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Forest ecosystem services at landscape level – Why forest transition matters?

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ABSTRACT

Forests in the humid tropics contribute to a wide range of globally demanded forest ecosystem services (FES) and are also beneficial to local communities, which are often highly dependent on natural resources. Approximately one-third of these forests are threatened by resource extraction, logging, and the expanding agricultural frontier. As a result of these developments, forest landscapes are shaped by a transition gradient representing areas with a high forest cover to locations resembling agricultural-forest mosaics. These transition gradients are often characterized by different types of forests and successional stages. We used inventory data from 331 plots collected in 24 landscapes in Ecuador and the Philippines, representing five forest-based land-use types. We used mixed linear effect models to analyze how the landscape transition gradient and forest type affect various forest ecosystem services. Additionally, we identified stand structure and landscape transition gradients that influence changes in these FES.

Results show country and forest type specific reactions for different FES. For example, aboveground carbon, non-timber forest products, biodiversity, and timber volume in natural forests are not only affected by logging but also decline along the landscape transition gradient. This includes the risk of extinction of high conservation species and long-term depletion of timber resources. We show that tree-based secondary land-use systems may partially compensate for the loss of some FES, especially timber supply, but found evidence for increased nutrient depletion in agroforestry systems. Our results highlight the importance of connected forest landscapes and structurally diverse forest stands in early transition landscapes. We suggest conservation and restoration strategies sensitive to the transition context for FES and to make better use of the various benefits of tropical forests in a sustainable manner.

1. Introduction

Moist tropical forests provide a wide range of benefits to humankind, referred to as ecosystem services (MEA, 2005; Watson et al., 2018). These include carbon storage regulating the global climate (Mitchard, 2018; Brinck et al., 2017) and the support of rural livelihoods in communities with high dependencies on natural resources (Asprilla-Perea and Díaz-Puente, 2019; Angelsen et al., 2014). Additionally, moist tropical forests harbor half of all described and a potentially larger proportion of undescribed species (Cardinale et al., 2012; Gibson et al., 2011). According to a recent estimate, 325 million ha, or 25.7% of their total land area, have been deforested or degraded between 1990 and 2019 (Vancutsem et al., 2021). In addition, half of the remaining tropical forests are in poor structural condition or face human pressure (Hansen et al., 2020) due to timber harvesting (Asner et al., 2010), the advancement of the agricultural frontier (Bourgoin et al., 2020), and climate change (Asner et al., 2010; Brienen et al., 2015). On the contrary, planted forests which are often monocultures with exotic and commercial species, have increased by 27 million ha in the tropics between 1990 and 2015 (FAO, 2015). These systems, however are insufficient to provide the whole range of ecosystem services required to mitigate climate change mitigation, biodiversity loss and maintain overall forest multifunctionality (Wilson et al., 2017; Bremer and Farley, 2010; Lewis et al., 2019).

The need to reverse degradation and deforestation and promote the restoration of forested landscapes receives increasing international

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attention (Chazdon et al., 2017). Examples include the United Nations Program on Reducing Emissions from Deforestation and Degradation (REDD+) (UNFCCC, 2013), which intends to mitigate climate change, and the Bonn Challenge (CBD, 2012), which committed to restoring 350 million ha of deforested or degraded ecosystems by 2030 or the recent Glasgow declaration to "halt and reverse forest loss and land degradation by 2030″ (COP, 2021). These initiatives primarily aim at conserving or enhancing forest cover and carbon stocks. They recognize the diverse roles of forests and multiple services provided but mainly focus on the extent of forest cover (Mackey et al., 2015; Watson et al., 2018). However, forest restoration and conservation initiatives have shown to be most successful when they include next to globally relevant FES as the storage of carbon also locally demanded ones (Höhl et al., 2020; Chazdon et al., 2017).

The forest transition theory is a theoretical model that suggests that a region or country that experiences forestation and-deforestation undergoes three distinctive stages. The early stage has largely undisturbed forests with high forest cover and low deforestation rates. The subsequent intermediate stage has accelerated deforestation and a reduction of forest cover, and finally, a late stage where forest cover stabilizes with eventual increases. This theoretical model implies two aspects: First, it refers to a ***forest-type gradient*** of different tree-based land-use systems ranging from structurally diverse undisturbed forests to young, often planted homogenous forest types with multiple uses resulting from reforestation and natural regeneration (Wilson et al., 2017; Reed et al., 2017). Second, it describes ***a landscape gradient*** from high and connected forest cover to fragmented and low forest cover (Arroyo-Rodríguez et al., 2017; Haddad et al., 2015; Rudel et al., 2005).

Case studies using the concept of the forest transition theory have predominantly focused on the land-use and forest type component. These showed that natural forests mostly outperform monocultures and agroforestry systems in most regulating ecosystem services and biodiversity, with intermediate values for second growth forests (Labrière et al., 2015; Veridiano et al., 2020; Eguiguren et al., 2020; Wilson et al., 2017).

These transitions are often driven by a mix of socio-economic conditions and the demand for ecosystem services (Angelsen and Rudel, 2013; Mather, 1992): common reasons include planting trees to respond to the scarcity of forest products, regeneration of former agricultural lands that have been abandoned in favor of more fertile or accessible areas (Rudel et al., 2005), planting of tress in agroforestry systems to intensify land-use and stabilize crop yields (Lambin and Meyfroidt, 2010) or to foster services as carbon storage or water regulation (Wilson et al., 2019). Finally, the forest transitions theory only describes an empirical regularity: Transitions may or may not occur under similar conditions with different outcomes (Redo et al., 2012; Mather, 1992). Even though the concept of the forest transition is well established theoretically, transitions' outcomes are context-specific. In this regard, there remains a lack of comparative cross-country studies addressing diverse landscape contexts and potential cross-country patterns to understand better how forest transition stages influence FES (Cavender-Bares et al., 2015; Wilson et al., 2017). The changes in FES triggered by the forest transition are driven by different natural and anthropogenic factors occurring at different scales: For example, stand structural characteristics determine biomass (Slik et al., 2013; Poorter et al., 2015), but these are subject to disturbance and their duration and intensity, climate conditions or geographic conditions. Landscape dynamics such as habitat reduction, fragmentation, and changing land-use pressure influence and often reduce the capacity of the forest to provide different FES (Grimaldi et al., 2014; Renó et al., 2016; Ordway and Asner, 2020; Hernández-Stefanoni et al., 2011). For example, landscape composition and soil properties explained 45% of the variance in ecosystem services for two Amazonas regions (Grimaldi et al., 2014). Therefore, the different scales contribute to the supply of FES: this aspect, however, has been less researched.

We aim to investigate how forest transitions change the supply of ecosystem services (FES) under consideration of forest type and landscape characteristics to identify management options that can maintain and enhance FES in the long run. We base this study on a high number of forest inventory data (331 plots) originating from Ecuador and the Philippines. The empirical data represents different forest types and tree-based land-use systems from diverse landscapes of the two countries from the moist tropical biome. Our analysis differentiates (i) to what degree landscape and respective fragmentation characteristics on different scales determine FES and (ii) to what degree different forest types and their respective stand characteristics influence this aspect. We highlight that FES by definition relate to local or global benefits and discuss these in the context of both countries and studied landscapes.

2. Methods

2.1. Site Selection

Ecuador and the Philippines were chosen because both belong to the humid tropical biome, are biodiversity hotspots (Mittermeier, 1997; Myers et al., 2000), and have experienced some degree of deforestation, degradation, and recovery in the past decades (FAO, 2020; Ferrer Velasco et al., 2020; Hosonuma et al., 2012). Following the forest transition theory, currently, Ecuador represents an early transition stage with high forest cover and deforestation rates (Hosonuma et al., 2012). Forests in Latin America are a biodiversity hotspot and hold 45% of the biomass of the tropics (Saatchi et al., 2011). Even though half of Ecuador is covered by natural forests, there has been constant loss in the last 25 years (FAO, 2015) driven by the expanding agricultural frontier, timber logging (Ojeda Luna et al., 2020; Mejia et al., 2015), road construction, oil extraction, mining, and growing population pressure (Armenteras et al., 2017). Ecuador made the pledge to restore 0.5 million ha of forest through revegetation with native species, agroforestry and ecological corridors (MAE, 2019). Using the same context, the Philippines represents a post-transition stage (Hosonuma et al., 2012): Although at the beginning of the 20th century, forests still covered more than half the archipelago, by 1990 only 22% of forest cover remained, and forest resources were severely depleted due to intensive legal and illegal logging and the conversion to agriculture (Chokkalingam, 2006; Guiang, 2001). In the last decades, several national government initiatives have been launched to reverse this development such as a logging moratorium, community-based forest management initiatives, and public and private reforestation programs. These initiatives result in the pledge to either restore or reforest 8.6 million ha corresponding to a third of its area with the specific aim to reduce poverty (DENR, 2016). Although there are still local losses (Perez et al., 2020; Araza et al., 2021), forest cover had increased by 2015 to 27% at national level (FAO, 2015). As a result, Philippine forest landscapes show a mixture of remaining natural forests, agroforestry, and tree plantations (Bagarinao, 2010).

2.2. Landscape transition gradient classification

We focused in both countries on two forested regions, where we collected data from 24 landscapes (12 landscapes per country) of approximately 10 km × 10 km (see Fig. 1). The landscapes were located along the forest-agricultural frontier with diverse land-use types. The extent of deforestation and reforestation however differed considerably (see Fig. 1a). We identified representative forest types (step 3, Fig. 2) for each landscape and collected inventory data (step 4, Fig. 2). Landscapes were grouped in regional clusters representing the landscape transition gradient with three distinct stages defined as **early**, **middle**, and **late** (later referred to as 'landscape transition gradient') (see Fig. 2). These clusters were characterized by a gradient in decreasing forest cover, increasing patch density, and increasing dynamics of forest cover change (see Fig. 1).

