogsstyrelsen.se/Skogsdataportalen/ (©Swedish Forest Agency)
Water bodies	http://ext dokument.lansstyrelsen.se/Gemensamt/Geodata/Datadistribution/ZIP/VM_Vattenforekomster.zip https://www.lantmateriet.se/sv/Kartor-och-geografisk-information/oppna-data/	Henestål and Björkert, 2017a; Henestål and Björkert 2017b; Swedish Land Survey 2019

3.4.3. Areas of secondary forests

To find secondary forests with environmental conditions similar to those in each primary forest, buffers of 15 km were created outside the borders of each original primary forest polygon – i.e., this was done before any areas were excluded from the original primary forest polygons (Figure 3). After the creation of the buffers, the procedure for delimiting secondary forests followed the same principles as when delimiting primary forest areas – the difference being that areas of felling were not excluded and that areas of for example nature conservation and intact forest landscapes were excluded (Table 3). Table 3 provides a full list of layers used when making exclusions from the buffers surrounding the original primary forest polygons. From here on, *secondary forests* refer to the areas within the 15 km buffers remaining after making these exclusions.

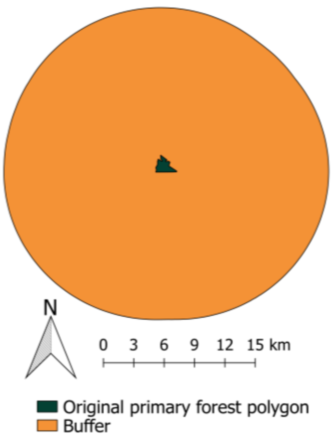

Figure 3. Original primary forest polygon with surrounding 15 km buffer.

Table 3. GIS-layers of land use/land cover used for excluding areas within buffers surrounding primary forests. The areas remaining after exclusions were considered secondary forests for the remainder of the study.

Excluded land use/land cover	Source	Metadata/Producer
Areas not classified as *forest* or *temporarily not forest* in Swedish land cover raster	http://gpt.vic-metria.nu/data/land/NMD/NMD2018_basskikt_generaliserad_Sverige_v1_0.zip	Ahlkrona et al. 2019
Areas not classified as *productive forest land* in the Swedish national land cover raster	http://gpt.vic-metria.nu/data/land/NMD/NMD_Produktivitet_v1_0.zip	Keskitalo et al. 2019
Intact Forest Landscapes	http://www.intactforests.org/data.ifl.html	Potapov et al. 2008
Natura 2000 – Sites of Community Importance (SCI)	http://gpt.vic-metria.nu/data/land/SCI_Rikstackande.zip	http://www.naturvardsverket.se/Var-natur/Skyddad-natur/Natura-2000/ (©Swedish Environmental Protection Agency)
Natura 2000 – Special Protection Areas (SPA)	http://gpt.vic-metria.nu/data/land/SPA_Rikstackande.zip	Ibid
National parks	http://gpt.vic-metria.nu/data/land/NP.zip	Ibid
Nature reserves	http://gpt.vic-metria.nu/data/land/NR.zip	Ibid
State-owned forests worthy of protection (SNUS)	http://gpt.vic-metria.nu/data/land/Skyddsvarda_statliga_skogar.zip	Löfgren, Henriksson and Hultgren 2004
Nature conservation agreement	http://geodpags.skogsstyrelsen.se/geodataport/feeds/Naturvardsavtal.xml	http://skogsdataportalen.skogsstyrelsen.se/Skogsdataportalen/ (©Swedish Forest Agency)
Objects of nature conservation value	http://geodpags.skogsstyrelsen.se/geodataport/feeds/Naturvarden.xml	Ibid
Key-biotopes (Nyckelbiotoper)	http://geodpags.skogsstyrelsen.se/geodataport/feeds/Nyckelbiotoper.xml	Ibid
Key-biotopes (Nyckelbiotoper) in specific companies' forests	http://geodpags.skogsstyrelsen.se/geodataport/feeds/StorskogsbrNyckelb.xml	Ibid
Protected biotopes	http://geodpags.skogsstyrelsen.se/geodataport/feeds/biotopskydd.xml	Ibid
Water bodies (layers from both the Swedish Water Agency and from the Swedish Land Survey)	http://ext-dokument.lansstyrelsen.se/Gemensamt/Geodata/Datadistribution/ZIP/VM_Vattenforekomster.zip ftp://download-opendata.lantmateriet.se/GSD-Terrangkartan_vektor/Sverige/Sweref_99_TM/mapinfo/tk_riks_Sweref_99_TM_mapinfo.zip	Henestål and Björkert, 2017a; Henestål and Björkert 2017b; Swedish Land Survey 2019

3.4.4. Data extraction to NFI data points

To coordinate points indicating where – within primary and secondary forests – NFI field inventory had been conducted (hereafter NFI data points), raster values representing dry weight of biomass (t/ha) and basal-area weighted tree height (dm) were extracted. Data on what year(s) specific areas were scanned for imagery used to produce the biomass raster (hereafter scan year) were also extracted to the NFI data points. All values were extracted without interpolation.

3.4.5. Cleaning and handling of NFI data points: primary and secondary forests

87% of NFI data points within primary forests were classified as productive forest in the NFI field inventory data. The remaining points were classified as montane needleleaf forest (11%) and mires and impediments (2%). Montane needleleaf forest and mires and impediments are described in the NFI field inventory instructions as forests of low productivity (growth of <1 m^3 of stem per year and ha over 100 years) and normally having low tree density (SLU 2017a; SLU 2018). In other words, even after the process of delimiting productive primary forests, some areas classified in the NFI as montane needleleaf forests, mires and impediments were included. These points were included in the analysis – the exclusion of these points would mean that the biomass raster evaluation would be based on the premises that the biomass raster cells on which these points were superimposed belonged to a land cover class which they in fact did not belong to.

Any NFI data points within primary forests marked with felling, thinning, cleaning, ground clearing or planting were excluded from further analysis. Since neither the biomass raster nor the layer with scan year information covered areas in the Swedish mountain birch forests (Nilsson et al. 2017; Swedish Forest Agency 2020), any NFI data points in these areas were excluded from subsequent analyses.

To correct for tree growth between NFI field inventory year and scan year, a biomass gross growth parameter available in the NFI field inventory data was utilized. Any growth values that were negative (due to e.g. previous felling or fire) were set to 0 as they did not represent growth and could hence not be used in calculations. For any positive gross growth value the yearly growth rate was multiplied with the number of years between the scan year and the year of NFI field inventory – if the field inventory year was later than the scan year, a negative growth was applied and vice versa. The calculated growth was then added to the total biomass stated in the NFI field inventory data. After updating the total biomass, any negative biomass values were set to 0. These updates were undertaken before any further analyses or exclusions were made.

