



Carbon cycle in tropical upland ecosystems: a global review

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Abstract. Along with habitat transformation, climate change has profound impacts on biodiversity and may alter ecosystem services on which human welfare depends. Many studies of the carbon cycle have focused on lowland tropical forests; however, upland forests have been less explored despite their pivotal role in carbon sequestration. Here, I synthesized the state of knowledge on the allocation of carbon in its different stocks (aboveground, belowground, and soil) as well as in its main fluxes (plant decomposition, respiration, and litterfall) in tropical upland ecosystems of the planet. In November 2020, a systematic review was carried out to identify references published from 2000 to 2020 through a combination of key terms in Google Scholar and Scopus databases, thus analysing bibliographic, geographical, methodological, and carbon cycling information of the global upland tropics (between 23.5° N–23.5° S). After analysing a total of 1967 references according to inclusion–exclusion criteria, 135 references published in the last 20 years were selected. Most of the studies were conducted in the tropical and subtropical moist broadleaf forest of South America. The main factors studied were elevation and forest type. Forest structure and soil variables were largely associated when studying carbon cycling in these ecosystems. Estimations of carbon stocks comprised three-fourths of the total studies, while the remaining fraction focused on carbon fluxes. Aboveground biomass and carbon in soils were highly investigated, while plant decomposition and respiration were the components that received the least attention. Even though in the last 20 years there was a slight increase in the number of studies on carbon cycle in tropical upland forests, I found bias associated with the biomes and ecoregions studied (especially in the Andes). Elevation was the main factor examined but other essential aspects such as the successional gradient, landscape management, diversity–productivity relationship, faunal and microbial effect, trophic cascades, and Gadgil effect require more attention. The inclusion of different litter species and origins (i.e. roots and stems) and theoretical frameworks including home-field advantage, substrate–matrix interaction, and phenology–substrate match may provide explanatory mechanisms to better understand litter decomposition over these forests. Despite respiration being a paramount link that is closely tied to above- and belowground compartment, this flux constitutes one of the important gaps to fulfil in future research. For a comprehensive understanding of the carbon cycle in upland forests, it is necessary to obtain information on its main fluxes and integrate them into climate change mitigation plans.

1 Introduction

Climate change is one of the major socio-environmental concerns worldwide (IPCC, 2014; Cuervo-Robayo et al., 2020). Global changes in mean atmospheric temperature and rainfall have changed dramatically over the last 140 years with increases up to 0.95 °C, as well as extreme precipitation and drought events (NOAA, 2021). Altogether with habitat transformation, climate change can cause profound impacts on

biodiversity and, consequently, may disrupt ecosystem processes and services on which human well-being depends (Sala et al., 2000; Loreau et al., 2001) such as food, fibre, and wood production (Beer et al., 2010). Therefore, quantifying carbon sequestration in each of its compartments as well as its main fluxes is critical for designing effective policies that are intended to reduce greenhouse emissions and

mitigate climate change, especially in developing countries (de la Cruz-Amo et al., 2020).

Tropical forests play a key role in carbon sequestration since they account for a quarter of global carbon storage (Bonan, 2008; Poorter et al., 2015) and a third of terrestrial net primary production (NPP) (Beer et al., 2010; Poorter et al., 2015). Within tropical forests, mountain regions represent a significant proportion of the world's biodiversity. Indeed, despite the relatively small area in mountain forests (ca. 25 % land surface of the Earth) (Körner, 2007), this region hosts 87 % of Earth's species of amphibians, birds, and mammals, many of which are entirely restricted to tropical mountains (Rahbek et al., 2019). In particular, tropical upper montane ecosystems are highly idiosyncratic because of their ecological and evolutionary singularities, which are very different from the lowland tropics (Malhi et al., 2010). Beyond constituting an upslope extension of lowlands, tropical upland forests are characterized by extraordinary local endemism and high rates of beta-diversity (Olson and Dinerstein, 2002; Calbi et al., 2021; Hurtado-Martilieti et al., 2021), which are mainly explained by the topographic heterogeneity (Pierick et al., 2021), the broad range of climatic environments (Malhi et al., 2010), and the complex geophysical structures (Körner, 2007; Körner and Spehn, 2019). These characteristics, at the same time, hinder mountain research, and many ecological questions remains to be answered, especially in ecosystem functioning. In fact, fundamental processes such as the carbon cycle are understudied in comparison to lowland tropical forests, which has received more attention (Malhi et al., 2010; Rubiano et al., 2017). Furthermore, the role of land use in the conservation status and carbon storage of these ecosystems as well as the interactions between climate change and land use change add an extra layer of complexity that is still not fully understood. Considering the importance of tropical mountain forests to climate change (Duque et al., 2021; Bendix et al., 2021), improving our understanding of the carbon cycle is critical to evaluate potential climate change impacts on natural resources from this region and, in this way, to further implement adaptation strategies to global warming.

It has been estimated that biotic carbon allocated into terrestrial plants counts for about 80 % of all taxa on Earth (450 Gt C), from which 320 Gt C is bound to aboveground biomass, mainly in stems and tree trunks, and 130 Gt C is accumulated in plant roots (Bar-On et al., 2018). Moreover, belowground biomass including microorganisms residing in the soil is also an important stock, especially along highland forests (de la Cruz-Amo et al., 2020). Despite some studies have quantified carbon stocks in tropical mountain forests by using several approaches including allometric equations (Phillips et al., 2019; Asrat et al., 2020; Calderón-Loor et al., 2020), fine root biomass in soil cores (Moser et al., 2011; Werner and Homeier, 2015), and carbon in soil pits (Wilcke et al., 2008; Zimmermann et al., 2010a), the estimation of carbon allocation is not clear or comprehensive, and the information about carbon stocks remains sparse, contrary

to lowland ecosystems (e.g., grasslands, Amazonian basin). Also, the analysis of the fluxes is generally excluded when scrutinizing carbon cycling in spite of being essential to establish the relationships between above- and belowground compartments.

Gathering information about how carbon is allocated aboveground, belowground, and in the soil organic matter, also how it is recycled in its principal fluxes, can be useful to evaluate the progress in the study of the carbon cycle in the tropical upland region. This way, it is possible to identify knowledge gaps and define future research avenues in these ecosystems within the context of climate change. Therefore, the objective of this systematic review was to synthesize the state of knowledge of the allocation of carbon stocks in its different compartments (i.e. aboveground biomass, belowground biomass, and soil organic matter) and its main fluxes (i.e. plant decomposition, respiration, and litterfall) in tropical upland ecosystems. I discuss the general patterns of bibliographic, geographical, methodological, and carbon cycle information identified in the contents of the scientific studies found in this review.