In *Ecuador*, eight are landscapes located in the Amazonas region. Four have a higher and connected forest cover representing an early

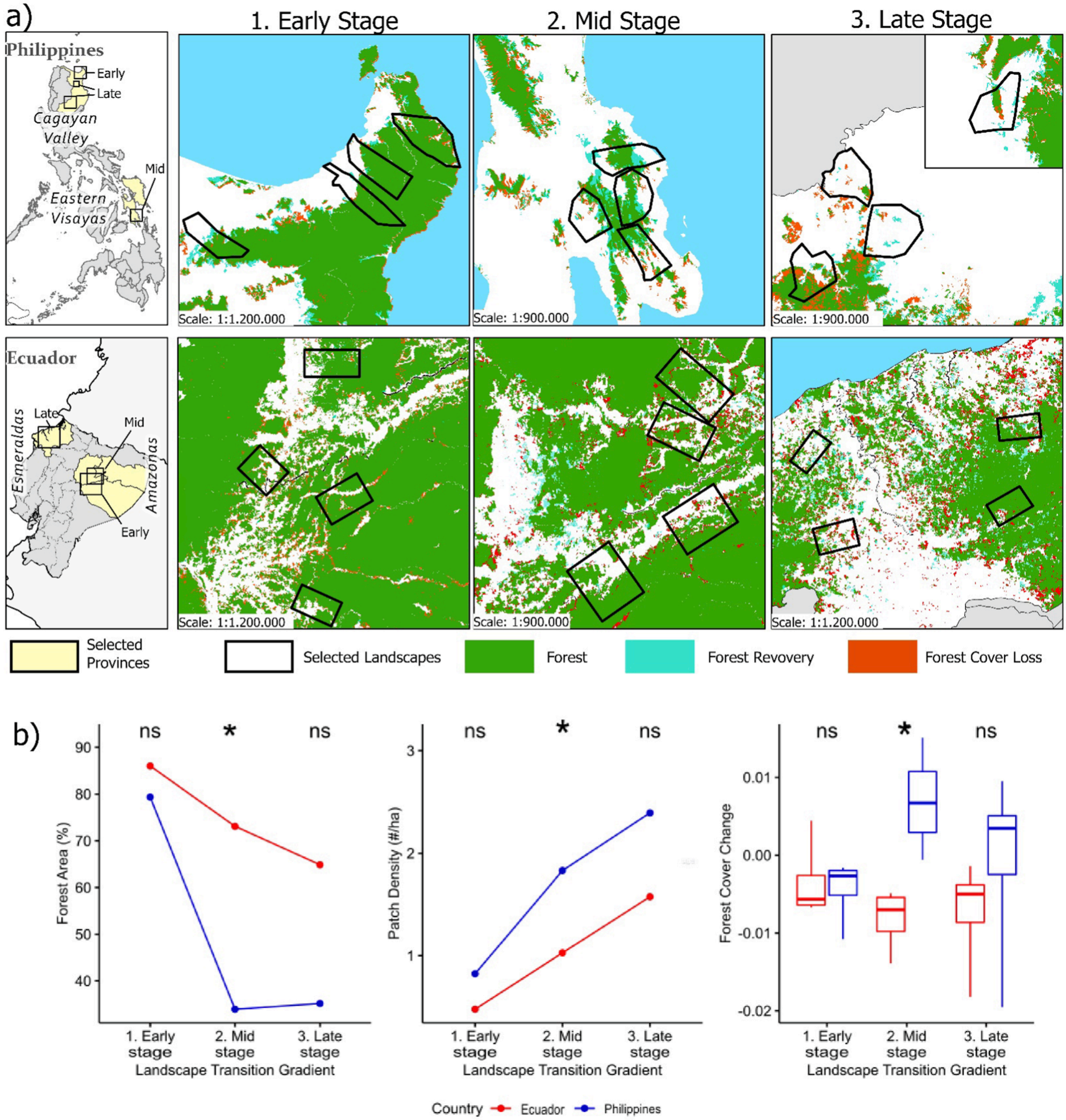

Fig. 1. Location of Study Regions and Landscapes within Ecuador and the Philippines. Displayed Forest Cover is based on national land use maps highlighting constant forest cover (dark green colored), new forest cover (cyan colored), and disappearing forest cover (red color). Note: harmonized forest cover maps were used for the later analysis. b) Overview of landscape transition stages (initial, middle, late) in relation to forest area (%), patch density (ha^{-1}) and forest cover change (see below for calcutions); Asterisks indicate significant differences in descriptive statistics for both countries within a landscape transition stage and ns indicates no significant differences.

transition stage, while the other four landscapes located are more fragmented, which describes a mid-transition stage (see Fig. 1). The final four landscapes are located in the Choco-Darién Mois Forest of province of Esmeraldas, where forest cover decreased from 70% to 50% due to extensive logging (López et al., 2010; SUIA, 2022). The selected landscapes reflect this development and hence represent the late transition stage. Eight Philippine landscapes are located in northeastern Luzon island. The northern landscapes intersect some of the country’s last connected forests. In contrast, perennial and annual crops and commercial species plantations characterize the four southern landscapes (Snelder and Persoon, 2007; NAMRIA, 2017). These two clusters represent an early and a late transition stage. The cluster resenting a mid-transition stage is located in the Eastern Visayas region on Leyte island. Patches of old-growth forests in less accessible areas and remnants of forest intermixed coconut plantations characterize these landscapes (NAMRIA, 2017)

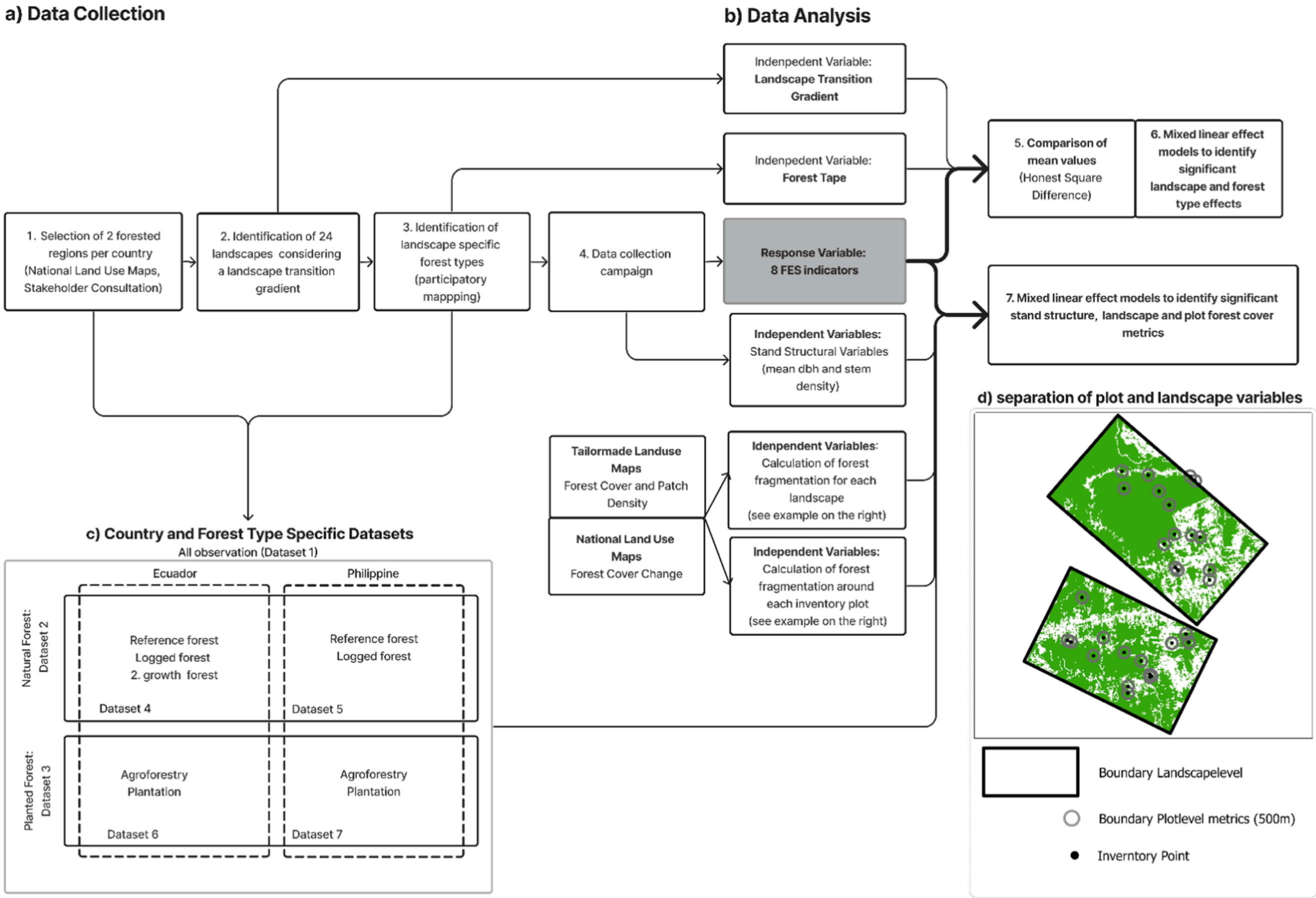

Fig. 2. Summary of the workflow highlighting both the data collection (a) and data analysis (b): The landscapes were located along the forest-agricultural frontier with diverse land-use types, the extent of deforestation and reforestation however differed considerably (see Fig. 1). We identified representative forest types (step 3) for each landscape and collected inventory data to ecosystem service indicators (step 4). We first analyzed the influence of the landscape transition gradient in interaction with the forest type comparing untransformed values and using mixed effect models (step 5–6). Second we addressed the influence of stand structural, forest cover fragmentation on plot and landscape level on each FES (step 7). We did this separately for natural and planted forests addressing country specific and cross-country effects.

Table 1
Values show the number of inventory plots per transition cluster, and forest type. Values in brackets indicate the number of plots with soil samples with each sample consisting of 2–4 mixed samples. excluded due to a small sample size (<3). The table reflects the nested design where different forest types were sampled across a gradient of landscapes representing different forest landscape transition gradient. The black arrows indicate the progress of the forest transition on both levels and also the degree of anthropogenic influence on landscape and plot level.

	Country	Ecuador			Philippines		
	Region	Amazonas		Esmeraldas	Cayagan Valley	Leyte	Cayagan Valley
	Sub Region	*West Napo Pastaza*	*East Napo Orellana*	/	*North Cayagan Valley*	/	*South Cayagan Valley*
	# landscape	*4*	*4*	*4*	*4*	*4*	*4*
	landscape transition gradient	**Early**	**Mid**	**Late**	**Early**	**Mid**	**Late**
forest type	Reference forest	12 (12)	12 (12)	12 (12)	21(13)	16 *(8)*	7(6)
	Logged forest	12 (12)	12 (12)	9 (9)	23 (11)	23 *(9)*	-
	Second growth forest	12 (12)	12 (12)	12 (12)	-	-	-
	Agroforestry	12 (12)	12 (12)	12 (12)	11 (11)	18 *(8)*	27 (23)
	Plantation	-	6 (6)	9 (9)	-	4 (-)	26 (26)
	Total	48 (48)	54 (54)	54 (54)	55 (34)	61 (25)	72 (55)

Advanced landscape forest transition on level landscape level

Advanced forest transition gradient country level

2.3. Forest inventory and classification

The location of the different forest types was identified through participatory land use mapping with local communities and stakeholders for each study landscape prior to the start of the fieldwork campaign. This resulted in a second gradient on a plot level ranging from low disturbance forests to plantation monoculture (later referred to as 'forest type') (see also Table 1). Although specific forest types dominated different landscapes, we found a broad gradient of undisturbed forests to plantations in most landscapes. Based on this information, three forest plots with a size of 40 × 40 m were selected randomly along a 200 m grid for each landscape and forest type. As an additional requirement, the location of reference forest and logged forest plots had to be at least 100 m inside a forest fragment to minimize effects of anthropogenic activities. We measured trees and palms with a diameter at breast height (dbh) ≥ 10 cm in the field. Mixed soil samples were collected to a depth of 20 cm for all plots in Ecuador and due to budget constraints for a subset in the Philippines. All trees were identified, if possible, to species level (887 species) or elsewise to genus (62 estimated species) or family level (2 estimated species). The total number of resulting plots in each region is summarized in Table 1. We obtained data from 331 plots corresponding to 52.96 ha with 24,403 individual recordings.