When producing the biomass raster, cell values were set to 0 if basal-area weighted stand height in that cell was <3 m (Nilsson et al. 2017; Swedish Forestry Agency 2020). Hence, any points where field inventory biomass was >0 t/ha, the extracted biomass raster value was 0 t/ha and, as indicated by the stand height raster, the basal-area weighted tree height was <3 m were excluded from the analysis.

3.4.6. Cleaning and handling of NFI data points: secondary forests only

This section only describes cleaning of NFI data points within secondary forests.

The NFI land classifications of data points within secondary forests were productive forestland (96%), impediments and mires (3%) and montane needleleaf forest (1%). With the same motivation as described in the previous section, these points were included in the analysis.

NFI data points with discrepant biomass values (0 t/ha from raster and >0 t/ha in NFI data or vice versa) and where the NFI data indicated management or disturbance between the scan year and the year of NFI field inventory were excluded from the analysis (Table 4). The exclusion of NFI data points marked with ground clearing, planting and/or cleaning between NFI field inventory year and scan year was made as such management is indicative of previous felling, not least in the context of the biomass discrepancy. NFI data points with field inventory biomass >0 t/ha, biomass raster value of 0 t/ha and extracted mean basal-area weighted tree height <3 m were excluded from the analysis. The specifics of NFI data point cleaning within secondary forests are given in Table 4.

Table 4. Specifics of NFI data point cleaning in secondary forests.

Time sequence	Biomass discrepancy	Reason for exclusion
Scan year < Disturbance year < Field inventory year	Biomass raster value >0 (t/ha) Field inventory biomass = 0 (t/ha)	NFI indicated disturbance: felling, thinning, planting, ground clearing or cleaning
Scan year < Field inventory year	Biomass raster value >0 (t/ha) Field inventory biomass = 0 (t/ha)	NFI indicated unknown disturbance: negative growth in NFI data
Scan year > Disturbance year > Field inventory year	Biomass raster value = 0 (t/ha) Field inventory biomass >0 (t/ha)	NFI indicated disturbance: felling, thinning, planting, ground clearing or cleaning
Any	Biomass raster value = 0 (t/ha) Field inventory biomass >0 (t/ha)	Basal-area weighted mean stand height < 3 m

3.5. Relationship enhancement and forest biomass estimation

The relationship between NFI field inventory biomass (t/ha) and extracted biomass raster values (t/ha) was tested by plotting the two biomass measures of each NFI data point against each other. In order to account for structural differences and hence potential differences in carbon storage mechanisms, primary forests and secondary forests were treated separately in terms of the relationship between NFI field inventory biomass (t/ha) and biomass raster values (t/ha).

The relationship between NFI field inventory biomass (t/ha) and biomass raster values (t/ha) were not of 1:1 character in primary forests nor secondary forests. In other words, the biomass raster values did not represent the same thing as the NFI field inventory biomass values. To attain a 1:1 relationship, the biomass raster values extracted to NFI data points in primary and secondary forests were multiplied with the slope coefficient of the respective linear regression. The slope coefficients were also used for resampling the biomass raster (i.e. multiplying raster cell values with the slope coefficients), producing one new biomass raster for primary forest biomass and one new for secondary forest biomass.

3.6. Paired analysis

The resampled biomass rasters were used to extract mean biomass densities (t/ha) across individual primary forests and surrounding secondary forests. Biomass raster cells that did not overlap with primary or secondary forest areas were excluded from the analysis. In order to compare individual primary forests with secondary forests of similar environmental conditions, mean biomass density (t/ha) of each primary forest was plotted against the mean biomass density (t/ha) of the surrounding secondary forest – i.e. each primary forest and surrounding secondary forest was considered a pair. By plotting mean biomass densities (t/ha) in a pairwise manner the relative biomass storage of individual pairs was illustrated.

3.7. Parameters influencing biomass storage

Differences between primary and secondary forest mean stand age (years), mean altitude (m), mean slope (°) and mean soil wetness (unitless, Metria index) were tested for potential influence on difference between primary and secondary forest biomass storage (t/ha). In addition, potential effects of temperature (°C) and forest latitudinal position (°N) on difference in biomass density (t/ha) was tested for. For all rasters, cells that did not overlap with primary or secondary forest areas were excluded from the analyses. The raster cells that did overlap with forest areas were used to extract mean values across individual primary and secondary forests.

Potential effects of temperature (°C), soil wetness (unitless), altitude (m) and latitude (°N) on biomass density (t/ha) in both primary and secondary forests were tested for with linear regressions – i.e. the general effect was tested, not the difference between forests.

Due to the continuous accumulation of carbon in trees during their lifetime and the cyclic nature of secondary forests, biomass stored in these forests is a function of stand age (Routa, Kellomaki and Strandman 2012; Seely, Welham and Kimmins 2002). Hence, unless the stands in the secondary forests are evenly distributed across the ages represented in that forest areas average rotational cycle, the analysis described thus far can only describe how the biomass density of Swedish primary forests compared to biomass density in Swedish secondary forests at one particular point in time. To get an indication on whether the mean stand age of the secondary forests investigated was affecting their biomass densities, a simple index was used. The index is based on the fact that the Swedish Environmental Protection Agency has classified forests as old-growth if the mean stand age is more than 130 years in parts of Sweden south of approximately 60°N and more than 150 years in parts north of approximately 60°N (Swedish Environmental Protection Agency 1999). The mean stand age of each secondary forest area was divided by 130 if they were located south of 60°N and by 150 if they were located north of 60°N. This yielded a value between 0 and 1 (none of the forests had a mean stand age higher than that of the old growth limits) which was plotted against the biomass density (t/ha) of the forest. In addition, a potential dependency of this index on latitude was investigated.

3.8. Statistical analyses

All data distributions used in statistical tests were tested for normal distribution with one-sample Kolmogorov-Smirnov tests (Massey 1951).

To test whether the relationship between field inventory biomass (t/ha) and biomass raster values (t/ha) was of 1:1 character for primary and secondary forests respectively, 95% confidence intervals of linear regression slopes were calculated and plotted to see if they overlapped with 1:1 lines. To test the correlation between field inventory biomass (t/ha) and biomass raster values (t/ha), Pearson correlation tests (Pearson 1895) were conducted for primary and secondary forests respectively with a significance level of 0.05. Due to the number of NFI data points available for analysis after all exclusions and data cleaning processes (171 within primary forests and 6 358 within secondary forests), the Pearson correlation test could be conducted in spite of non-normally distributed data. The Pearson correlation test was favoured over a Spearman correlation test as a linear relationship was desired (Hauke and Kossowski 2011).