2 Methods

2.1 Data searching

On 1 November 2020, I conducted an extensive review through the academic databases of Google and Scopus, searching for the available scientific literature from 2000 to 2020 that contained in the title, abstract, and/or keywords the following search terms with all the possible combinations: ("Carbon stock" or "Aboveground biomass" or "Net primary production" or "Productivity" or "Fine root biomass" or "Belowground biomass" or "Litterfall" or "Soil organic carbon" or "Soil respiration" or "Litter decomposition" or "Carbon cycle") and ("Mountain forests" or "Montane ecosystems") and ("Tropics").

It is worth mentioning the limitation of search terms, considering the stringent key words used, as the objective of this systematic review was to evaluate the upland ecosystems only. In particular, the selection of the terms "Mountain forests" and "Montane ecosystems" provides a useful combination of words to obtain a wide range of studies carried out on mountain ecosystems. This was done with the intention of including all the possible studies carried out in the uplands since many of them could be part of investigations that assess altitudinal transects from lowland to upland mountain ecosystems. However, a literature search with more flexible key terms and considering the elevation as the only criteria to select upland ecosystems could provide a higher number of studies (see inclusion criteria), rather than the more restricted but direct and ecological criteria that this review attempts to address.

2.2 Inclusion–exclusion criteria

After removing duplicate documents and grey literature (e.g. theses, conference proceedings, and technical reports), I evaluated a total of 1967 references retrieved by Google scholar and Scopus according to the following inclusion criteria by reviewing the title, keywords, and abstract: (1) the forests were located in the tropics (23.5° N and 23.5° S), and (2) the study focused on at least one of the allocation components (aboveground biomass, belowground biomass, soil organic carbon) or carbon fluxes (decomposition rates, respiration, litterfall). This reduced the results to 564 references. Posteriorly, I excluded the references in which the analysed ecosystems belonged to the “Lowlands” according to the bioclimatic belts proposed by Körner et al. (2011). That is, thermal belts of “Remaining mountain area with frost” and “Remaining mountain area without frost” were excluded. This way, upland ecosystems examined in the selected studies pertained to the thermal belts of “Upper montane”, “Lower montane”, “Lower alpine”, and “Upper alpine” (Körner et al., 2011), thus removing 429 references from the 564 previously included (Fig. A1). To do this, I used the Global Mountain Explorer platform (<https://rmgsc.cr.usgs.gov/gme/gme.shtml>, last access: 12 March 2021) for assigning the thermal belt to each study site. Despite tropical montane forests having been defined as ecosystems between 23.5° N and 23.5° S above 1000 m elevation (Spracklen and Righelato, 2014), montane belts based on temperature seem to be a better ecological criterion than altitude itself (Körner, 2007; Körner et al., 2011; Körner and Sphen, 2019), because altitude represents an indirect variable and an arbitrary measure of the zonation of mountain forests that can be confounded with several local and regional characteristics such as the inclination and direction of slopes, architecture of plants, drought, or even land use, among others (Körner, 2007).

2.3 Data analysis

The selected references were organized in Microsoft Excel 2016 using mainly crosstabs. From each document, the information was collected according to bibliographic, geographical, methodological, and carbon cycling information as described in Table 1. To analyse co-occurrence of key words from all the studies, VOSviewer 1.6.16 was employed.

When an article covered different characteristics (e.g. different topics, factors, components, variables), each characteristic was accounted for independently. Based on the description and coordinates of study areas for each document, biomes and ecoregions were obtained according to the platform Ecoregions 2017 © Resolve (<https://ecoregions2017.appspot.com/>, last access: 24 February 2021) (Olson et al., 2001; Dinerstein et al., 2017). The percentage of publications of each function was quantified with a respective number of studies (n).

3 Results

3.1 Bibliographic information

The search in Scopus yielded 987 results while in Google Scholar 980 results were found, which were reviewed entirely, thus obtaining a total of 135 documents that coincide with the inclusion–exclusion criteria described in the methodology (Fig. A1 and Table B1). Four clusters were identified in co-occurrence of keywords as is depicted in Fig. 1. The number of publications showed a slightly positive but not significant trend in the 20 years analysed ($p = 0.121$; $R^2 = 0.12$; $n = 135$; Fig. 2a), especially after the end of the first decade of the 2000s. The studies were published in 64 peer-reviewed scientific journals (Table B1). The journals with the highest number of studies were *Journal of Tropical Ecology* ($n = 8$), *Forest Ecology and Management* ($n = 8$), and *Global Change Biology* ($n = 6$).

The main topics on which these investigations were developed included elevational gradients ($n = 82$), carbon balance and estimation ($n = 76$), and soil properties ($n = 51$), while the least investigated topics were related to studies of landscape ecology ($n = 1$), functional diversity ($n = 3$), and landslides and erosion ($n = 2$) (Fig. 2b). Regarding the type of study, empirical investigations focused on the estimation of aboveground biomass were of high research interest ($n = 93$), followed by experimental studies that calculated mostly belowground biomass and leaf-litter decomposition ($n = 19$). In a sharp contrast, syntheses ($n = 3$) and meta-analyses ($n = 2$) were uncommon (Fig. 2c). In line with this, most of the studies were original articles ($n = 127$) while short communications ($n = 1$) and review papers ($n = 2$) were scarce (Fig. 2d).

3.2 Spatial information

The country where more research on carbon cycle was carried out was Ecuador ($n = 47$), followed by Peru ($n = 28$) (Fig. 3a). Tropical and subtropical moist broadleaf forest was the biome where most studies were conducted ($n = 115$), while montane grasslands and shrublands were the second ones with more investigations ($n = 43$) (Fig. 3a). The vast majority of studies were concentrated in three biogeographic realms: Neotropics ($n = 97$), Afrotropics ($n = 13$), and Oceania ($n = 11$) (Fig. 3b). This is mirrored in different ecoregions such as the Eastern Cordillera Real Montane Forest ($n = 39$), Peruvian Yungas ($n = 23$), and Central Andean Wet Puna ($n = 16$) (Fig. 3b). In terms of bioclimatic belts, the lower montane belt was the thermal life zone where the most studies took place ($n = 106$), while the upper montane ($n = 39$) and lower alpine belts ($n = 11$) were the least studied.

Table 1. General description of the components identified in the individual assessment of the article contents.