2.3.1. Natural forest

i. **Reference forest**: these forests in both countries correspond to the most mature forest stands found in each region with the relative absence or lowest presence of recent anthropogenic interventions.
ii. **Logged forest**: this forest type was characterized by a known past timber extraction. For Ecuador, these were plots with selective logging 2 to 5 years before field measurements. In Esmeraldas, these were programs with a 15-year cutting cycle and mechanized hauling, whereas in the Amazon programs this referred to a 5-year cycle and non-mechanized drag extraction. Since almost all Philippines' forests have experienced some degree of formal and informal extractions, forest plots were chosen based on documented logging activities before the first logging ban and favorable access for harvesting. Due to the paucity of locally available information, no further distinction could be drawn between formal and information extraction. As both, formal and informal extractions, can be regarded as a form of intervention, inventory plots were characterized by stands of remnant forest mixed with natural regeneration.
iii. **Second growth forest**: these included 11–29-year-old naturally regenerating forest patches on previously abandoned agricultural land, mainly pastures, in Ecuador. A corresponding class of abandoned agricultural fallows was not found in the Philippines and hence not included.

2.3.2. Planted forests

iv. **Agroforestry**: Although they do not meet the national definition criteria for forest areas, we include them due to their importance for local livelihoods. As a highly diverse system, they range from home gardens to traditional shifting cultivation systems, but are generally characterized by the combination of crops and trees (MAE, 2016; DENR, 2019; FAO, 2002).
v. **Plantations:** they correspond to forests planted with commercial timber species (FAO, 2020). For Ecuador, we considered plantations with 2- to 3-year-old *Ochroma pyramidale* in the Amazon region with a six-year cutting cycle and 4 to 18-year-old Tectona grandis with a cutting cycle of 18 years in the Esmeraldas region. In the case of the Philippines, most plantations were mixed- and monocultures of approximately 10 years age with locally popular timber species such as *Acacia mangifera*, *Gmelina arborea*, *Swietenia macrophylla* or *Tectona grandis*. Plantations were not representative of the early transition regions.

2.4. Ecosystem Service indicators

We obtained indicators for ecosystem services based on the data collected in the field. All values represent stocks, volumes or densities measured in the plot as opposed to estimated or extrapolated growth rates. The following section presents an overview of forest-specific regulating, provisional, and supporting ecosystem services and biodiversity indicators built on recommendations by the Millennium Ecosystem Assessment (MEA) framework (MEA, 2005). Each of the following sections provides a short rationale for including a particular indicator. Methodological details are summarized in Annex 1 and average values are summaized in Table 2.

2.4.1. Regulating services

The regulation of the global climate by storing carbon is one of the globally most important FES (Brinck et al., 2017; Mitchard, 2018).

Total Aboveground Carbon (AGC) (t/ha): AGC pools were derived from in situ aboveground biomass measurements and consisted of living biomass (trees and most important palms species > 10 cm), downed and standing deadwood from the whole 40x40 plot, and forest floor litter from 0.25x0.25 m^2 sublots. All values were extrapolated to t/ha.

Soil Organic Carbon Stocks ($Cs_{oil.org}$) (t/ha): $C_{soil.org}$ was based on total amount of carbon stored in the top 20 cm using carbon concentrations and bulk density obtained from mixed samples. All values were extrapolated to t/ha.

2.4.2. Biodiversity

Endangered Species (species/plot): Rare and iconic species indicate an ecosystem's uniqueness, and can be part of an ecosystem's cultural heritage (Dee et al., 2019). We used each plot's total number of species, which were recognized by the International Union of Conservation and Nature (IUCN) as critically, near extinct, endangered, and vulnerable (IUCN, 2022), as an indicator.

Shannon index (-): Biodiversity indicated by tree species is closely related to other aspects of FES and important for the functioning of an ecosystem (Isbell et al., 2011; Cardinale et al., 2012). Using the Shannon index includes the number of species and their abundance (Spellerberg and Fedor, 2003; Daly et al., 2018).

2.4.3. Provisioning services

Timber volume (m^3/ha): the provision of timber is one of the essential FES (MEA, 2005) as construction material for either subsistence needs or sold commercially (Ojeda Luna et al., 2020; Wiebe et al., 2022). We based the indicator on regional data and reported harvested species (Ojeda Luna et al., 2020; Wiebe et al., 2022; ITTO, 2015; Soerianegara and Lemmens, 1993). We used the standing volume of recognized as commercially important timber species (dbh > 10 cm) based on dbh measurements per ha.

Non-Timber Forest Products (NTFP) – (number / ha): NTFP from forest and agroforestry trees represent a non-destructive form of forest usage and support alimentation, nutrition, livelihood, and welfare in communities (Asprilla-Perea and Díaz-Puente, 2019; Reed et al., 2017). We included the number of individual trees or palms per plot containing edible parts as fruits and nuts. We matched tree and palm species listed in household survey data (Ojeda Luna et al., 2020), regional and global secondary sources (Amaro et al., 2010; Orwa et al., 2009; Propuesta Normativa, 2018; Razal and Palijon, 2009; van der Vossen and Umali, 2001; Westphal et al., 1991) with value as supplementary or staple foods with our inventory data. The most common species were *Theobroma Cacao* and *Coca nucifera* in agroforestry systems and *Iriartea deltoidei* and *Ficus nota* in natural forests.

Table 2
Mean Values of FES in the different forest types and transition stages. Values in brackets indicate standard deviations.

	Ecuador									Philippines								
	N	AGC	$C_{soil.org}$	Timber Volume	NTFP	N_{soil}	P_{soil}	Endangered Species	Shannon Index	N	AGC	$C_{soil.org}$	Timber volume	NTFP	N_{soil}	P_{soil}	Endangered Species	Shannon Index
1. Initial																		
1. Reference Forest	12	125.11 (26.54)	42.64 (6.50)	184.85 (80.76)	4.13 (0.23)	3.99 (0.91)	3.95 3.28)	0.6 (0.89)	3.59 (0.46)	21	131.68 (80.31)	51.93 (15.35)	225.33 (108.95)	1.71 (1.12)	3.32 (1.02)	4.18 (3.64)	6.76 (2.53)	2.05 (0.44)
2. Logged Forest	12	94.29 (21.53)	36.39 (11.28)	100.12 (54.73)	3.99 (0.25)	3.47 (0.95)	3.51 (2.38)	0.75 (0.87)	3.49 (0.45)	23	56.51 (30.38)	61.95 (14.40)	99.66 (58.47)	1.52 (0.94)	4.56 (2.22)	4.55 (4.00)	6.09 (1.50)	2.14 (0.40)
3a. Second Growth Forest	12	65.79 (26.02)	35.96 (9.76)	79.00 (72.63)	3.33 (0.38)	3.67 (1.10)	4.21 (3.15)	0.58 (0.79)	2.88 (0.52)									
3b. Agroforestry	12	17.60 (8.90)	39.51 (14.51)	20.84 (15.34)	3.53 (0.58)	4.42 (1.20)	5.09 (3.35)	0.33 (0.49)	1.55 (0.47)	11	27.45 (33.99)	55.65 (10.90)	53.06 (115.13)	3.08 (1.43)	3.97 (0.91)	10.34 (11.65)	1.27 (1.19)	1.05 (0.64)
2. Mid																		
1. Reference Forest	12	125.81 (28.86)	31.08 (5.87)	187.14 (89.72)	4.20 (0.20)	3.27 (0.77)	4.69 (1.94)	0.92 (1.00)	3.49 (0.38)	16	260.27 (136.67)	141.95 (60.44)	394.06 (342.37)	1.55 (0.93)	7.50 (1.84)	1.73 (1.43)	7.75 (3.75)	2.27 (0.53)
2. Logged Forest	12	81.92 (34.45)	31.03 (7.42)	106.49 (64.00)	3.99 (0.23)	3.69 (0.65)	3.75 (2.56)	0.75 (0.75)	3.43 (0.22)	23	99.60 (52.09)	175.60 (76.62)	101.28 (99.36)	1.57 (0.85)	7.34 (2.34)	0.99 (1.56)	7.17 (3.61)	2.44 (0.39)
3a. Second Growth Forest	12	72.77 (22.16)	32.55 (7.10)	82.30 (32.63)	3.75 (0.53)	3.89 (0.98)	3.33 (1.88)	0.33 (0.65)	3.00 (0.40)									
3b. Agroforestry	12	17.91 (9.65)	30.51 (8.24)	29.81 (27.39)	3.88 (0.41)	3.11 (1.37)	3.88 (4.86)	1.0 (0.51)	0.96 (0.23)	18	26.96 (41.64)	94.73 (57.35)	41.64 (99.50)	2.53 (0.89)	3.62 (1.82)	4.02 (6.44)	0.94 (1.06)	1.08 (0.52)
3c. Plantation	6	9.60 (5.08)	31.45 (5.72)	57.38 (40.76)	0 (0)	3.72 (0.62)	2.16 (1.52)	0 (0)	0 (0)	4	59.85 (29.43)		136.09 (94.30)	0 (0)	NA	NA	0 (0)	0 (0)
3. Late																		
1. Reference Forest	12	97.95 (35.88)	36.29 (8.19)	122.57 (80.76)	3.49 (0.45)	4.20 0.62)	8.94 (5.94)	2.58 (1.62)	2.76 (0.29)	7	44.93 (26.10)	67.70 (22.72)	36.48 (35.95)	2.16 (0.69)	6.23 (2.32)	49.62 (32.60)	2.00 (2.00)	1.64 (0.39)
2. Logged Forest	9	68.05 (30.57)	31.56 (8.70)	53.94 (36.42)	3.24 (0.65)	3.82 (1.32)	6.37 (4.55)	2.44 (1.67)	2.80 (0.29)									
3a. Second Growth Forest	12	57.12 (26.35)	37.17 (8.61)	54.50 (40.37)	3.08 (0.61)	4.57 (1.05)	10.30 (7.18)	0.75 (1.14)	2.45 (0.60)									
3b. Agroforestry	12	22.34 (13.59)	27.80 (5.30)	40.24 (36.86)	4.35 (0.38)	3.48 (0.96)	10.05 (6.23)	0.33 (0.65)	1.02 (0.50)	27	23.50 11.26)	46.45 (13.26)	34.53 (27.62)	1.48 (0.92)	3.89 (3.43)	23.47 (36.84)	0.74 (0.71)	0.95 (0.59)
3c. Plantation	9	51.66 (15.77)	27.06 (4.91)	129.44 (43.46)	0 (0)	3.50 (0.74)	17.56 (20.12)	0 (0)	0 (0)	38	31.81 (17.54)	51.93 (15.35)	76.47 (48.39)	0 (0)	5.06 (4.63)	33.43 (51.75)	0 (0)	0 (0)

2.4.4. Supporting services

Supporting services are necessary to produce or maintain all other FES (MEA, 2005). Phosphorus (P_{soil}) and Nitrogen (N_{soil}) are the two most limiting nutrients for primary production on tropical soils (Vitousek et al., 2010). The stock of both nutrients in the first 20 cm based on nutrient concentrations and bulk density obtained from mixed samples were used as indicators. N_{soil} was expressed in t/ha and P_{soil} in kg/ha.