When comparing mean biomass densities (t/ha) in primary forests with biomass densities (t/ha) in secondary forests (paired analysis), a Wilcoxon rank-sum test (Wilcoxon 1945; Mann and Whitney 1947) was conducted with a significance level of 0.05. The Wilcoxon test was favoured over a paired-sample t-test due to the non-normal distribution of mean biomass densities across both primary and secondary forests.

With the use of Spearman correlation tests (Spearman 1904), difference between primary and secondary forest biomass density (t/ha) was tested for correlation with temperature (°C) and latitude (°N) and with difference in stand age (years), soil wetness (unitless), altitude (m) and slope (°). The Spearman correlation test was applied due to non-normally distributed data and the correlations were tested at a significance level of 0.05. Biomass density (t/ha) in primary and secondary forests was tested for correlation with temperature (°C), soil wetness (unitless, Metria index), altitude (m) and latitude (°N) by applying Spearman correlation tests (due to non-normally distributed data) with a significance level of 0.05. The secondary forest stand age index was tested for potential correlations with biomass density (t/ha) and latitude (°N) with the use of Spearman correlation tests.

4. Results

4.1. Relationship between field inventory biomass and biomass raster values

Neither in primary nor secondary forests did the 95% confidence intervals of the linear regression slopes overlap with 1:1 lines – i.e. the relationships between field inventory biomass (t/ha) and uncorrected biomass raster values (t/ha) were not of 1:1 character in primary forests nor secondary forests (secondary forest slope = 0.67x, primary forest slope = 0.75x) (Figure 4a and 4b). Relative to the NFI field inventory data, the biomass raster overestimated the biomass density in both primary and secondary forests, but secondary forest biomass density (t/ha) was overestimated to a larger extent. Nonetheless, field inventory biomass (t/ha) and biomass raster values (t/ha) were significantly and strongly correlated in both primary and secondary forests (Pearson correlation coefficient = 0.68 and 0.83 respectively, $p < 0.05$ for both).

When biomass raster values had been multiplied with slope coefficients, a 1:1 relationship was attained (Figure 4c and 4d). In other words, after multiplication, the biomass raster values represented the same thing as the biomass from NFI field inventories – i.e. biomass in living trees and roots >2 cm diameter. After multiplication, mean biomass density was 56 t/ha across secondary forests (both raster and field inventory mean) and ~55 t/ha across primary forests (54 t/ha mean raster biomass and 56 t/ha mean field inventory biomass). In other words, based on NFI field inventory data, mean biomass density (t/ha) was approximately the same in primary and secondary forests.

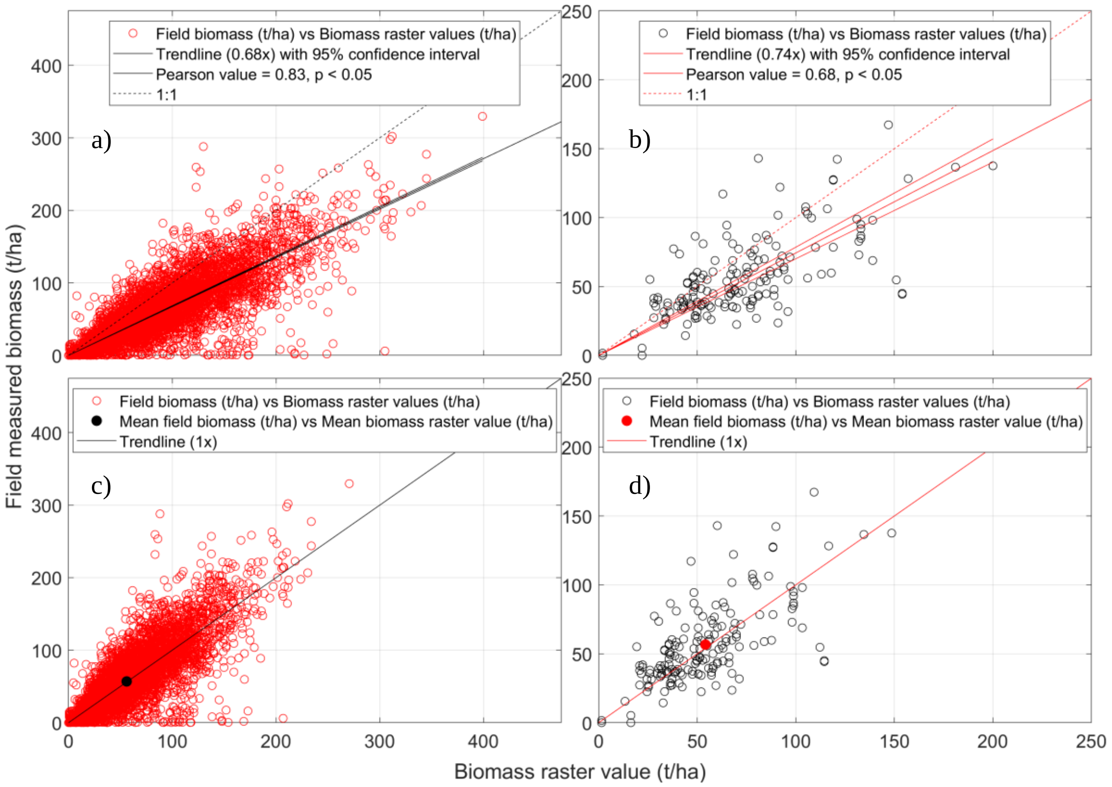

Figure 4. Relationship between field inventory (NFI) biomass (t/ha) and biomass raster values (t/ha) for secondary forests (a and c) and primary forests (b and d). Top images show relationships before multiplying biomass raster values with respective slope coefficients while the bottom images show relationships after such multiplication. The lines surrounding the middle lines on the top plots show the 95% confidence interval. The full circles on the bottom plots are mean biomass values (t/ha). Note the different scales on secondary forest plots and primary forest plots.

4.2. Paired analysis of mean biomass density across full forest extents

Mean biomass densities (t/ha) over the whole extents of individual primary forests were significantly different from mean biomass densities (t/ha) of surrounding secondary forests ($p < 0.05$). In 83% of the pairs, mean biomass density (t/ha) was higher in the primary forest than in surrounding secondary forest (Figure 5). The average biomass density of primary forests was 76 t/ha while the average biomass of secondary forests was 49 t/ha (27 t/ha difference). In other words, mean secondary forest biomass density amounted to 65% of mean primary forest biomass density.