Component assessed	Variable analysed	Description
Bibliographic information	Year	When was the study published?
	Type of publication	What was the format of the study?
	Study type	What was the nature of the study?
	Journal	In what journal was the study published?
	Disciplinary subject of the study	What was the framework of the study?
Geographical information	Site (country and city)	In what country was the study conducted?
	Altitude	In what altitudinal range was the study conducted?
	Realm	In what realm was the study conducted? ^a
	Biome	In what biome was the study conducted? ^a
	Ecoregion	In what ecoregion was the study conducted? ^a
	Mountain belt	In what mountain belt was the study conducted? ^b
Methodological information	Variables analysed	Which were the complementary variables analysed? Biotic (e.g. diversity, composition), climate (e.g. temperature, humidity, precipitation), soil (e.g. physicochemical properties), functional traits (e.g. foliar traits), forest structure (e.g. diameter at breast height, basal area), topography (slope), landscape (e.g. size, distribution).
	Factors evaluated	Which were the factors tested in the study? (e.g. elevation, time, landscape management, seasonality).
	Methods for carbon assessment	Which methods were employed to estimate carbon stocks and/or fluxes? Stocks (i.e. aboveground, belowground, and soil) and fluxes (i.e. plant decomposition, litterfall, respiration).

Table 1. Continued.

Component assessed	Variable analysed	Description
Carbon cycling information	Aspect analysed	What was the aspect of the carbon cycle analysed in the study? (e.g. aboveground biomass, fine root biomass, root decomposition, soil respiration).
	Component analysed	What was the component of the carbon cycle analysed in the study? Stocks (i.e. aboveground, belowground, and soil) and fluxes (i.e. plant decomposition, litterfall, respiration).
	Production fractions for each compartment	What were the specific fractions estimated of the above- and belowground production in the study? (e.g. NPP wood allocation, NPP to canopy, NPP to coarse roots).
	Production at ecosystem level	What were the estimations of production performed at the ecosystem level? (e.g. carbon use efficiency, ecosystem respiration, net ecosystem production).

^a According to Ecoregions 2017 © Resolve (<https://ecoregions2017.appspot.com/>, last access: 24 February 2021) (Olson et al., 2001; Dinerstein et al., 2017). ^b This was explored using Global Mountain Explorer (<https://rmgsc.cr.usgs.gov/gme/gme.shtml>, last access: 12 March 2021).

3.3 Methodological information

Within the main factors assessed, elevation ($n = 54$) and forest type ($n = 31$) were the most evaluated, while vertical stratification ($n = 3$), fertilization treatment ($n = 3$), and substrate ($n = 1$) were the least studied (Fig. 4a). Complementary variables associated with the analysis of the carbon cycle were forest structure like diameter at breast height, tree height, and basal area ($n = 68$); soil properties including physicochemical variables such as bulk density, C/N ratio, minerals, and nutrients ($n = 68$); and climatic variables which comprise temperature, precipitation, and humidity ($n = 68$). Conversely, biotic variables such as plant diversity, soil macrofauna, and microbial biomass were less assessed ($n = 22$) (Fig. 4b).

Different methods were employed to estimate carbon stocks and/or fluxes; for the aboveground compartment, allometric equations ($n = 47$) were the most common method to assess aboveground biomass as well as the usage of dendrometers for track wood increment ($n = 15$) (Fig. 4c). Remote-sensing-based approaches ($n = 6$), direct collections of plant material ($n = 3$), and vegetation models for above-

ground biomass monitoring ($n = 1$) as well as volume of wood debris for necromass estimations ($n = 5$) were little investigated. In the belowground compartment, soil cores ($n = 20$) and allometric equations ($n = 8$) were the principal methods to calculate root biomass (fine and coarse), followed by ingrowth cores ($n = 7$) and rhizotrons ($n = 5$), which were mainly used to evaluate changes in root biomass over time (Fig. 4d). Other belowground less explored estimations include mass balance method ($n = 2$) and root diameter increment ($n = 1$). For the assessment of soil carbon storage, the bulk of studies analysed soil pits with different horizons ($n = 34$), followed by small soil cores considering the organic layer in the top of the soil only ($n = 22$) and allometric equations ($n = 6$) (Fig. 4e).

In terms of carbon fluxes, the litterbag technique was by far the principal method to estimate plant decomposition ($n = 19$) (Fig. 4f) as well as litter traps for measure litterfall dynamics ($n = 23$) (Fig. 4g). Other methods less frequently employed include soil bags ($n = 2$) and the mass balance method ($n = 2$) for estimating decomposition rates, as well as quadrats from the forest floor ($n = 7$) and the line inter-