2.5. Explanatory variables

To answer how different variables characterizing a forest transition from stand to landscape-level influence FES, we used three groups of explanatory variables: (1) stand structure and (2) forest fragmentation around each inventory plot and (3) forest fragmentation of each landscape (see Table 3).

We included mean dbh and stem densities deviation to reflect the range of diameter distributions and stocking densities along the gradient of old-growth forests to young regeneration stands. Forest fragmentation described the quantity, quality, and forest cover change dynamic as present forest cover (FC) in %, the density of patches (PD) in number per ha, and forest cover change (FCC) in %. FC represents the total area available as habitat and pool for forest resources and PD forest fragmentation and mosaics (Fahrig, 2003; Melito et al., 2018). FCC reflects the decrease and increase of forest cover described in the forest transition theory. Estimates of edge effects on biomass and species composition range from 100 to ~1500 m (Ordway and Asner, 2020; Melito et al., 2018; Pütz et al., 2014; Laurance et al., 1997). We chose a reference radius of 500 m based on a pantropical estimation of edge effects for moist tropical forests, which showed that globally biomass is decreasing by 25% within this distance from the forest edge (Chaplin-Kramer et al., 2015). We used the best available maps of forest cover to quantify the metrics. Hence, FC and PD were calculated based on a landscape-specific forest/ non-forest map derived from Landsat-8 and Sentinel-1 data with a 30 m resolution (Ferrer Velasco et al., 2022); while forest cover change was calculated using available national land use maps. Forest cover change on a landscape level was calculated as the annual rate of forest cover change (Eqn 1 (Puyravaud, 2003)), and forest cover change on plot level was calculated by an adapted formula (Eqn 2 (WRI, 1995)) using the plot area as a reference to avoid dividing by 0.

Table 3
Independent variables used for mixed effect models, describing stand structure, forest fragmentation on plot level and landscape level, and climatic gradients.

		Variable Name	Source
Stand Structure		Mean dbh	Mean dbh of all palm and trees per plot
		Stem density	Total number of all trees and palms per plot
Forest Cover Metrics	Plot level (500 m radius)	Forest Cover (FC_{Plot})	FNF map (resolution: 30 m) (Ferrer Velasco et al., 2022)
		Forest Cover Change (FCC_{Plot})	Reference period Ecuador: 2008 2016 Reference period Philippines: 2010 – 2015 (SUIA, 2022; NAMRIA, 2013; NAMRIA, 2017)
	Landscape level (10 × 10 km cut-out)	Forest Cover ($FC_{landscape}$)	Forest Non Forest Map (Ferrer Velasco et al., 2022)
		Patch Density ($PD_{landscape}$)	
		Forest Cover Change ($FCC_{landscape}$)	Reference period Ecuador: 2008 – 2016 Reference period Philippines: 2010 – 2015 (SUIA, 2022; NAMRIA, 2013; NAMRIA, 2017)

$$FCC_{landscape} = \log\left(\frac{FC_2}{FC_1}\right) * \frac{1}{t2 - t1} \quad (1)$$

$$FCC_{500\ m\ radius} = \frac{FC_2 - FC_1}{A^*(t2 - t1)} \quad (2)$$

where FC_1 was the forest cover in 2015 or 2016, FC_2 forest cover in 2008 or 2011, t_2 and t_1 years of measurement

2.6. Statistical analysis

We first tested for significant differences between mean values of FES in different forest types and transition stages using post hoc test and tukey honest square differences (Neter et al., 1985) and found substantial differences. Results are shown in Annex 2.

We used mixed linear effect models to identify significant variables related to ecological aspects of the forest transitions addressing the unbalanced sample sizes and nested design, while excluding at the same time spatial effects unrelated to the research question as geological or climatic differences between countries, regions or landscapes. Accordingly, random effects were defined by country, region, and landscape nested within each other for cross country analysis and region and landscape for country specific analysis (Zuur et al., 2009). Depending on the response variable, the statistical analysis was conducted with linear models or generalized linear models using a Poisson distribution (in case of Endangered Species and NTFP) (O'Hara and Kotze, 2010). Data with a Gaussian distribution were tested for normal distribution and log-transformed if normal distribution improved. We used log(x) for AGC, $C_{soil.org}$ and N_{soil} and log(x + 1) for Timber Volume and P_{soil}.

As a first step, the landscape transition gradient, forest types, and their interaction were used to explain individual FES in each country. The forest landscape transition gradient was transformed as a continuous variable from 1 to 3. Stepwise elimination was used for each model to identify significant fixed effects. We interpreted significant interactions as a forest type depended reaction to the landscape transition gradient of a particular FES. This can be either be related to increases or decreases. Since coefficients of interactions do not identify increases or decreases which we plotted predicted fixed effects (Kruschke, 2015).

In a second step, significant stand structure, forest fragmentation (landscape and plot level), and variables were identified using the set of the 7 explanatory variables for each FES. We first tested models with all observations. Based on different reactions of forest types to landscape transition gradients, we replicated each model first only for natural forest types and second only for planted forest types. We finally replicated the model for country specific subsets (see Fig. 2c). All variables with a Gaussian distribution were centered and scaled. We used a variance inflation factor (vif) to identify collinearity between independent variables and to avoid overfit (Neter et al., 1985; Chatterjee and Simonoff, 2020). We removed variables with as vif > 5, as found for combinations of $PD_{landscape}$ and $FC_{landscape}$ in all datasets. Hence, backward regression was conducted for two models, each containing only one of the two variables, and the better model was chosen based on the Akaike information criterion (AIC). We considered variables with a p-value lower than 0.05 significant. Statistical analysis was conducted with the software R using the packages *lmer* (Bates et al., 2015) and *lme4Test* (Kuznetsova et al., 2017) for mixed-effects models. We used the Pseudo-R^2 of the package MuMIn (Barton, 2020) to compare explained variance by random and fixed effects between the different FES and datasets, and the difference of the AIC between a null model containing only random effects and the most parsimous model (DeltaAIC) for overall model validity. We presented only DeltaAIC for four models due to R^2 values exceeding 0.95.

3. Results

3.1. Differences in ecosystem services between forest types

We tested the effect of the landscape transition gradient and forest types on each individual FES. We ran this test for each country separately. The interaction between landscape transition gradient and forest type was significant in most models. According to the DeltaAIC and R^2, AGC, Timber Volume, NTFP, Endangered Species, and Shannon index were explained mainly by these fixed effects ($R^2_{\text{fixed}} > 0.33$). In contrast, $C_{\text{soil.org}}$, N_{soil} and P_{soil} were explained mainly by random effects ($R^2_{\text{fixed}} < 0.33$) (see Fig. 3). Mean values of FES and significant differences are shown in Table 2 and Annex 2. Vegetation-related FES were highest in reference forest in most cases, followed by logged forest and second growth forests, and depending on the service, lowest in plantation (biodiversity and NTFP) or agroforestry systems (Timber volume and