Furthermore, the highest mean primary forest biomass density was little more than double that of the highest mean secondary forest biomass density (181 t/ha and 89 t/ha respectively). The lowest mean primary forest biomass density was 18 t/ha and the lowest mean secondary forest mean biomass density was 25 t/ha.

In the north of Sweden, particularly in the northwestern montane areas, biomass density (t/ha) in primary and secondary forests was often similar (Figure 6). The south of Sweden hosted both pairs where primary forests had the highest and the lowest biomass density (t/ha) relative to that in surrounding secondary forest. Apart from that, there were no clear geographical patterns in biomass difference (t/ha).

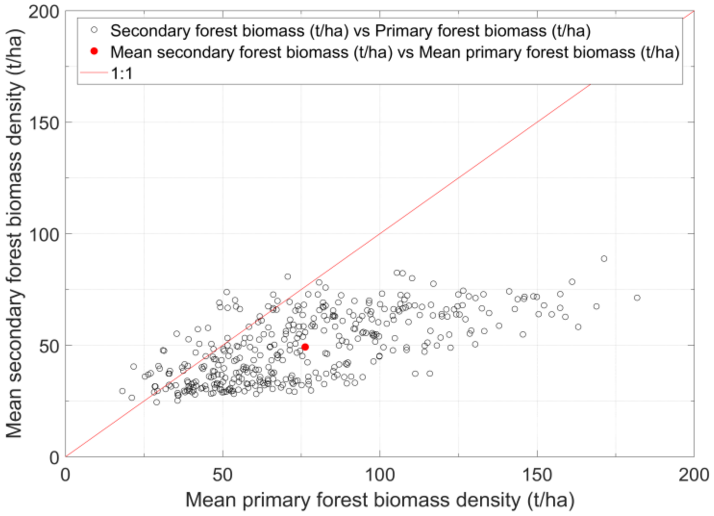

Figure 5. Paired analysis of mean biomass density (t/ha) across individual primary forests and surrounding secondary forests. Full red circle shows mean biomass densities (t/ha).

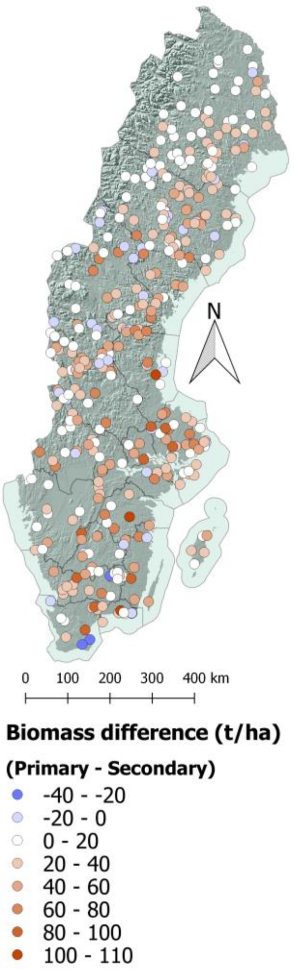

Figure 6. Distribution of difference in biomass (t/ha) across Sweden. Primary = primary forest and Secondary = secondary forest.

4.3. Biomass difference with difference in age and environmental parameters

Biomass density difference (t/ha) increased with increasing difference in stand age (years), difference in slope (°) and with mean annual temperature (°C) (Figure 7a, 7c and 7e). With increasing latitude (°N) and increasing difference in altitude (m) and soil wetness (unitless, Metria index), difference in biomass density (t/ha) decreased (Figure 7b, 7d and 7f). More specifically, difference between mean primary and secondary forest biomass density (t/ha) exhibited a moderate positive correlation with difference in mean stand age (years) (Spearman correlation coefficient = 0.35), weak positive correlations with temperature (°C) and difference in slope (°) (Spearman correlation coefficient = 0.23 and 0.25 respectively) and weak negative correlations with difference in mean altitude (m) and latitude (°N) (Spearman correlation coefficient = -0.21 and -0.18 respectively). The correlation between biomass density (t/ha) and soil wetness (unitless, Metria index) was negative but very weak (Spearman correlation coefficient = -0.12). All correlations were statistically significant ($p < 0.05$).