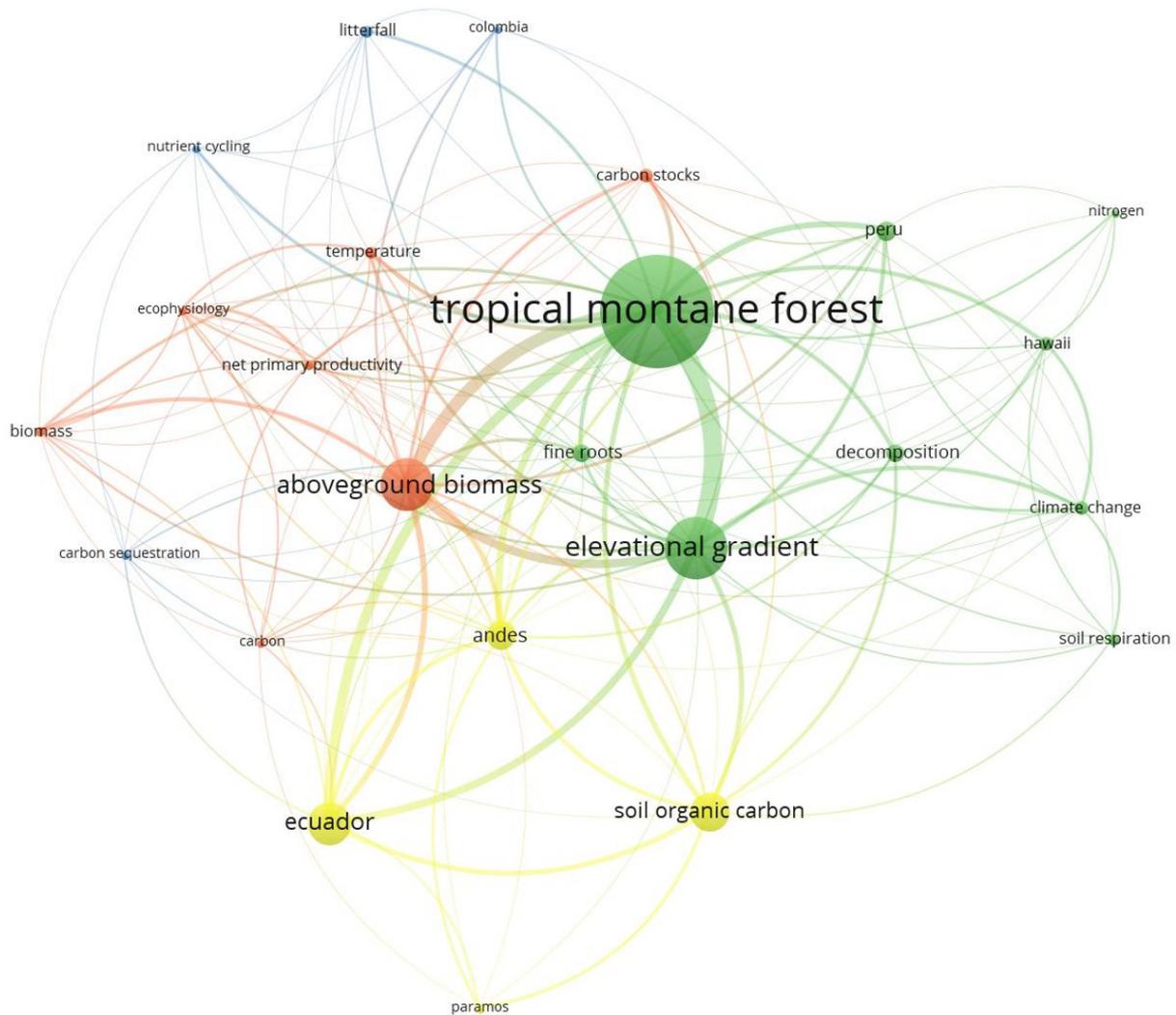


Figure 1. Analysis of the co-occurrence of keywords in publications of the carbon cycle in tropical upland ecosystems. Each colour corresponds to a different cluster. The size of each node shows the frequency of occurrence. The distance between two nodes indicates the number of co-occurrence of the two keywords; that is, the larger the distance between two nodes, the lower the co-occurrences of the two keywords. The co-occurrence in the same publication is represented by the curves between the nodes.

section method ($n = 1$) for quantify litterfall (Fig. 4f and g). Finally, CO_2 fluxes from the soil, root, wood, and leaves were analysed in most of the studies by using an infra-red gas analyser (IRGA) ($n = 15$), but other methods such as substrate-induced respiration ($n = 2$), the inverted-box method ($n = 2$), static chambers ($n = 2$), vegetation models ($n = 1$), and laboratory incubations ($n = 1$) were rarely used (Fig. 4h).

3.4 Carbon cycle information

Estimates of carbon stocks encompassed three-fourths of the total studies, while the remaining fraction focused on fluxes in the carbon cycle (Fig. 5a). Within the studies of carbon stocks, aboveground biomass ($n = 69$) and carbon in soils ($n = 66$) were the most evaluated, while within the fluxes,

both respiration and plant decomposition received less attention, with 26 and 25 studies respectively (Fig. 5b and c). Although litterfall was the most investigated component within the fluxes ($n = 28$), it is still understudied when compared to carbon stock estimates, since major components such as aboveground biomass and soil carbon stocks presented at least twice as many studies as for litterfall (Fig. 5b). When analysing the specific aspects assessed, for both above and belowground stocks, the necromass was little investigated along with measurements across the time (production), while for fluxes, root, wood, and microbial respiration was largely neglected combined with decomposition of roots (Fig. 5c).

Even though production estimations were little investigated for both compartments ($n = 34$), especially belowground ($n = 7$), I found 15 fractions (along with the total pro-

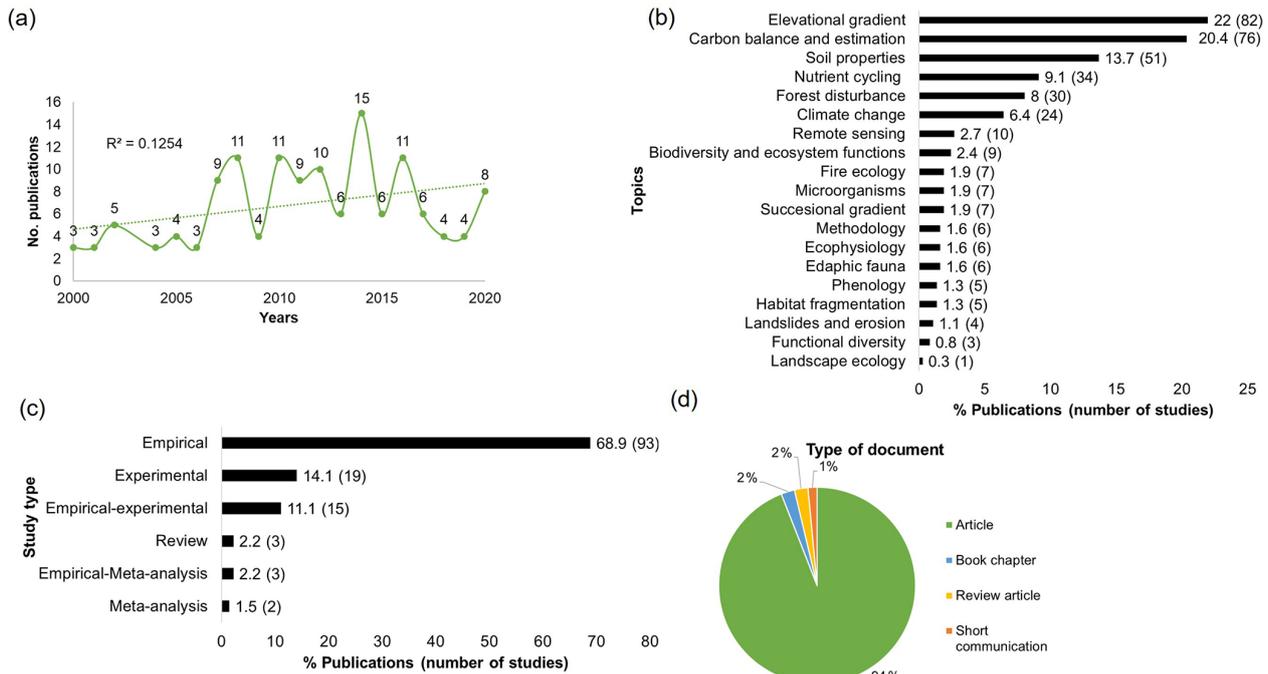


Figure 2. Bibliographic information of carbon cycle in upland tropical ecosystems. (a) Years, (b) topics, (c) type of study, and (d) type of document.