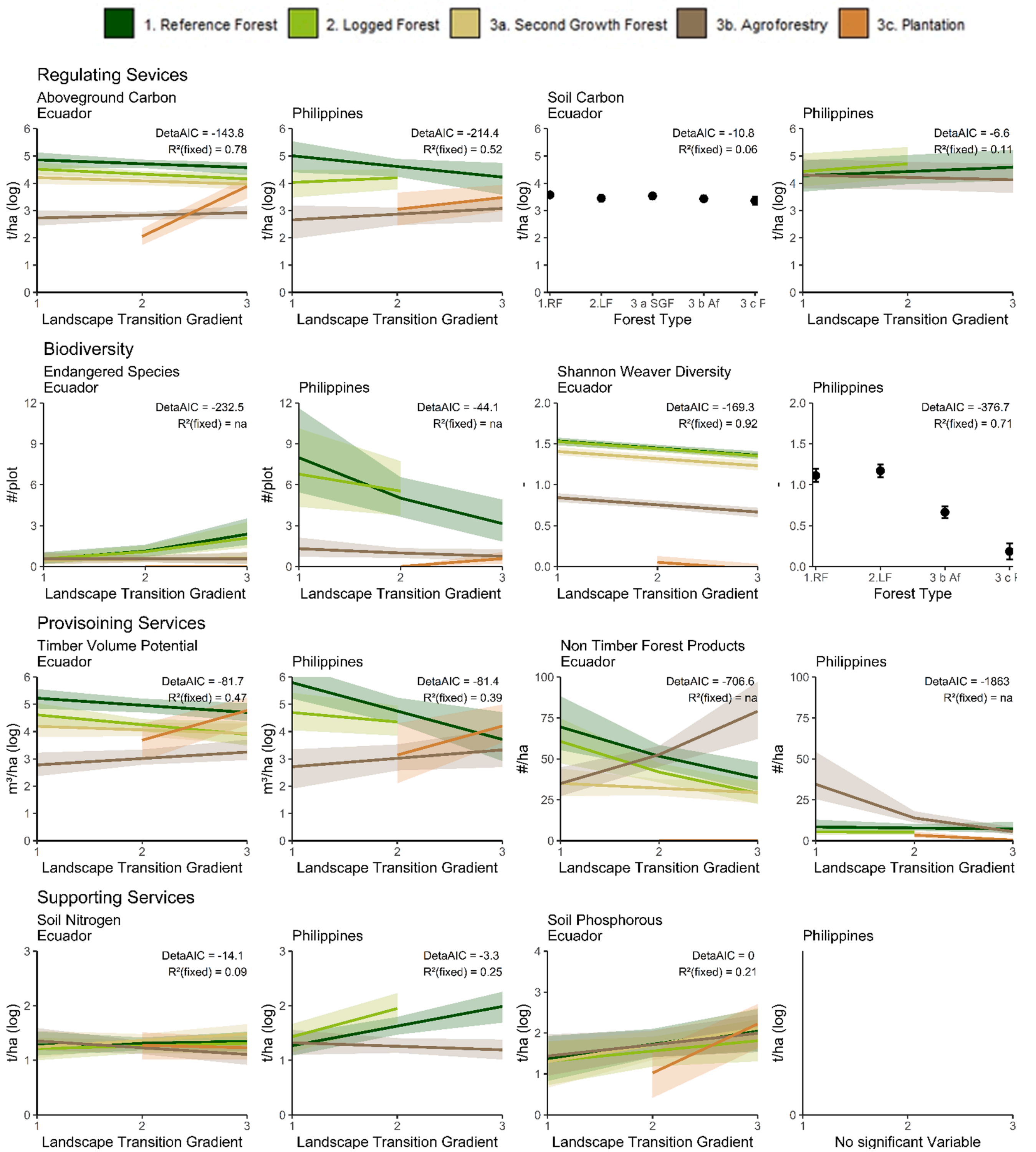

Fig. 3. Predicted values of FES in different forest types along a forest landscape transition gradient based on significant fixed effects from mixed effect models. R^2-value indicate the explained variance by both fixed effects, and DeltaAIC shows the improvement compared to a null model containing only fixed effects. Landscape transition effects were not significant in two models and therefore not displayed.

AGC). For natural forests, especially reference and logged forests, late transition stage landscapes had lower values compared to mid and early stage landscapes in reference forests with the notable exceptions for Endangered Species and NTFP (described in more details below). Even though reference forests were only found in two of the four landscapes in the Philippines representing the mid-transition phase, they showed exceptional high untransformed values of AGC, $C_{soil.org}$ and Timber Volume (see Annex 2).

AGC was highest for all regions in the reference forest (116 mean t/ha (Ecuador) and 166.7 mean t/ha(Philippines)), followed by logged forest (82.8 mean t/ha (Ecuador) and 78.06 mean t/ha), and second-growth forest (65.34 mean t/ha). The relative differences between reference and logged forest in the Philippines exceeded the one in Ecuador. $C_{soil.org}$ was highest in the more disturbed second growth forests in Ecuador and slightly higher in logged forests compared to reference forests in the Philippines, but mainly determined by regional differences.

The impacts of anthropogenic disturbances on both biodiversity indicators were relatively low, and only second growth forest in Ecuador showed distinctly lower values. While agroforestry had intermediate values, only few individual plantations in the Philippines had more than one species per plot. Endangered Species had a higher presence in the Philippines than in Ecuador, where these species were mainly found in logged and reference forests in late phase (see Fig. 3).

Considering provision services, Timber Volume followed the trend described for AGC, but the declines and increases along landscape transition gradients were even stronger. In late stages, Timber Volume in plantations exceeded the least disturbed natural forest, although in the Philippines, these plantations did not exceed 76.5 m^3/ha on average. Overall agroforestry system in the Philippines had a higher value for Timber Volume and lower values for NTFP compared to Ecuador. Finally, late transition agroforestry systems compared to earlier stages had higher NTFP densities in Ecuador, and lower ones in case of the Philippines (see Fig. 3).

3.2. Scale effects

We used 7 variables to explain 8 diverse FES. We split the dataset in natural forest (reference, logged and second growth forest), and planted forests (agroforestry and plantations) (see Fig. 2c). First, we used all observations (dataset 1, see Table 4) to identify general trends. In a second step we used specific effects for natural and planted forests (dataset 3 and 4, see Tables 5 and 6) and in a final step country specific effects for natural (dataset 4 and 5, see Table 7) and planted forests (dataset 6 and 7, see Table 7), respectively.

When using the **complete dataset** (see Table 4), seven FES benefitted high from stem densities. AGC, Endangered Species, and Timber Volume consistently increased with higher mean dbh, but NTFP reacted model depended, e.g. with decreases in planted forest (see Table 6) and natural forest in the Philippines (see Table 7). High forest cover within a 500 m radius mainly indicated higher levels of FES. N_{soil} showed the most susceptibility to forest cover dynamics on both levels with higher values in plots with forest cover increases and patch-rich landscapes (see Table 4).

The influence of forest fragmentation increased in the subsets: In **natural forests**, we found an increased and positive influence of FC_{plot} on AGC, NTFP, and Timber Volume, which was explained additionally by $FC_{landscape}$. Shannon Weaver Diversity exclusively and Endangered Species mainly benefitted from high landscape forest cover. N_{soil} and P_{soil} were higher in low fragmented forest cover landscapes with net increases (see Table 5). Country specific we found evidence for a stronger influence of forest cover fragmentation and on larger scales in the Philippines. Landscape variables were significant for 6 FES in the Philippines but only 2 in Ecuador. For example, only in the Philippines AGC was significantly explained by FC_{plot}, or Timber Volume in the Philippines increased with $FC_{landscape}$ and with FC_{plot} in Ecuador (see Table 7a).

In **planted forests**, FES reacted differently to forest cover fragmentation compared to natural forests. AGC, Timber Volume, NTFP, and Shannon index were explained best by the models. Local deforestation was associated with high NTFP and Shannon index and local regrowth with high Timber Volume. AGC and Timber Volume were higher in patchy landscapes, and NTFP was higher in high forest cover landscapes (see Table 6, see Table 7b).

Table 4
Summary of standardized coefficients of significant effects from mixed effect models using backward regressions on fixed effects on the complete dataset. Delta AIC indicated the difference between the most parsimonious model to the AIC of a null model without fixed predictors.

		Complete Dataset							
		AGC	Soil C	Endangered Species	Shannon Index	Timber	NTFP	Soil N.	Soil P.
Stand Structure	Mean dbh	0.52***			0.18***	0.42***	0.05**		
		(0.03)			(0.05)	(0.04)	(0.02)		
	Stem Density	0.56***	0.12**	0.23***	0.14*	0.54***	0.27***	0.14*	
		(0.04)	(0.04)	(0.05)	(0.06)	(0.05)	(0.02)	(0.07)	
Forest Cover Metrics 500 m radius	Forest Area	0.28***		0.43***	0.43***	0.16**	-0.08***		
		(0.04)		(0.06)	(0.06)	(0.05)	(0.02)		
	Forest Cover Change	0.06*					-0.09***	0.14*	
		(0.03)					(0.02)	(0.06)	
Forest Cover Metrics 10 × 10 km landscape	Forest Area			0.40***			0.41***		
				(0.10)			(0.12)		
	Patch Density							0.28**	
								(0.11)	
	Forest Cover Change								
	Constant	0.02	0.32	0.43	0.05	-0.001	2.82***	0.09	-0.12
		(0.07)	(0.66)	(0.74)	(0.19)	(0.06)	(0.42)	(0.11)	(0.23)
	Observations	331	270	331	331	331	331	270	269
	AIC	517.1	496.3	1094.3	736.9	720.1	5567.5	734.4	632.6
	DeltaAIC	-398.5	-4.7	-159.1	-124.3	-203.7	-305.7	-8.4	0.0
	R^2_{Fixed}	0.73	0.01	0.29	0.31	0.50	0.41	0.10	0.00
	$R^2_{(fixed + random)}$	0.76	0.81	0.87	0.50	0.54	0.96	0.26	0.53

Table 5
Summary of standardized coefficients of significant effects from mixed effect models using backward regressions on fixed effects on the complete dataset. Delta AIC indicated the difference between the most parsimonious model to the AIC of a null model without fixed predictors.

		Natural Forest (Cross Country) (*Reference Forest. Logged Forest. Second Growth Forest*)							
		AGC	Soil C.	Endangered Species	Shannon Index	Timber	NTFP	Soil N.	Soil P.
Stand Structure	Mean dbh	0.67*** (0.04)				0.42*** (0.06)			
	Stem Density	0.42*** (0.04)		0.14*** (0.04)		0.43*** (0.06)	0.20*** (0.02)		
Forest Cover Metrics 500 m radius	Forest Area	0.20*** (0.04)				0.14* (0.07)	0.20*** (0.02)		
	F. Cover Change								
Forest Cover Metrics 10 × 10 km landscape	Forest Area			0.49*** (0.08)	0.33*** (0.10)	0.17* (0.08)		-0.45*** (0.12)	
	Patch Density								0.52** (0.17)
	F. Cover Change							0.34** (0.12)	
	Constant	0.01 (0.15)	0.41 (0.63)	1.04 (0.76)	-0.07 (0.32)	-0.02 (0.07)	2.81*** (0.62)	0.15 (0.10)	-0.11 (0.41)
	Observations	194	152	194	194	194	194	152	152
	AIC	247.2	257.9	687.6	396.8	436.8	1844.3	364.1	300.7
	DeltaAIC	-257,4	0,0	-23,1	-7,1	-88,1	-203,1	-12,4	-5,0
	R^2_{Fixed}	0,72	0,00	0,13	0,12	0,47	0,10	0,34	0,17
	$R^2_{\text{(fixed + random)}}$	0,84	0,84	0,89	0,58	0,52	0,96	0,49	0,84

Table 6
Summary of standardized coefficients of significant effects from mixed effect models using backward regressions on fixed effects on the complete dataset. Delta AIC indicated the difference between the most parsimonious model to the AIC of a null model without fixed predictors.

		Planted Forest (Cross Country) (*Agroforestry and Plantation*)							
		AGC	Soil C	Endangered Species	Shannon Index	Timber Volume	NTFP	Soil N.	Soil P
Stand Structure	Mean dbh	0.56*** (0.07)				0.51*** (0.08)	-0.38*** (0.05)		
	Stem Density	0.63*** (0.07)	0.23** (0.08)		-0.21* (0.09)	0.60*** (0.09)	0.40*** (0.03)		
Forest Cover Metrics 500 m radius	Forest Area								
	F. Cover Change				-0.24** (0.08)	0.21** (0.07)	-0.49*** (0.03)	0.18* (0.09)	
Forest Cover Metrics 10 × 10 km landscape	Forest Area				0.45*** (0.14)		0.63*** (0.17)		
	Patch Density	0.28* (0.12)							
	F. Cover Change				0.32* (0.14)				
	Constant	-0.03 (0.12)	0.08 (0.75)	-0.58* (0.25)	0.02 (0.11)	-0.13 (0.14)	2.47*** (0.17)	0.004 (0.09)	-0.13 (0.20)
	Observations	137	118	137	137	137	137	118	117
	AIC	271.3	254.6	295.4	372.7	321.31	2340.5	341.8	314.8
	DeltaAIC	-86.6	-5.3	0.0	-15.2	-59.3	-412.3	-1.5	0.0
	R^2_{Fixed}	0.50	0.03	0.00	0.20	0.34	0.71	0.03	0
	$R^2_{\text{(fixed + random)}}$	0.73	0.82	0.18	0.33	0.65	0.99	0.03	0.34

Table 7
Summary of standardized coefficients of significant effects from mixed effect models using backward regressions on fixed effects on country specific. Delta AIC indicated the difference between the most parsimonious model to the AIC of a null model without fixed predictors.