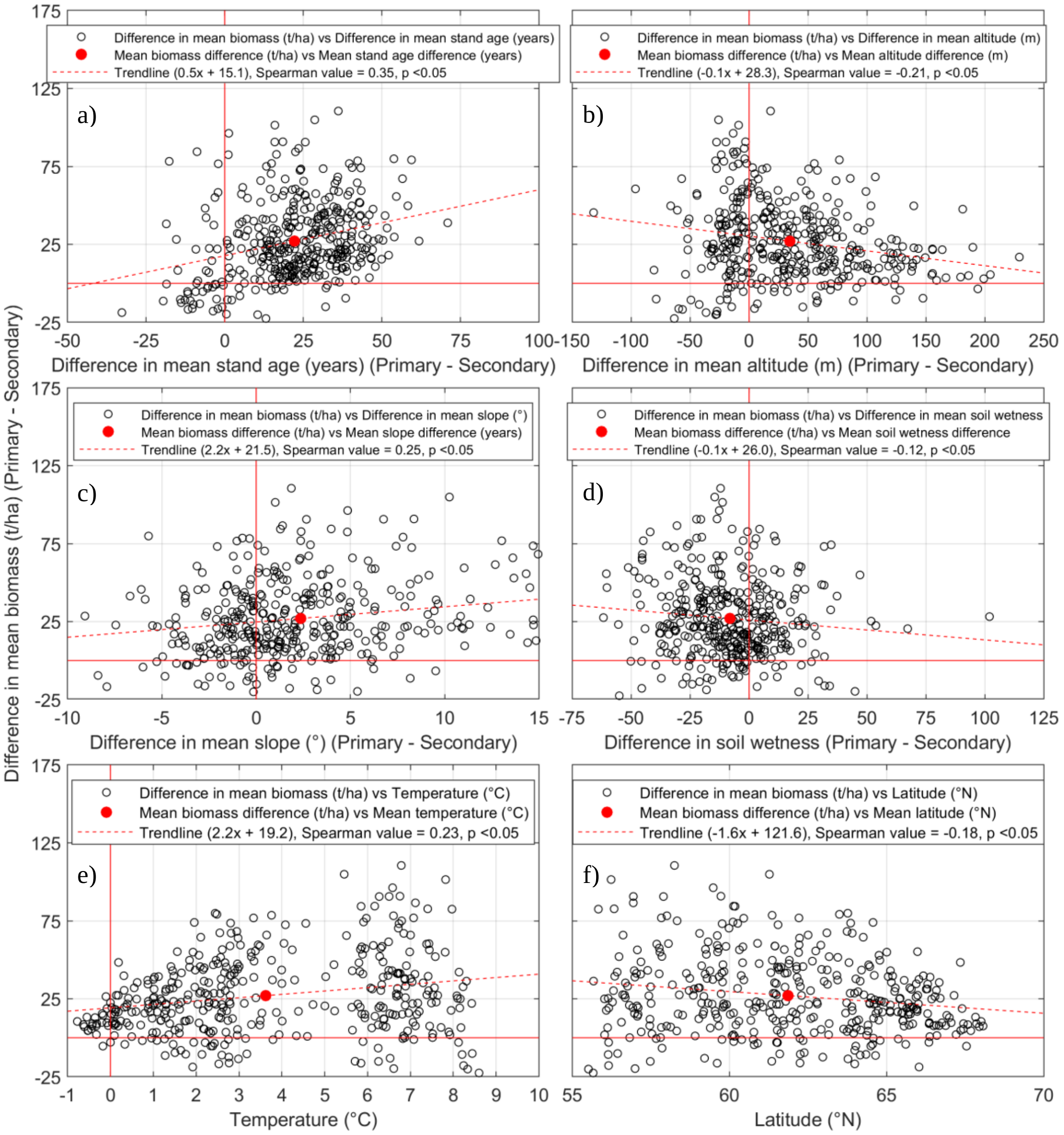

Figure 7. Difference between primary forest biomass (t/ha) and secondary forest biomass (t/ha) as a function of difference in mean stand age (years) (a), difference in mean altitude (m) (b), difference in slope (°) (c), difference in soil wetness (d), mean annual temperature (°C) (e) and latitude (°N) (f). Primary = primary forest and Secondary = Secondary forest.

4.4. General relationships between biomass and environmental parameters

Biomass density (t/ha) in primary and secondary forests was moderately and strongly positively correlated with increasing temperatures (Spearman correlation coefficient = 0.63 and 0.86 respectively) (Figure 8a). There was no correlation between primary forest biomass density (t/ha) and primary forest soil wetness (Metria index) and the correlation in secondary forests was positive but very weak (Spearman correlation coefficient = 0.16) (Figure 8b). Biomass density (t/ha) in both primary and secondary forests exhibited moderate to strong negative correlations with increasing latitudes and altitudes (Spearman correlation coefficient = -0.54, -0.79, -053 and -0.69 respectively) (Figure 8c and 8d).

The effects of temperature (°C), latitude (°N) and altitude (m) on biomass density (t/ha) was more pronounced in primary forests than in secondary forests. With the exception of primary forest soil wetness, all correlations were statistically significant ($p < 0.05$). For all parameters, secondary forest biomass densities (t/ha) were distributed more closely around its linear regressions as compared to primary forest biomass densities.

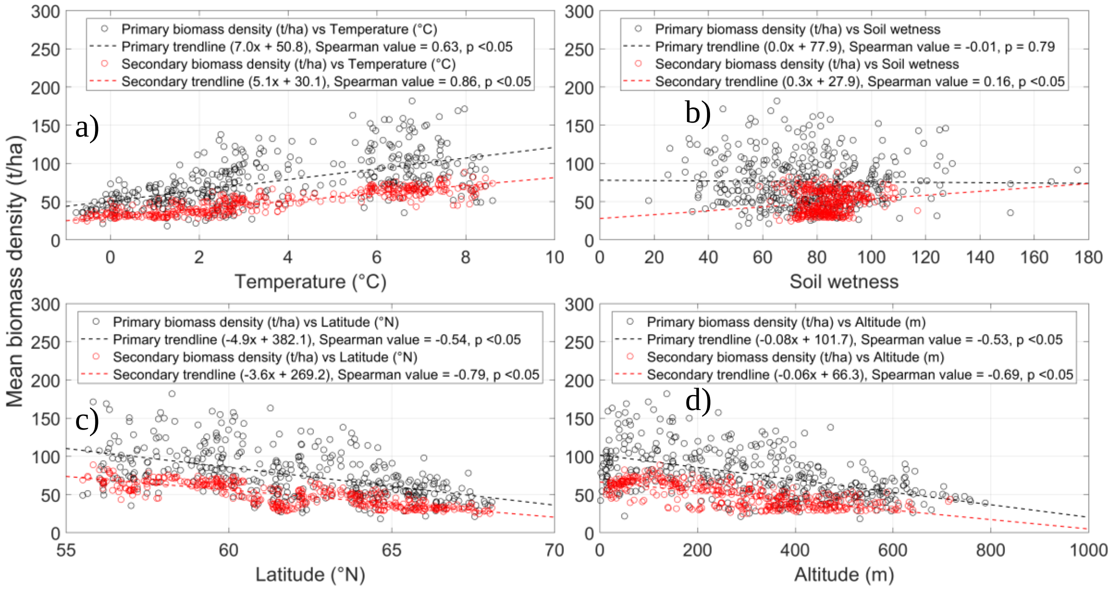

Figure 8. Mean biomass density in primary forests (black) and secondary forests (red) as a function of temperature (°C) (a), soil wetness (unitless) (b), latitude (°N) (c) and altitude (m) (d). Primary = primary forest and Secondary = secondary forest.

4.5. Stand age in secondary forests

In both northern and southern Sweden, biomass density (t/ha) decreased slightly with an increase in the stand age index and the stand age index increased with increasing latitudes (Figure 9). However, in the south of Sweden, the stand age index was not correlated with biomass density (t/ha) (Spearman correlation coefficient = -0.07, p = 0.44). For the north of Sweden, the stand age index exhibited a moderate correlation with biomass density (t/ha) (Spearman correlation coefficient = -0.46, $p < 0.05$). The stand age index was moderately positively correlated with forest latitudinal position (°N) in both southern and northern Sweden. Only three secondary forests had a stand age index <0.3 (all of them located south of 60°N) and the majority (73%) of secondary forests had a stand age index between 0.3 and 0.5.