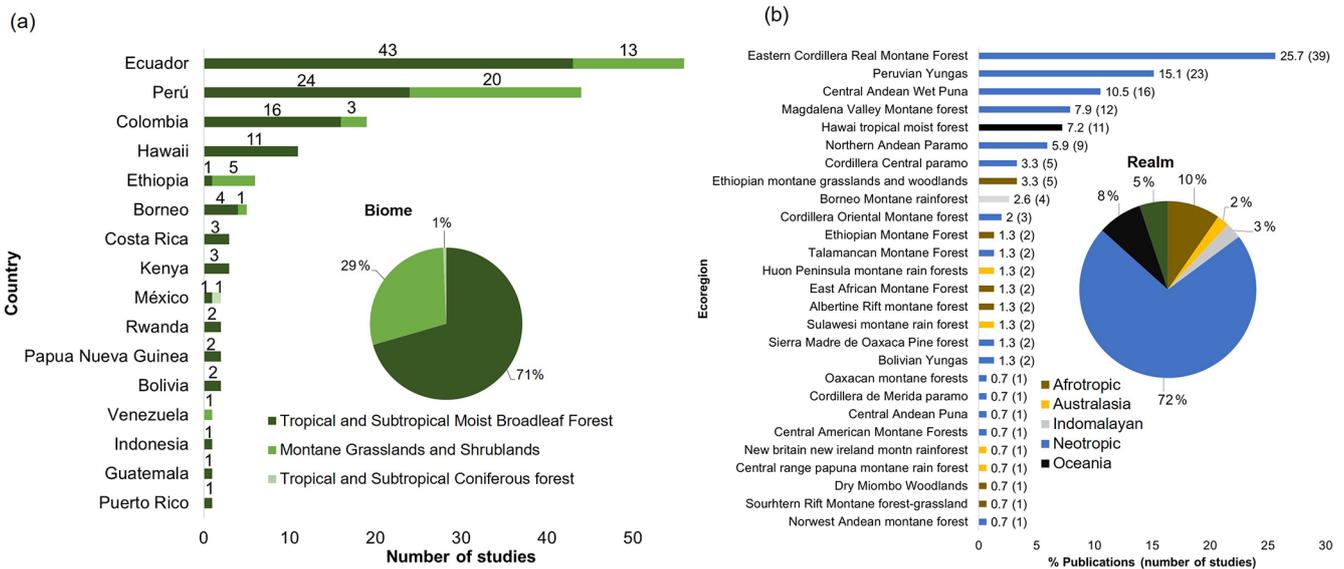


Figure 3. Geographical information from work done on the carbon cycle in tropical upland ecosystems. (a) Country and biome and (b) ecoregions and realms. The colours for each country and ecoregion indicate the evaluated biomes and realms, respectively.

duction) that were quantified for aboveground and six for belowground where stem wood increment and NPP of fine roots concentrated the highest number of studies (Fig. 6a and b). In the same way, calculations at ecosystem level of carbon production were very scarce: net ecosystem production (including both above- and belowground NPP, $n = 6$) and carbon use efficiency ($n = 4$) were more quantified. Other ecosys-

tem estimations that were rarely calculated were root / shoot ratio ($n = 2$), ecosystem respiration ($n = 1$), and NPP aboveground and NPP soil respiration ($n = 1$) (Fig. 6c).