		Natural Forest (Reference Forest. Logged Forest. Second Growth Forest)															
		AGC		Soil C		Shannon ndex		Endangered Species		Timber Volume		NTFP		Soil N.		Soil	
		EC	PH	EC	PH	EC	PH	EC	PH	EC	PH	EC	PH	EC	PH	EC	PH
Stand structure	Mean dbh	0.76***	0.61***			0.21*		0.33***		0.50***	0.41***	0.08***	-0.11*				
		(0.04)	(0.05)			(0.10)		(0.08)		(0.07)	(0.08)	(0.02)	(0.05)				
	Stem Density	0.57***	0.38***				0.16***			0.47***	0.48***	0.21***	0.14**				
		(0.05)	(0.05)				(0.04)			(0.08)	(0.08)	(0.02)	(0.05)				
Forest Cover Metrics 500 m radius	Forest Area		0.24***							0.19*		0.16***					
			(0.06)							(0.08)		(0.02)					
	F. Cover Change									-0.16*							
										(0.07)							
Forest Cover Metrics 10 × 10 km landscape	Forest Area						0.65***		0.74***		0.31***				-0.61***		-1.04***
							(0.10)		(0.18)		(0.09)				(0.15)		(0.23)
	Patch Density				0.24*											0.50*	
					(0.09)											(0.20)	
	F. Cover Change					0.29*											
						(0.12)											
	Constant	-0.01	0.02	-0.01	0.19	0.02	1.86***	-0.23	0.12	-0.00	-0.02	3.71***	1.87***	0.001	0.05	0.02	-0.27
		(0.08)	(0.27)	(0.17)	(0.49)	(0.35)	(0.46)	(0.45)	(0.69)	(0.07)	(0.09)	(0.08)	(0.17)	(0.18)	(0.15)	(0.20)	(1.00)
	Observations	105	89	105	47	105	89	105	89	105	89	105	89	105	47	105	47
	AIC	135.5	91.2	288.0	99.5	282.4	392.0	259.9	237.7	228.8	201.04	1002.2	782.1	2812	118	212.5	96.6
	DeltaAIC	-161.7	-132.5	0	-3.9	-6.3	-24.7	-14.8	-3.48	-69.1	-36.2	-246.8	-9.9	0	-5.8	-2.5	-5.9
	R^2_{Fixed}	0.77	0.71	0.00	0.07	0.13	0.44	0.10	0.25	0.55	0.50	0.58	0.08	0.00	0.37	0.26	0.31
	$R^2_{(fixed + random)}$	0.83	0.88	0.28	0.61	0.39	0.85	0.49	0.69	0.55	0.53	0.86	0.70	0.33	0.47	0.70	0.93

(*continued on next page*)

Table 7 (*continued*)

		Planted Forest (*Agroforestry and Timber Plantations*)															
		AGC		Soil C		Shannon Index		.Endangered Species		Timber Volume		NTFP		Soil N		Soil P	
		EC	PH	EC	PH	EC	PH	EC	PH	EC	PH	EC	PH	EC	PH	EC	PH
		Planted Forest (*Agroforestry and Timber Plantations*)															
																	AGC
Soil C		Shannon Index		.Endangered Species		Timber Volume		NTFP		Soil N		Soil P					
		EC	PH	EC	PH	EC	PH	EC	PH	EC	PH	EC	PH	EC	PH	EC	PH
Stand structure	Mean dbh	0.79*** (0.08)	0.44*** (0.06)							0.58*** (0.11)	0.41*** (0.08)	-0.51*** (0.04)				0.36*** (0.10)	
	Stem Density	0.27** (0.08)	0.69*** (0.06)		0.48*** (0.11)		0.28* (0.12)			0.26* (0.11)	0.60*** (0.08)	0.34*** (0.04)	0.41*** (0.03)				
Forest Cover Metrics 500 m radius	Forest Area											-0.10*** (0.03)					
	F. Cover Change								-0.33** (0.11)		0.22** (0.08)	-0.32*** (0.03)	-0.51*** (0.05)				
Forest Cover Metrics 10 ×10 km landscape	Forest Area							0.46** (0.16)				0.36** (0.13)	0.63* (0.25)				
	Patch Density	0.32*** (0.08)	0.45*** (0.10)							0.36** (0.12)	0.39** (0.14)					0.45** (0.17)	
	F. Cover Change				0.23* (0.10)												
	Constant	-0.00 (0.07)	-0.05 (0.11)	0.05 (0.25)	0.57 (0.50)	-1.0** (0.38)	-0.34* (0.16)	0.03 (0.15)	0.15 (0.19)	-0.01 (0.11)	-0.09 (0.15)	3.56*** (0.14)	1.83*** (0.29)	0.005 (0.26)	-0.00 (0.12)	-0.03 (0.16)	-0.07 (0.21)
	Observations	51	86	51	67	51	86	51	86	51	86	51	86	51	67	51	66
	AIC.	93.0	129.7	137.3	173.6	88.6	202.4	142.0	239.7	122.5	183.7	1464.9	747.7	131.9	197.1	112.5	183.3
	Delta AIC	-48.9	-91.3	0.0	-12.1	0.0	-3.5	-4.5	-6.6	-22.8	-56.5	-285.4	-242.9	0.0	0.0	-8.7	0.0
	R^2_{Fixed}	0.72	0.73	0.00	0.16	0.00	0.08	0.21	0.10	0.50	0.56	0.76	0.46	0.00	0.00	0.36	0.00
	$R^2_{\text{(fixed + random)}}$	0.72	0.82	0.56	0.52	0.10	0.16	0.32	0.35	0.54	0.72	0.96	0.97	0.64	0.00	0.65	0.28

4. Discussion

Moist tropical forests provide a wide range of services and benefits to humankind (FES), which describe the aspects of ecosystems utilized (actively or passively) to produce human well-being (MEA, 2005). This capacity is severely threatened by timber extractions and ongoing deforestation (Asner et al., 2010). Therefore, we used the framework of forest transition theory, which describes patterns of forest decline and recovery (Mather, 1992), to explain how and which FES in different forest types change when forested landscapes transition from connected forests to agricultural-forest mosaics landscapes. We linked these dynamics on different scales describing stand structure and forest fragmentation on two levels. We included data from two countries and four regions to highlight cross-country and context-specific trends. Our results confirmed highest values in reference forest, reduced values of FES in logged forests, intermediate values in second growth forests and lowest values in agroforestry systems for Timber Volume and AGC and the absence of biodiversity in plantations (Veridiano et al., 2020; Mukul et al., 2020; Eguiguren et al., 2020; Labrière et al., 2015). In agreement with these studies our result also highlight overall lower impacts on soil properties and faster recovery of selected biodiversity indicators than biomass (Poorter et al., 2021). Our results, therefore, shed light on decline and recovery in the context of forest transition dynamics. For example, our findings highlight how landscape effects lead to a degradation of the FES in the remaining forest stands. Our results add to empirical findings on the influence of landscape context on bundles of FES (Renó et al., 2016; Lamy et al., 2016; Grimaldi et al., 2014). However, the presented study includes a wider spatial variability due to the cross-country context. Our selected FES indicators relate on the one hand to global demands, backed by international commitments as the regulation of the global climate and the conservation of Endangered Species (CDB, 2012; UNFCCC, 2013), and on the other hand to rural income sources.

4.1. Limitations

We worked in this cross-country study with indicators for FES, and did not quantify the actual benefits. For example, we deliberately chose NTFP as an indicator to highlight a non-destructive form of forest resource usage, but we did not relate this to real or in-kind income generated from NTFP. Even though the collection of edible forest products is documented in both countries (Wiebe et al., 2022; Ojeda Luna et al., 2020), we acknowledge that other potentially more relevant products were not part of our dataset, either because they were not recorded in the inventory, which focused trees and palms with a dbh > 10, or because the consulted secondary sources did not list them. Additionally, our results describe in detail per ha value of a wide set of FES and not their total supply within a landscape. Hence, neither total quantity of particular a FES, nor the total degradation and restorations of particular FES is revealed, which would require further research.,

There is some overlap in the selected regions and landscape transition stages. Although the landscape transition gradient was not linear, we therefore rejected treating the landscape transition gradient as a categorical variable, and included a comparison of mean values (see Annex 2). This way interpreting the results in combination with the output of mixed linear effect models allowed to estimate declines of FES along the analyzed transition gradient (see Fig. 3).

We faced the overall challenge matching forest types with particular different deforestation histories. While all disturbances in the Philippines were related exclusively to logging, available information was insufficient to identify where a complete removal of forest cover and where a partial removal of forest cover had taken place in the past. Similarly, the landscape transition gradient has probably different components, and numerous factors can drive spatial variability in FES. To address the fuzziness of forest type boundaries in a cross-country context, we used substitute variables for further analysis as stem density, mean dbh, and forest cover change.

4.2. Forest type and landscape transition gradient influences

Both countries lie in the humid tropical zone and share a high dependency on natural resources from the forest and agricultural sector: Ecuador harbors more intact forest areas but experienced increased deforestation in the last years (Armenteras et al., 2017; FAO, 2015). In contrast, commercial logging in the Philippines led to a large-scale forest cover decline in the last century, but recent efforts led to a net increase (FAO, 2015; Chokkalingam, 2006). Logging led to declines in Timber Volume and AGC with significant differences, and in NTFP and Endangered Species in absolute numbers. In reference forests, the landscape transition gradient led to a decline in Timber Volume and AGC. Neither logging nor the landscape transition gradient consistently affected the Shannon index in the pre-clearing forest, but additional analysis showed that also this indicator declined with forest cover on the landscape level. Low FES-values in the early stage compared to early and mid-transition stages drove this decline (see Annex 2). For example, the Timber Volume in the late stage was only 16% in the Philippines and 66% in Ecuador of the values compared to the early stage (see Table 2). This pattern suggests that indirect effects of natural and anthropogenic disturbances mainly become visible in landscapes with an intensive deforestation history. In general, soil carbon accounts for 36–60% of tropical forests' carbon pools and can be influenced by deforestation (Mahli and Jarvis, 1999). Pools in the top 20 cm in this study accounted for 20% (reference forest middle stage Ecuador) and 78% (agroforestry middle stage Philippines) of total meassured carbon. However we found only minor influences of forest types or transition gradients on total carbon pools, and thereby highlight the role of soils for carbon storage as relatively stable pools.