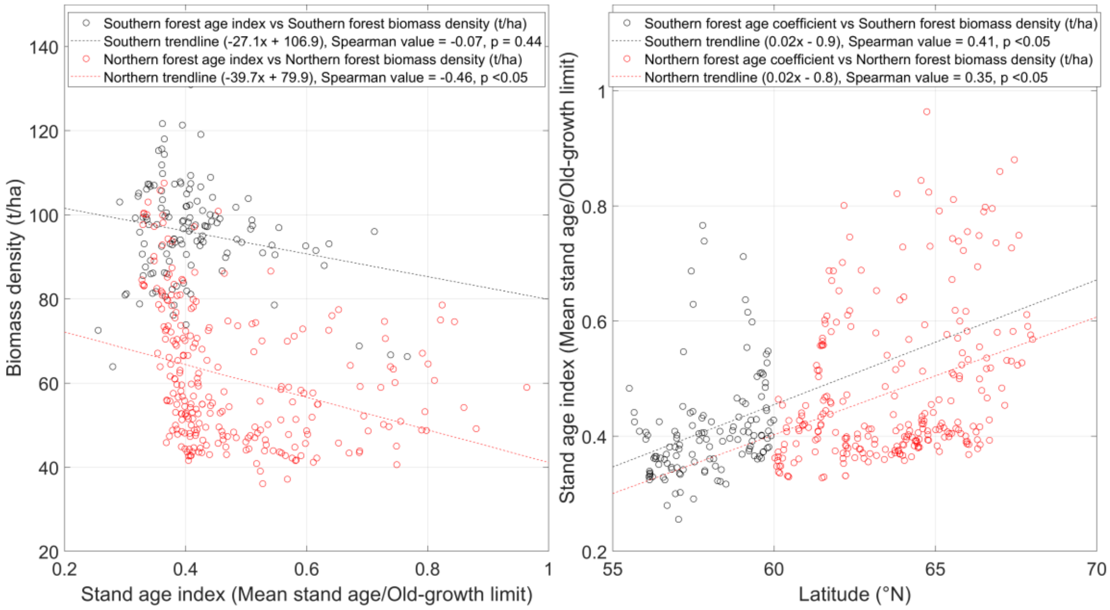

Figure 9. Biomass density (t/ha) as a function of the stand age index (left) in southern Sweden (black) and northern Sweden (red). On the right, the stand age index as a function of latitude (°N) in southern Sweden (black) and northern Sweden (red). The stand age index is the mean stand age across individual secondary forest areas divided by the age limit for being classified as old-growth by the Swedish Environmental Protection Agency (1999) – 130 and 150 years in southern and northern Sweden respectively.

5. Discussion

5.1. Main results

This study has shown (I) that with a simple correction, the biomass raster produced by SLU and the Swedish Forest Agency allows for estimation of biomass stocks (AGB and roots >2 cm) in both primary and secondary forests across the full extent of Sweden, (II) that primary forests in Sweden store more biomass than surrounding secondary forests in the majority of cases as well as on average and (III) that the higher biomass storage in primary forests is largely resulting from age-related processes.

5.2. Usability of the biomass raster

The biomass raster produced by SLU and the Swedish Forestry Agency (Nilsson et al. 2017; Swedish Forest Agency 2020) overestimated the biomass density in both primary and secondary forests, but the reason for the discrepancy is unknown. However, the reason seems to be systematic in character as the overestimation was evenly distributed (linear) across NFI data points. The fact that the magnitude of the overestimation differed between primary and secondary forests is most likely a consequence of the biomass raster being a “one-size fits all” product while the mechanisms governing biomass storage in primary forests are different from those in secondary forests (Bråkenhielm 1982; Keith, Mackey and Lindenmayer 2009; Seedre et al 2020).

The stronger correlation between field inventory biomass and raster biomass values in secondary forests than in primary forests is most likely a result of the vast difference in number of data points available for evaluation of the biomass raster. Nonetheless, the correlation between primary forest field inventory biomass and biomass raster values was strong. In fact, considering the environmental gradients in Sweden (e.g. in temperature and precipitation (SMHI 2020)), one might even conclude that the raster performed very well in estimating biomass on large scales. In sum, this study shows that with a simple correction, the biomass raster can be used for large scale estimation of Swedish primary and secondary forest biomass stocks (AGB and roots >2 cm).

5.3. Relative biomass storages

In line with what was expected, primary forests stored more biomass than surrounding secondary forests in the majority of cases as well as on average – 76 t/ha mean biomass density across primary forests and 49 t/ha across secondary forests. In addition, the difference between the highest primary and the highest secondary forest biomass densities was about 90 t/ha – the highest primary forest biomass density being twice as high as the highest secondary forest biomass density. For further context, it should be noted that the primary forests investigated in this study often are located in areas characterised by lower site quality than surrounding secondary forests (Bråkenhielm 1982). Thus, it should be taken into consideration that the biomass storage potential in these forests may be limited relative to potential storage in surrounding secondary forests and that, consequently, differences in biomass would likely be larger if environmental conditions converged. Nonetheless, this study adds to a growing body of research showing that primary forests can, when and where conditions allow, store large amounts of C in biomass (Harmon, Ferrell and Franklin 1990; Finér et al. 2003; Luyssaert et al. 2008; Keith, Mackey and Lindenmayer 2009; Nord-Larsen et al. 2019; Erb et al. 2018).

A lot of primary forests had similar biomass densities as surrounding secondary forests, not least in the northern and north-western areas of Sweden. AGB in particular decreases with increasing latitudes (Vucetich et al. 2000; Jacob et al. 2013; Seedre et al. 2015), and the high proportion of similar biomass densities in northern Sweden are likely the result of environmental conditions – temperatures in particular (SMHI 2020) – applying a general constraint on the productivity of these ecosystems. This notion is supported by the relatively low spread of biomass differences at the lower end of the temperature scale and the higher end of the altitude scale. However, while this study has only investigated living biomass, high latitude primary forests have been shown to store much C in dead wood and soil (Vucetich et al. 2000; Jacob et al. 2013).

The three forest pairs where secondary forest biomass density was at least 20 t/ha higher than in the primary forest were all located in the south of Sweden. The three areas where primary forest biomass density was at least 100 t/ha higher relative to surrounding secondary forests were evenly distributed between approximately 62°N (on the east coast near Hudiksvall) and 56°N (on the south coast of Blekinge). In other words, the southern and middle parts of Sweden hosted primary forests with biomass densities both lower and much higher than in surrounding secondary forests. Except for one primary forest being very dry and on being very wet, environmental conditions were similar within pairs where biomass density was higher in secondary forests than in primary forests. Environmental conditions were also similar within pairs on the opposite end of biomass density difference. However, the three primary forests storing most biomass relative to surrounding secondary forests had soil wetness levels within the soil wetness window where the majority of secondary forests were found. These results are confounding, especially as soil wetness generally had no effect on biomass storage. In all of the forest pairs mentioned, mean stand age in the primary forests was higher than in secondary forests, but the relative differences were generally larger in the cases where primary forest biomass density was higher than secondary forest biomass density. This relative increase in stand age difference may partly explain the differences in relative biomass storage, but reasons not uncovered here are likely to influence this relationship as well.