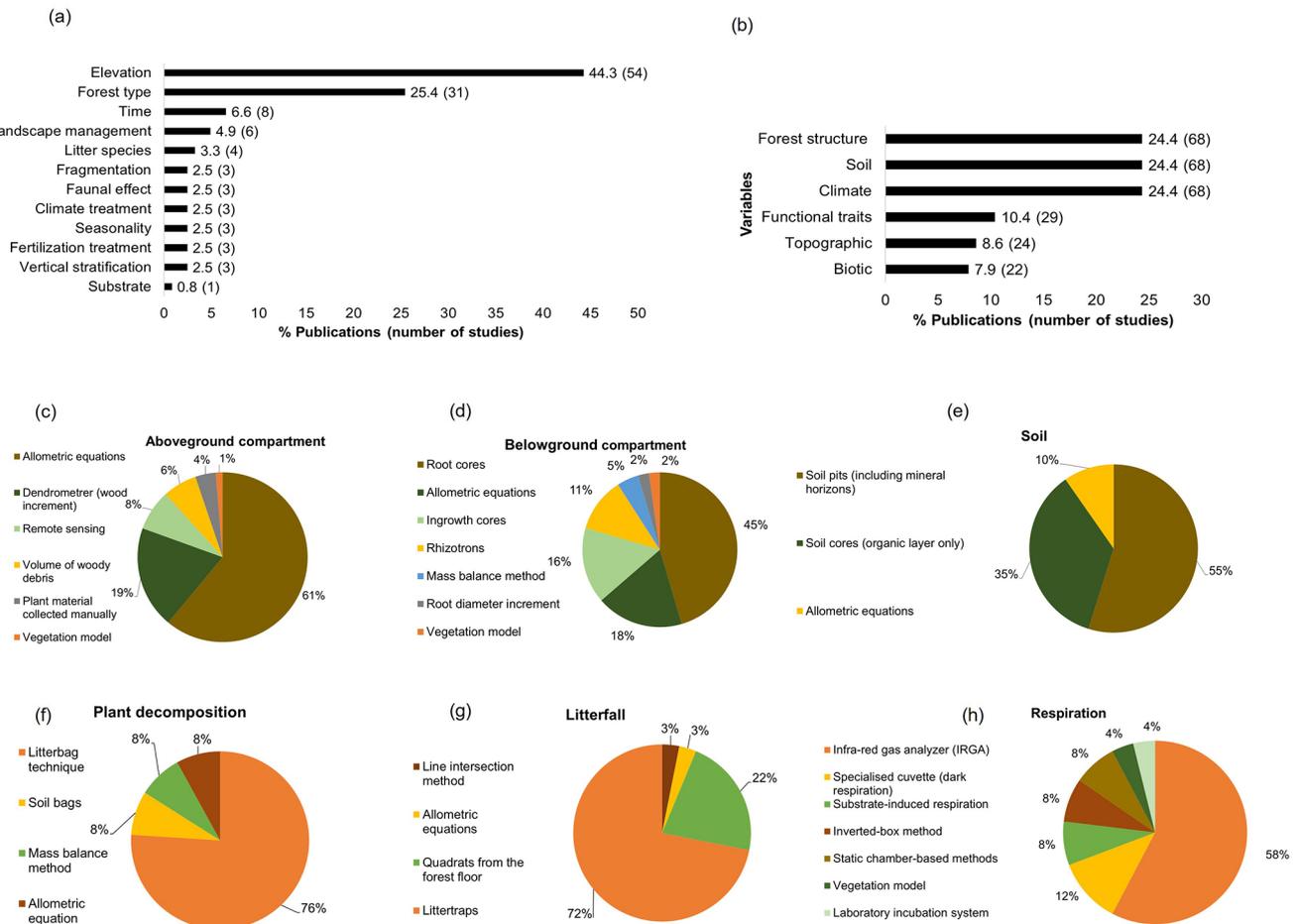


Figure 4. Methodology employed in the studies of the carbon cycle in tropical upland ecosystems. (a) Factors analysed in the studies, (b) complementary variables evaluated in the studies of the carbon cycle, (c) methods employed to quantify carbon in the aboveground compartment, (d) belowground compartment, (e) and soil organic matter. Methods used to estimate fluxes of (f) plant decomposition, (g) litterfall, and (h) respiration.

4 Discussion

4.1 General bibliographic trends

The scientific production of the carbon cycle in the last two decades was more focused on the estimation of carbon stocks rather than on carbon fluxes. Most of the studies focused on elevational transects rather than other disturbance or successional gradients (Fig. 2b). This can be explained because altitudinal gradients have historically been explored as one of the most remarkable ecological gradients, even since the first Humboldt expeditions in the 19th century (Malhi et al., 2010; Rahbek et al., 2019).

In stark contrast, successional gradients have been studied in depth for a relatively short time (Brown and Lugo, 1990). Considering the remarkable expansion of secondary forest due to the rapid formation of human-modified landscapes in tropical mountain regions (Etter and van Wyngaarden, 2000; Rubiano et al., 2017; Hurtado-Martilleti et al.,

2021), the study of successional gradients becomes critical for understanding how carbon sequestration is affected by anthropogenic pressures. Furthermore, these kinds of studies allow us to know how the carbon sequestering potential is changed by the rate of recovery across time, which is very useful for major decision-making that promotes forest recovery in the context of climate change mitigation. In doing so, other topics which are less studied such as habitat fragmentation, landscape ecology, forest disturbance, and fire ecology can complement this research line.

One missing aspect in our understanding of the carbon cycle in upper montane ecosystems is the inclusion of eco-physiology and functional diversity, which are of substantial relevance because they provide a framework to understand the linkages between functional traits, especially the hard ones, that predict biomass gain and storage. This way it is possible to scale from the individual to ecosystem level by studying informative traits related to carbon balance such as maximum rate of photosynthesis, maximum chlorophyll flu-

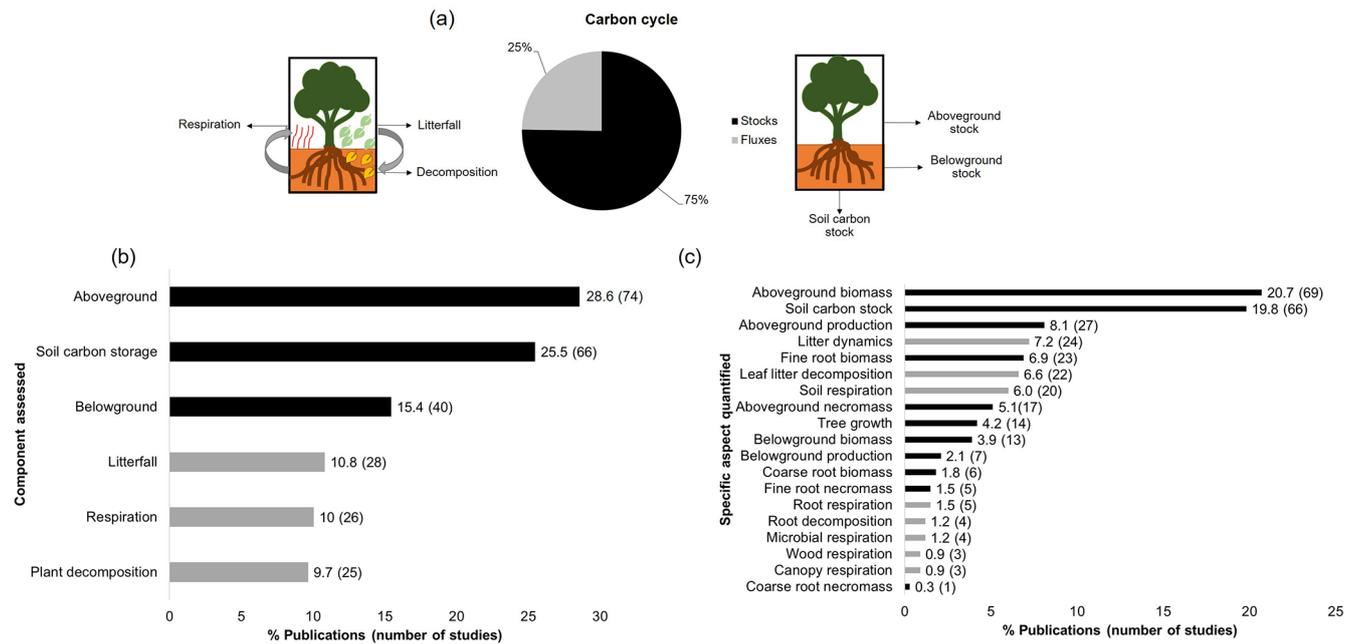


Figure 5. Information on the carbon cycle in tropical upland ecosystems. (a) Percentage of studies that estimate carbon stocks and fluxes, (b) assessed component of the carbon cycle, and (c) specific aspect quantified. The colours represent the evaluated functions (carbon stocks, fluxes).

orescence, and time to maximum photosynthesis (Rawat et al., 2015). Additionally, functional traits can also be critical for understanding the dynamics of fine roots in the carbon storage and nutrient acquisition, but this is still in its infancy (Pierick et al., 2021). Traits such as root diameter, specific root length, root branching intensity, root tissue density, root nitrogen concentration, mycorrhizal association type, carbon translocation to symbionts, and others (Freschet et al., 2021; Pierick et al., 2021) may have important effects on soil carbon and nutrient cycling in upland ecosystems. It is important to note that correlations between above- and belowground traits can be integrated at the whole-plant level (Weigelt et al., 2021), showing the level of coordination between both compartments from which significant functions can emerge like plant growth and carbon accumulation. This combination of traits is even more challenging to scrutinize under the variety of environmental and climatic conditions typical from mountain regions but can contribute to integrating and better understanding the role of both compartments in carbon storage.