Natural Forests had more Endangered Species in the Philippines and a higher Shannon index in Ecuador. Regarding the Shannon index this highlights the differences between the high diversity rainforests of Ecuador compared to the less species rich ones of the Philippines. Regarding Endangered Species, the results are in line with the overall number of red-list species registered by the *International Union of Conservation* in both countries (IUCN, 2022). This is likely due to the long deforestation history since 96% of Endangered Species in our dataset were also valuable timber species, and also due to high levels of endemism. However, Endangered Species declined with an ongoing landscape transition in the Philippines, and increased in Ecuador along the studied gradient (see Fig. 3). On the one hand, the late transition region in case of Ecuador (Esmeraldas) is more influenced by logging and deforestation. On the other hand, due to the separation by the Andes, species composition is different compared to the studied Amazon regions, and overall, 25% of vascular plants are considered endemic (Mittermeier et al., 2002). Further deforestation would pose a risk that these species become regionally extinct, a process that is likely already ongoing in the late transition region of the Philippines. The low density (0.56 species per plot) of Endangered Species in second growth forests adds to these risks. Restoration strategies with mixed species plantations have the potential to bridge this gap (Keenan et al., 1999). For example, species composition in close-to-nature reforestation in the Philippines showed similar species composition to logged forest (Veridiano et al., 2020).

As discussed earlier, the effect of logging on AGC and Timber Volume species exceeded in the Philippines the one found in Ecuador, even though forests had up to 40 years to recover. AGC and Timber Volume in the Philippines had high regional differences: High AGC, $C_{soil.org}$, and Timber Volume values in the middle stage and low values in the late stage stand out. In the middle stage, the values can be attributed to plots in two landscapes located at high altitudes and are therefore not typical for region as a whole, and participatory mapping indicated poor accessibility which might have hindered logging activities. The contrasting low values in the late stage belonged to the last remnant forests of highly deforested and hurricane-prone landscapes. The contrast between these landscapes and these types of forests indicates that reference values have not been achieved even 30 years after a nationwide logging ban. Some studies have shown that forest biomass stocks recovered decades after logging, e.g. 27–70 years (Susanty, 2021). For example, selective logging led to 40% lower biomass in a forests in Borneo even after 22 years of recovery due to the removal of large-diameter trees (Hector et al., 2011). Recent estimates even assume that second growth forests take up to 120 years to recover biomass (Poorter et al., 2021). Hence, forests either had insufficient time to recover from past interventions, or current policies are not enforced sufficiently. Although logged forests had less time to recover in Ecuador, only values of relative degradation of the once completely deforested second growth forests in Ecuador were comparable to those in the Philippines. We focused on relatively recent selective timber extractions within designated concession areas in Ecuador; these extractions are not necessarily representative of all local timber extractions (Bonilla-Bedoya et al., 2017; Mejia et al., 2015). For example, in the Ecuadorian Amazon, characterized by high forest cover and low deforestation, timber used by local communities is often a byproduct of clearing agricultural land rather than gained by active extraction (Ojeda Luna et al., 2020). Considering the recovery rates mentioned above, cutting cycles of 5–12 years, as permitted under PSFU and PSAFI management schemes in case of Ecuador, are likely insufficient to recover harvested biomass. In order to avoid long-term degradation or drastic protection measures such as the Philippine logging moratorium, harvesting intensities should be reduced and cycles extended.

The landscape transition effect on NTFP (increase by 5% the Philippines and decrease by 44% in Ecuador) was country-specific. In Ecuador this correlated with a decrease of overall species diversity and biomass, but also the collection of NTFP provided a higher share to forest income in particular in the Amazon region (Ojeda Luna et al., 2020). In the Philippines this development could be attributed to one particular species (*Ficus Nota)* which shows how individual NTFP species can benefit from degraded forest landscapes.

The number of landscapes with timber plantations and Timber Volume stored within this forest typ increased along the transition gradient. Plantations are likely to be more widespread and older in regions of late transition stages exhibiting low forest cover. The differences in Timber Volume and AGC between plantations in the middle and late transition stages can be attributed to the age structures of 2–3 years *Ochroma pyrimidale*-plantations (mid stage) compared to 4–18 years *Tectona grandis*-plantation (late stage) in Ecuador (Eguiguren et al., 2020). Agroforestry systems are highly diverse and likely to provide more goods than timber and alimentary support (FAO, 2002). Overall the provided services in the agroforestry system reflected the local availability of forest resources. Ecuador had higher NTFP, and the Philippines had a higher Timber Volume. Additionally, NTFPs increased along the gradient in the Ecuadorian agroforestry system. In the early and mid-stages, these systems are characterized by integrating trees with perennial and annual crops such as *Manihot esculenta* or *Musa paradisa* (non-published inventory data, (see Eguiguren et al., 2020 for details). The late-stage agroforestry system in Ecuador included a higher proportion of NTFP trees, especially *Theobroma cacao*, and annual crops are cultivated separately in the respective landscapes. In the Philippines, timber trees such as *Gmelina arborea* replaced frequent palm species in the earlier stages of *Cocos nucifera, Areca catechu,* and *Livistonia rotundifolia*. Famers on the island of Luzon in the Philippines for example meet subsistence needs and sell to local markets, and as a result, decide to grow more timber and less fruit trees in less forest-dominated landscapes (Schuren and Snelder, 2008). Additionally, the national policy promotes growing trees on farms to regenerate tree cover (Pulhin et al., 2007).

These results stress that FES from "new" forests are distinctively lower compared to FES in the initially cleared forests, unless particular FES are actively promoted, like NTFP in agroforestry systems. The decline of FES either as a result of the landscape transition gradient or due to logging highlightsthe exceptional values of undisturbed forests for FES conservation.

The previously discussed FES provide different benefits, but they have in common that they are quantified based on aboveground vegetation. As such, they depend on the landscape's capacity to sustain primary production (MEA, 2005). Our study indicates this capacity through the supportive services of P_{soil} and N_{soil}. Since nutrient concentrations in natural forest soils are often relatively stable (Binkley and Fisher, 2020), changes in relative of soil properties in agroforestry and or plantations can shed light whether these systems lead to the degradation or restoration of supporting services. P_{soil} increased along the landscape transition gradient in all forest types, but P_{soil} in plantations compared to reference forest was 54% lower in the Amazon landscapes and 96.5% higher in the Esmeraldas landscapes. This suggests some potential of forest plantations to contribute to soil restoration, which is supported by above average values of P_{soil} in plantations in the Philippines. This assumption however is driven by two individual species in distinct site conditions. In the Amazon, *Ochroma pyrimidale* plantations are often established on sites with low soil fertility (Villacís et al., 2016), while *Tectona grandis* grandis altering properties of the as the accumulation of litter-based nutrients in the soil and transport of nutrients from the deeper depth layer (Boley et al., 2009; Ikhajiagbe et al., 2020). An alternative possibility could be attributed to the establishment on high fertility sites. However, N_{soil} in agroforestry decreased compared to reference forests values (13% decrease late stage Ecuador, 51-33% descrease mid and late stage Philippines (see Annex 2)). A possible explanations could be N_{soil} depletion, especially in more intensively used agroforestry systems in landscapes representing advanced transition stages. Possible reasons include losses through fires (Vitousek and Howarth, 1991; Wong et al., 2020), increased nutrient loss from erosion after vegetation clearings and removal of nitrogen through harvested crops (Asio et al., 2009; Alfaia et al., 2004). These developments highlight both the potential of soil restoration and degradation through active reforestation.

4.3. Scale effects on ecosystem services

Our analysis revealed how the studied scales from stand to landscape affect FES. These forest transition-related variables can positively and negatively influence FES (Ali, 2019; Steur et al., 2020; Bennett et al., 2009). This analysis, in turn, sheds light on optimal stand and landscape structures for maintaining FES in natural forest and how modifications on plot level and developments on landscape relate to higher FES in planted forests.

Structural variables at the stand level had the strongest influence on FES (see Table 4-7). This can point to complementary effects, where trees with different sizes share resources more efficiently, or selective effects, where the dominance of a group or individual with particular traits influences the total values of a particular FES (Ali, 2019; Poorter et al., 2015). Overall positive effects of mean dbh, and stem density on AGC and Timber Volume are well documented (Slik et al., 2013). For example, the density of large diameter trees accounts for 70% of variation in aboveground biomass across humid tropical forests (Slik et al., 2013). However, knowledge gaps on less studied services such as NTFP still exist (Steur et al., 2020).

In natural forest, lower mean dbh means less competition for resources from dominant trees and allows more space for different species and individuals to coexist. In planted forests, this indicates a trade-off between systems with fruit trees with a low dbh and timber producing systems with a high dbh. Based on these results, timber harvesting practices that maintain different age classes, large diameter trees, and high tree densities, possibly through regeneration, is best suited to maintain multiple ecosystem services. Afforestation that reflects stand structures of natural regeneration would likely be suited to combine provisioning services with regulating service as AGC and biodiversity.

High forest cover and to a lesser degree and low fragmentation supported multiple FES in natural forests, highlighting the importance of landscape integrity. Forest cover and fragmentation at plot and landscape level are a product of deforestation and natural disturbances. Plot-level metrics were frequently significant in models including both natural and planted forests, which displayed largest variation in FES. Immediate positive influence of forest recovery comparable in scale to the used 500 m radius have been documented for both biodiversity and AGC (Chazdon, 2003; Hernández-Stefanoni et al., 2011), and forest recovery rates (Schwartz et al., 2017). Our results show that the wider landscape context can exceed this influence. Additionally, our results highlight stronger landscape effects in the highly deforested Philippines than in the less deforested Ecuador.