5.4. Difference in age and environmental conditions as drivers of biomass storage – indications of LU

Stand age has been shown to drive biomass accumulation both in general and in primary forests (Bradford et al. 2008; Chatterjee, Vance and Tinker 2009; Jacob et al. 2013). The difference between primary and secondary forest biomass density (t/ha) in this study was related to differences in mean stand age, indicating that the greater biomass storage in primary forests is resulting at least partly, and probably largely, from age-related processes. While the mechanistic reasons behind this was beyond the scope of this study, a hypothesis of multiple tree layers and partially stand-replacing disturbances as drivers of primary forest biomass storage has been proposed (Luyssaert et al. 2008; Keith, Mackey and Lindenmayer 2009). However, while disturbance seems to be one of the components driving C storage in primary forests, considerable uncertainty in terms of mechanisms behind primary forest C storage remain (Seedre et al. 2020).

In terms of environmental differences between primary and secondary forests, the parameters examined in this study were only weakly to moderately (or, in the case of soil wetness, very weakly) correlated with difference in biomass storage. Of the more interesting, and perhaps more surprising correlations, was that between biomass difference and difference in slope. Differences in biomass storage generally increased with an increased difference in slope, suggesting that a relative inaccessibility of the primary forests may lead to increased biomass storages. In other words, in the cases where biomass difference increased with increasing difference in slope, slope may be an indirect measure of LU and/or land use history. Such a hypothesis is supported by Bråkenhielm (1982) who stated that it is unlikely that Sweden hosts any deciduous forest that have not been affected by humans, but that if they do exist, they are likely to be found in areas that are inaccessible due to rough terrain. However, the use of slope is at best an indirect way to account for land use history and differences in primary and secondary forest biomass due to differences in slope should therefore be interpreted carefully. Still, land use history has been shown to influence biomass storage in primary forests (Keith, Mackey and Lindenmayer 2009) and inclusion of explicit measures of LU in future studies is encouraged.

The effects of altitude, temperature and latitude are interconnected (Vucetich et al. 2000; Körner 2007; Jacob et al. 2013; Seedre et al. 2015). The spread in biomass difference was, relatively speaking, higher at the higher end of the temperature scale as well as at the lower ends of the altitude and latitude scales. In other words, the main factors limiting biomass storage in southern, low-lying, and relatively warm areas do not seem to be related to the environmental parameters investigated here. The combination of the secondary forest biomass values closely convening around the linear regressions of temperature, altitude and latitude, and the spread in biomass differences in warm and low-latitude areas, show that the spread in the difference plots are due to a spread in primary forest biomass. Hence, the large spread in biomass difference may be an indication of differences in LU and land use history in the primary forests. Such a hypothesis is supported by the history of intensive LU in the south of Sweden (Bråkenhielm 1982; Emanuelsson 2002). Primary forests in these areas may have been, and may still be, affected by LU in two main ways: (I) LU itself (cutting for firewood, grazing etc) may limit the biomass storage of these forests and (II) in areas where LU is or has been intensive, primary forests may be pushed into less fertile areas. Again, this study offers only indications of such processes and relationships, and future studies should, if possible, include explicit measures of LU to reveal the effects of different types of land use.

5.5. General effects of environmental parameters on biomass storage

The wide range in biomass densities was expected due to the distribution of forests across Sweden and hence across environmental gradients. The decrease in biomass density with increasing altitude and latitude is in line with previous studies (Vucetich et al. 2000; Jacob et al. 2013; Seedre et al. 2015). In addition, both temperature and precipitation have been related to biomass storage (Keith, Mackey and Lindenmayer 2009), and this study confirmed that biomass storage in both primary and secondary forests is influenced by temperature. Soil wetness on the other hand, had no effect on biomass storage in primary forests and, if any, only a slight effect on biomass storage in secondary forests. In short: warm, low-lying and southern parts of Sweden have greater potential for storing forest biomass than cold, high-altitude and northern areas. It should be noted, however, that while only living biomass was investigated in this study, high elevation and high latitude primary forests have been shown to store high proportions of total ecosystem biomass in dead wood and soil (Vucetich et al. 2000; Jacob et al. 2013).

While the soil wetness index did not affect biomass storage, it did reveal an interesting clustering of secondary forest biomass storage around a rather narrow window of soil wetness (narrow relative to the primary forests' spread across the soil wetness gradient). This clustering indicates that the secondary forest sites are either specifically chosen for their moisture levels or drained to achieve desired moisture levels. Whichever of the two, the clustering acts as an evaluation of the process of delimiting secondary forest areas, indicating that these forest areas are indeed managed.

5.6. Stand age in secondary forests

Biomass in secondary forests is a function of stand age (Routa, Kellomaki and Strandman 2012; Seely, Welham and Kimmins 2002). The stand age index was correlated with biomass density in Swedish secondary forests above 60°N, but not with biomass density in forests south of 60°N. Stand age index values increased with increasing latitude (indicating that rotation length in secondary forests increased with increasing latitude), yet most secondary forests (73%) were found within a stand age index window between 0.3 and 0.5 – i.e. stand age mainly ranged between approximately 40 and 65 years in the south of Sweden and between 45 and 75 years in the north. Only three secondary forests had a stand age index value of less than 0.3 – all of them residing south of 60°N.

Swedish forestry laws stipulate that felling may not be undertaken in stands that are less than 35 or 45 years (depending on species composition) (Swedish Forestry Agency 2019; SFS 1979:429) and major Swedish forestry corporations recommend felling when stands are between 60 and 100 years old (Stora Enso 2017; BillerudKorsnäs n.d.; SCA n.d.; Sydved n.d.). Hence, mean stand ages across secondary forests investigated in this study indicate that many of these forests are close to, or within, the age range of when forest managers are advised to harvest. However, as long as the actual average rotational lengths of the secondary forests are unknown, it is difficult to evaluate how the mean stand ages found in this study are related to those rotational lengths. It follows that it is unclear whether this study overestimated the biomass densities of secondary forests relative to mean biomass densities across several rotations, but it is unlikely that biomass densities in these forests were underestimated.