There is a pervasive lack of data about how biotic factors influence carbon storage. Biotic interactions play a prominent role in carbon dynamics; for example, feedbacks between plants and their associated soil organisms can influence species growth (Pizano et al., 2019), changes in aboveground arthropods can determine herbivory (Ebeling et al., 2014), and soil macrofauna can drive leaf-litter decomposition (Cárdenas et al., 2017; Four et al., 2019), thus making major contributions to carbon and nutrient cycling in tropical

ecosystems (McNaughton et al., 1989; Metcalfe et al., 2014). The effects of biomass and faunal, fungal, and bacterial diversity on different functions such as decomposition, litterfall, aboveground biomass, and fine root production are little known in upland forests. In this regard, experimental studies allowing inclusion and exclusion of these groups may be useful to know the role of these organisms in each component of the carbon cycle (Powers et al., 2009). On the other side, it would be important to examine how carbon allocation and release influence the taxonomical and functional structuring of these biotic communities to extend our view about the implications of carbon cycling on biodiversity processes (see more discussions later).

4.2 Geographical patterns

The mountain chain of the tropical Andes is one of the most biodiverse areas globally, and its more than 7000 km in length encompasses different countries in the region with many populous cities of South America, including La Paz (Bolivia), Cuzco (Peru), Bogotá (Colombia), Mérida (Venezuela), and Quito (Ecuador) (Seyfried et al., 1998; Duque et al., 2021). In addition, Andean mountain forests represent a significant aboveground carbon sink globally and are considered a future carbon refuge due to the declining of carbon sequestering capacity in lowland old-growth tropical forests (Duque et al., 2021). This tropical region was where more studies were conducted, unlike other continents that do

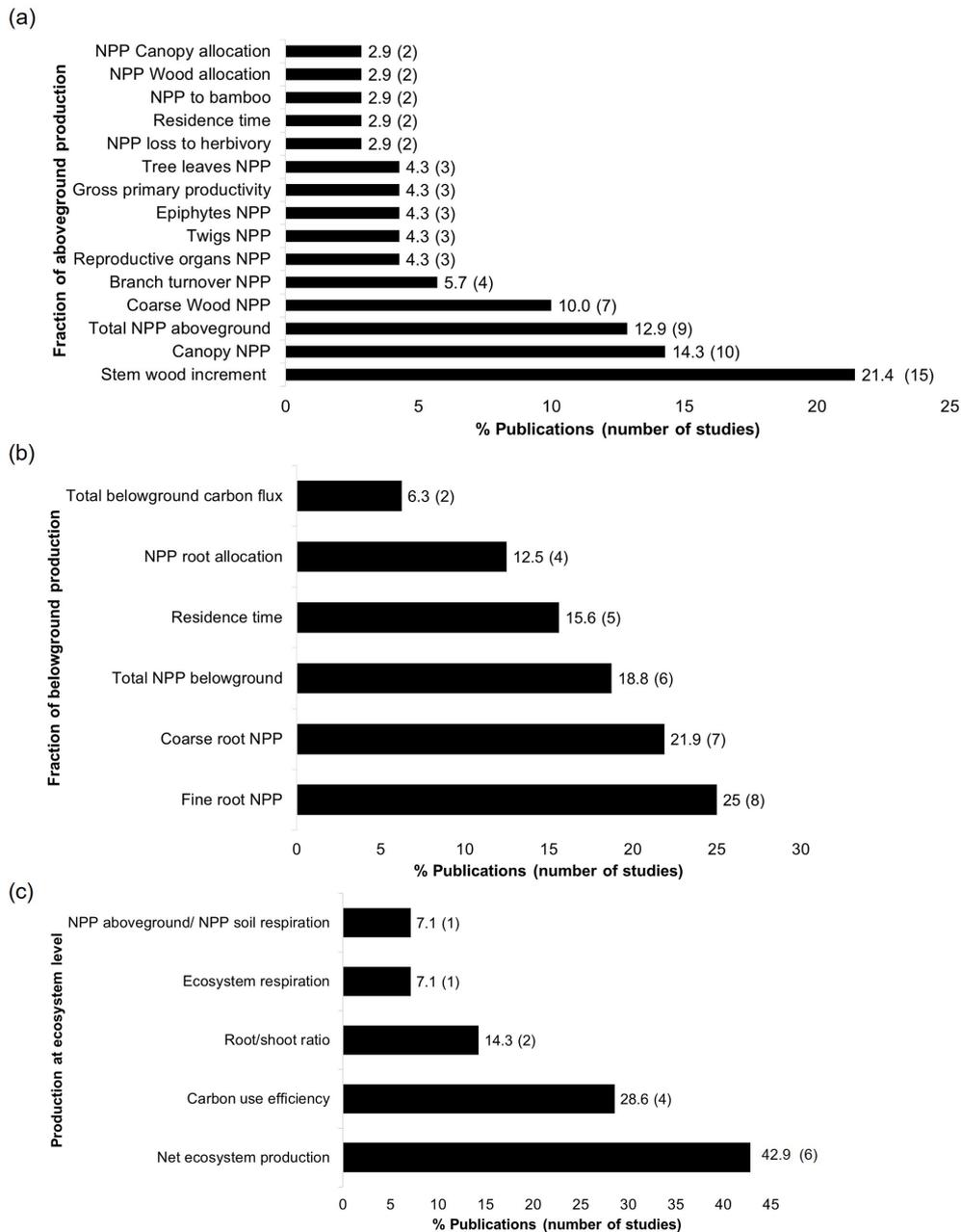


Figure 6. Production fractions for the (a) aboveground compartment, (b) belowground compartment, and (c) ecosystem level.

not have such extensive mountain systems that involve different countries and regions.