In natural forests, AGC reacted to reduced forest cover in a 500 m radius, biodiversity indicators responded to lower forest covers within a 10x10 landscape cutout, whereas Timber Volume reacted to both variables. Population density is a deforestation driver in both countries, increasing pressure on forest resources (Rebugio et al., 2007; Ferrer Velasco et al., 2020). When available forest resources within a landscape are low and not provided through external markets, pressure on remaining resources increases through timber extraction, grazing, or firewood collection (Geist and Lambin, 2002; Hosonuma et al., 2012). These clearings open the canopy and allow for the emergence of lianas and shorter-lived successional trees, which store substantially less carbon than old-growth trees (Laurance et al., 2011; Ordway and Asner, 2020; Chaplin-Kramer et al., 2015). This deforestation increases forest fragmentation and thereby forest edges. Mortality of large trees increases near forest edges through microclimatic changes and increased wind turbulence (Brinck et al., 2017). Since these disturbances can penetrate several kilometers deep into the forest (Briant et al., 2010), edge effects can account for 31% of the direct carbon emissions from tropical forests due to land-use changes (Silva Junior et al., 2020; Brinck et al., 2017). Considering biodiversity, local disturbances can lead to a variation in habitat, allowing for more diverse species to regenerate or to isolating habitats patches with reduced dispersion and regeneration (Attiwill, 1994; Fahrig, 2003). Overall these are stronger in the Philippines: landscapes are more fragmented (see Fig. 1) and old-growth reference forest have disappeared from half of the landscapes representing an advanced transitions. Intense timber harvesting of valuable timber trees and reduced regeneration through isolated and smaller patches are possible drivers behind this reduction.

The influence of fragmentation variables on FES in planted forests was heterogeneous. Decreases in forest cover change in a 500 m radius explained NTFP and increases Timber Volume. First, this shows high forest dynamics around agroforestry systems and timber plantations. Overall forest cover decreased around 43 out of 93 agroforestry plots, suggesting that agroforestry can be not attributed only to landscape restoration, but also to short-term forest loss (Dewi et al., 2017) and timber plantations to short-term gain. High forest cover landscapes had lower NTPFs and Endangered Species, and patchy landscapes higher Timber Volume and AGC. Although timber plantations had barely any tree diversity, forest patcheshave the potential to make an indirect contribution by providing services not mentioned, e.g. regulating the hydrological cycleand improving the connectivity of the forest mosaic, when replacing degraded lands (Bauhus, 2010; Bremer and Farley, 2010)

N_{soil} and P_{soil} increased with an advancement of the forest transition, either expressed as $PD_{landscape}$, $FC_{landscape}$ or $FCC_{landscape}$. This effect is relatively weak and disappeared with smaller sample sizes. Agricultural expansion is associated with higher soil fertility (Ferrer Velasco et al., 2020). For example low soil fertility is one reason for the delayed agricultural expansion in the Amazon (Pichon, 1997). The South Cayagan Valley in the Philippines, where the late transition landscapes are located, has a history of agricultural cultivation due to favorable soil conditions (BSWM, 2013). Another possible explanation would be the conversion of carbon and nutrient pools from aboveground to belowground after disturbances: Large mature trees store nutrients and carbon in stems with reduced mineralization, whereas the residence time of nutrients in secondary trees, lianas, and vines are shorter (Laurance et al., 2011). After a disturbance, primary production increases, and a larger proportion of biomass accumulates in roots and litter (Ordway and Asner, 2020). Our results suggest that nutrient stock increases due to deforestation and timber extractions are more likely for N_{soil} and $C_{soil.org}$. The increase of N_{soil} along the gradient second growth, logged and reference forest support this explanation (see Fig. 3). The contrasting influence of landscape integrity on P_{soil} and N_{soil} on the one hand and AGC, Timber Volume and biodiversity indicators on the other hand suggest some trade-off on landscape level forests between agricultural potential and AGC, Timber Volume, and biodiversity.

4.4. Recommendation for FES conservation, restoration and future research

We showed considerable variation of FES of global and local importance in both natural forest systems and planted forest systems. The results highlight that simple land-use classes cannot capture this heterogeneity since landscape effects have an additional influence. Hence, monitoring, assessment, and compensation for the conservation of FES as AGC under schemes as REDD+, should account for this heterogeneity. For example, carbon losses caused by the edge effect are an additional flux that can counteract carbon emissions avoided by reducing deforestation (Silva Junior et al., 2020; Brinck et al., 2017). Advancements in earth observations that capture stand structure attributes will close this gap and provide standardized information for AGC, which was explained well by stand structure. We propose that context information derived from simple forest non-forest cover maps, such as forest fragmentation used in this study, can potentially improve these estimations for less frequently studied FES as Endangered Species, which were explained poorly by stand structure.

Consideration the very broad geographical context of both countries at opposite positions of the globe, we can confirm previously published pathways of recovery and degradation of FES (Wilson et al., 2017): For example, low disturbance reference forests had the highest values of FES, followed by logged forests, whereas different forms of planted forests only reach these values for provision services, which confirms the exceptional importance of these forests for multiple FES (Watson et al., 2018). We showed that in cases of severe biomass reductions, they still provide a habitat for Endangered Species. One motivation to include the Shannon index was its relationship to other FES which this study could not address (Cardinale et al., 2012; Isbell et al., 2011). The low impact of logging on the Shannon index also indicates that these FES recover faster than AGC. We confirm that structurally diverse forests and connected landscapes support multiple FES (Lamy et al., 2016; Grimaldi et al., 2014). However, we found an inconsistent effect of dbh on the abundance of NTFP. As a non-destructive form of forest use, NTFPs can play a crucial role in forest conservation in tropical countries (Asprilla-Perea and Díaz-Puente, 2019; Ros-Tonen, 2000). The inconsistencies country-specific effects highlight that integrating NTFPs in forest management should be adapted and developed locally. Increasing carbon stocks might even result in outcompeting NTFP-providing species in some cases. Sustainable forestry depends on a minimum of timber resources: Mean values in late transition stages as low as 36 m^3/ha (Philippines) or 53.9 m^3/ha (logged forest in Ecuador) suggests that this form of forest usage not feasible anymore or only at the expense of the last remnant intact forest.

In Ecuador, “50% of household income comes from forest and agricultural activities” in the selected Ecuadorian landscapes, and “high deforestation context is associated with higher forest and agricultural income” (Ojeda Luna et al., 2020). This is mainly driven by high timber revenues () in the Esmeraldas province (late transition), whereas in the amazon forest income is rather related to the collection of firewood and lower proportions of timber (Mejia et al., 2015; Ojeda Luna et al., 2020).

Noteworthy, NTFPs contribute up to 18% to forest-based income in the Amazon landscapes when households participate in community-based forest conservation schemes. High timber stocks in plantations and low timber stocks in logged forests in the Esmeraldas region, and high NTFP in natural forests in the Amazonas regions reflect this pattern of forest dependencies. In the late transition landscapes, commercial timber stocks of undisturbed forests are with 122 m^3/ha twice as high as in logged forests (53.9 m^3/ha). This depletion, combined with the high local deforestation rate and the high income obtained from timber, highlights that alternative income sources are urgently needed to stop the conversion to other forms of land use. Timber plantations show potential as alternative income sources and thereby reduce pressure from natural forests in the late transition landscapes while providing additional regulating services (Bauhus, 2010). By providing economic incentives to introduce mixed plantations and native species, there is potential for increasing their direct and indirect biodiversity value (Bremer and Farley, 2010). This strategy would be in line with the implementation of the national restoration plan of Ecuador (MAE, 2016, 2019). In the Amazon landscapes, total household income was lower (Ojeda Luna et al., 2020). Although our results suggest that timber plantations can be a promising alternative especially for nutrient-depleted lands, less land for this form of reforestation is available due to the overall higher forest cover (MAE, 2016). So far, both economic development and deforestation have been hindered by poorly developed infrastructure and market access. The challenge consists in providing access to forests without affecting conservation priorities. High Timber Volume and high AGC in logged forests show some potential for sustainable forestry with even further reduced cutting cycles (Eguiguren et al., 2020) as long as landscape integrity is maintained. The high presence of NTFP, especially in low-disturbance forests, invites further research into the potential for their commercialization. Both steps depend on implementing existing government plans (MAE, 2016) to build bio-based economy related to forest products..6

In the Philippines, rural households' dependency on agriculture and forest sector on forest products is relatively low, while remittances and off-farm income have become increasingly important in recent years. Income from forest resources is mainly related to firewood, with timber only making a minor contribution and some regional contributions from NTFPs. In contrast, collecting edible plants from forests is a frequent activity of rural households but contribute relatively little to household income (Wiebe et al., 2022). There is also an increased official demand for regulation services beyond carbon storage as water air enhancement or water regulation (DENR, 2016). Despite high ambitions, restoration initiatives often fail. Reasons include weak institutions, lack of resources, inadequate site, and species selections, and lack of economic benefits (Höhl et al., 2020; Le et al., 2014). We found high variability in Timber Volume in plantations (76.47–136.09 m^3/ha), and relatively low AGC (35.3–59.9 t/ha) in monocultures of primarily commercial though native species. This indicates that overall, four times more area is required to store the same amount of AGC in plantation compared to reference forests. The availability of this land for reforestation is challenged by a high population growth and increasing demand for land (Ferrer Velasco et al., 2020). Relatively high stocks in agroforestry system (34.53–53.10 m^3/ha) suggest that this land-use system can provide timber as alternative to traditional management of forests. Natural regeneration on logged lands was relatively successful in providing a range of FES, especially biodiversity with values close to less disturbed lands. However, there is little evidence of active regeneration with mixed native species that mimic these systems in our landscapes. These systems have shown to be relatively successful in restoring some or multiple FES both inside and outside the Philippines (Hector et al., 2011; Veridiano et al., 2020; Bremer and Farley, 2010). We suggest upscaling best practice models with mixed species to enhance multifunctional forests.

Since we did not include FES's total demand and supply in terms of spatial coverage and growth, additional research is required to identify the optimal balance between timber production, carbon storage, and biodiversity.

5. Conclusion

We used a framework based on the forest transition theory to describe how landscape dynamics and forest types influence different FES. We showed that not only logging reduces the capacity of forest areas to supply a wide range of FES, but landscape transitions also lead to a decline of FES in remnant forests. In these late transition landscapes, planted forests, agroforestry and plantations, become import sources for timber supply. We could attribute these changes to different stand structures and fragmentation indicators. These results highlight that dense and structurally diverse forests support multiple vegetation FES in old-growth and regeneration forests and show the need to maintain connected forest landscapes to conserve multiple ecosystem services. Finally, we advocate for a forest transition specific forest restoration, that takes the demand of forest depended people into consideration.

CRediT authorship contribution statement

Ferdinand Peters: Conceptualization, Methodology, Software, Formal analysis, Data curation, Visualization, Writing – original draft. **Melvin Lippe:** Conceptualization, Methodology, Resources, Data curation, Supervision, Writing – original draft, Writing – review & editing, Project administration. **Paúl Eguiguren:** Data curation, Methodology, Writing – review & editing. **Sven Günter:** Conceptualization, Supervision, Writing – review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.120782.

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