It should be mentioned that the index used in this study is far from an ideal solution to a complex problem. The division of Sweden into two large areas is static as it does not account for the wide range of conditions across the south and the north of Sweden. Nonetheless, the crude normalization provided an indication that biomass storage in secondary forests was likely not overestimated in this study.

5.7. C content of Swedish primary forests in a regional perspective

The living biomass densities in this study's primary forests were lower, but comparable to that of primary forests in countries surrounding Sweden (Vucetich et al. 2000; Finér et al. 2003; Kenina et al. 2018; Kenina et al. 2019; Nord-Larsen et al. 2019). Assuming that 50% of biomass is C (Houghton 2007; Thomas and Martin 2012), mean biomass C density in the Swedish primary forests ranged between 9 t/ha and 91 t/ha, to compare with 28 t/ha and 229 t/ha in other studies on C storage in Nordic and Baltic primary forests (Vucetich et al. 2000; Finér et al. 2003; Kenina et al. 2018; Kenina et al. 2019; Nord-Larsen et al. 2019). Under the same assumption, mean biomass C density across primary forests was 38 t/ha. Hence, mean biomass C density of primary forests in this study was lower than averages of field inventoried boreal primary forests: 59 t/ha in dry forest and 64 t/ha in wet forest (Keith, Mackey and Lindenmayer 2009). However, excluding the C rich forests in Denmark and eastern Finland (Finér et al. 2003; Nord-Larsen et al. 2019), the range of living biomass C densities was very similar to that of field inventories in Europe: 25 t/ha to 105 t/ha (Vucetich et al. 2000; Keith, Mackey and Lindenmayer 2009; Kenina et al. 2018; Kenina et al. 2019).

5.8. Are the primary forests really primary forests?

Most forests labelled primary in this study are most likely not primary in the sense that they have been spared from anthropogenic activities for centuries. As illustrated when delimiting the areas of primary forests (Figure 2), felling had been undertaken in some and LU not reported to the Swedish Forestry Agency is likely to have affected many of them (Bråkenhielm 1982). In other words, except for perhaps a few forests in inaccessible northern montane areas, forests called primary in this study are rather forests where LU intensity is or has been lower than in surrounding secondary forests. However, it should be noted that while forests in remote and inaccessible areas of northern Sweden may be perceived as unaffected by anthropogenic activities, traces of low intensity land use from decades to centuries ago are still present (Josefsson, Östlund and Hörnberg 2009; Josefsson et al. 2010). Nonetheless, the difference between primary and secondary forest biomass storages does confirm that the primary forests in this study have not undergone the same development as the secondary forests. Hence, the biomass stocks of the primary forests investigated in this study still provide useful information for developing and defining baseline conditions.

5.9. Biomass storage potential in Swedish primary forests

Assuming that 50% of biomass is C (Houghton 2007; Thomas and Martin 2012) and that C density on all Swedish productive forestland (23.6 million ha) (SLU 2019b) would increase by an amount equivalent to the difference between this study's primary and secondary forest mean biomass C density (13.5 t/ha), an approximate amount of 1.2 Pg CO_2 would be sequestered (Eq 1):

Eq. 1: $13.5 \text{ tC/ha} \times 23.6 \text{ million ha} \times 3.7 \text{ (}CO_2\text{ to C ratio)} \sim 1.2 \text{ Pg } CO_2$

This amount is more than 70 times the Swedish transport sectors CO_2 emissions in 2018 (Swedish Environmental Protection Agency 2019b). There is no doubt that the estimate is crude, yet it does provide a rough reference as to the effect of LU on Swedish forest C stocks. It should also be noted that this estimate does not include C changes in dead wood or soil – pools in forests that together make up a large portion of total ecosystem C (Vucetich et al. 2000; Chatterjee, Vance and Tinker 2009; Jacob et al. 2013). In addition, this estimate does not include effects of for example substituting fossil fuels for biofuels, something which is necessary to account for in order to understand the full effect of LU and LUC on C cycling (Helin et al. 2013).

5.10. Main limitations and uncertainties

The main limitation of this study is that the raster used for estimating biomass did not include soil or dead wood biomass. Hence, the biomass storage in both primary secondary forests is in reality larger than the biomass storages presented in this study. The amount of dead wood in Swedish primary forests is normally high compared to that in secondary forests (Bråkenhielm 1982), and primary forests located at high latitudes and altitudes in particular store much of total C in dead wood and soil pools (Vucetich et al. 2000; Jacob et al. 2013). Therefore, it is likely that differences between primary and secondary forests total ecosystem C are larger than the differences presented in this study. However, the magnitude of this effect is unknown and further research is needed to elucidate differences in total biomass and C storages.

The fact that less productive forest areas were not included in this study may be regarded as a limitation as the primary forests investigated in many cases are located in areas characterised by lower site quality than surrounding secondary forests (Bråkenhielm 1982). However, in order to improve comparability between the two forest types and in that way get a better picture of the effect of land use, such areas were excluded. In other words, todays secondary forests were once primary forests located on productive forest land, and to get an indication of the effect of land use, environmental conditions should be as similar as possible.

The main uncertainty in regard to biomass storage in both primary and secondary forests is most likely embedded in the biomass raster. However, while it is not clear what models were used when producing the raster (Nilsson et al. 2017), the agreement between biomass raster values and field inventory biomass values was rather strong, not least considering the environmental gradients that the raster was used across. In addition, even though over- and underestimation of biomass storage certainly occurred on a pixel level, these effects largely cancelled each other out when the raster was uses across larger areas (similar amounts of NFI data points over and under the slopes in plots in Figure 4). In short, while there are uncertainties related to this study's biomass estimates, the evaluation process showed that the biomass raster provided robust estimates of biomass storage across both primary and secondary forests.

6. Conclusion

Forests are mitigating climate change by absorbing C from the atmosphere and storing it in the biosphere. This study was set out to answer (I) whether the biomass raster produced by SLU and the Swedish Forest Agency could be used for Sweden-wide estimation of living biomass and (II) how much living biomass that is stored in Swedish primary forests relative to surrounding secondary forests. The results showed that, with a simple correction, the biomass raster can be used for large scale estimation of biomass within both primary and secondary forests. The estimates showed that Swedish primary forests stored more biomass than surrounding secondary forests in the majority of cases (83%) and that the average biomass density across primary forests was 27 t/ha higher than the average biomass density across secondary forests. In addition, this study showed that primary forests have the potential to store large amounts of biomass and that land use in Sweden have had large effects on forest C storage. However, many forests labelled as primary in this study have been, and probably still are, affected by land use. Hence, future studies should, if possible, include explicit measures of land use when investigating primary forest biomass storage.

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