The consolidation of biological research stations over important natural areas of mountain forest such as the Zamora-Chinchipe Province in Ecuador (Leuschner et al., 2007; Moser et al., 2011; Pinos et al., 2017) or the biological station of Wayqecha in the Kosñipata Valley in Peru (Girardin et al., 2010; Segnini et al., 2011) probably have facilitated the study of carbon allocation, especially under elevational gradients ranging from Amazon forests to high-mountain forests and even paramo ecosystems. In this review most of the stud-

ies were conducted at both research stations (21 studies at Zamora Chinchipe and 20 studies in Kosñipata Valley), but it is worth highlighting the importance of other research stations in less studied areas in Bolivia, Argentina, and Colombia to understand the carbon dynamics in the Andean highland forests (Duque et al., 2021). Based on the studies conducted mainly in Ecuador and Peru, two different patterns have been identified regarding the allocation of carbon in the altitudinal gradient. In the Ecuadorian model, with the increase in elevation, most of the biomass is stored in the belowground compartment, while, in the aboveground com-

partment (biomass, wood density, and maximum tree height) an inverse relationship with altitude is shown (Moser et al., 2011; Calderón-Loor et al., 2020). On the other hand, in the Peruvian model, the allocation of carbon in the above- and belowground compartments is the same from lowland forests to mountain forests (Girardin et al., 2010).

Arguably, the high rainfall in Ecuador can increase runoff, generating more acidic soils with nitrogen limitations, thus requiring a greater investment in roots to compensate for the low availability of nutrients. Conversely, in Peru, when presenting a greater seasonality of rains, there is a higher rate of nutrient mineralization, a reason that would explain a similar allocation in all its compartments according to de la Cruz-Amo et al. (2020). It is important to note that investigations of these patterns in high Andean forests of Bolivia, Venezuela, Argentina, and Colombia can provide new information to better understand how carbon is allocated along this elevational gradient. In particular, the high Andean forests of Colombia show significant heterogeneity in the three branches of the Andes mountain range (Calbi et al., 2021; Hurtado-Martilieti et al., 2021), so that future studies could focus on investigating the carbon cycle over these forests.

I found very few studies in the realms of Afrotropics, Oceania, Indomalayan, and Australasia (Fig. 3b). For a global perspective of carbon cycling, it is necessary to obtain specific information about carbon dynamics over biomes and ecoregions of Asia and Africa, many of which harbour a significant level of plant endemism and are globally hyper-diverse sites (e.g. East African Highlands, Papua New Guinea). Hence, studies focused on root decomposition and turnover may provide important information to understand the contribution of the rhizosphere to belowground carbon storage and how this could be linked to the aboveground compartment (Rahbek et al., 2019). However, information on carbon flux (e.g. plant respiration and decomposition) and biomass allocation (e.g. belowground biomass) is underexplored in the upland forests of these regions, and more research is needed on the factors that regulate these components.

4.3 Factors analysed in the carbon cycle and methods employed

In line with previous results, the bulk of papers assessed the effect of elevation on forest biomass (Fig. 4). Overall, elevation has received more attention due to its importance as a natural laboratory that provides a broad climate gradient that allows assessment of the potential effects of global warming on key ecological processes such as carbon sequestration (Malhi et al., 2010; Girardin et al., 2014). Nonetheless, important factors including land use history need to be explored considering the increase in anthropogenic activities in the forests that modify the carbon stocks (Ziter et al., 2013) and promote the increase in greenhouse emissions (Brinck et al.,

2017). This is also linked with the effect of the successional stage to biomass and productivity, which is important to consider, taking into account that secondary forests are becoming a common natural coverage across tropical biomes (Melo et al., 2013; Arroyo-Rodríguez et al., 2017), but their effects on carbon accumulation have not been extensively tested besides some works performed in the Neotropics (Fehse et al., 2002; Farley et al., 2004).

One of the topics that has frequently been neglected in upland ecosystems is fire ecology although it is an important factor in the ecology and dynamics of tropical ecosystems (Román-Cuesta et al., 2011). Specifically, in the context of carbon cycling it is important to understand how fire can alter carbon release to the atmosphere through massive above- and belowground biomass losses and how this may influence other ecological properties associated with forest structure and recovery (Asbjornsen et al., 2005). Considering the high amount of carbon stored in the soil at higher elevations (Dieleman et al., 2013), the ongoing warming that mountain regions are coping with (Litton et al., 2020), and the widespread human-induced fires because of grazing and other agricultural activities (Farley et al., 2013), the vulnerability of these ecosystems to other events such as extreme droughts (e.g. ENSO) may have major impacts on ecosystem recovery, carbon balance, and nutrient cycling (Ponette-González et al., 2016), as well as the distribution of the tree-line (Román-Cuesta et al., 2011). In this review few studies assessed the effect of fire on carbon balance ($n = 7$), mainly by using paired-plot research design for burned and unburned sites. Additional research in this regard can provide essential information to encourage adaptive fire management and conservation strategies to prevent greenhouse emissions.

Remote sensing and landscape ecology may be useful to establish spatial relations with carbon stocks (Clerici et al., 2016; Taddese et al., 2020); however the results of this review show that this approach needs to be further explored in the upper montane regions (Fig. 4c). Despite some difficulties in the resolution of images linked to the climatic characteristics of the upland ecosystems such as sparse clouds that cause variations in illumination conditions (Clerici et al., 2016), remote-sensing-based approaches ease the measuring of carbon stocks and sequestration not only for producing spatial interpolations but also for including the temporal dynamics of the analysed ecosystems at plot and landscape levels. Nevertheless, more research is required to improve atmospheric and topographic corrections from images to obtain better estimates of aboveground biomass and other ecosystem properties (Clerici et al., 2016).

On the other hand, it is crucial to assess the effect of individual species on both above- and belowground biomass and productivity, especially in the belowground compartment where the individual contribution of species has rarely been the subject of study. Vertical stratification can complement the analyses of belowground production combined with nutrient cycling and distribution in the different soil layers,

bearing in mind the strong vertical variation and the dramatic changes in organic matter quality, nutrient availability, and hydromorphology along soil profiles (Bahram et al., 2015).

As aforementioned, somewhat critical to consider is the relationship between biomass and biotic variables. In line with this, a topic that remains to be examined is the biodiversity and ecosystem function relationship, especially the diversity–productivity relation. It seems that diversity enhances productivity but on a small scale (Homeier and Leuschner, 2020), and some studies have stressed that the effect of diversity on productivity can increase importantly in long-term experiments (Tilman et al., 2012; Eisenhauer et al., 2013); however, the debate is still open, especially over tropical upland forests. Furthermore, little is known about the top-down regulation of predators in soil food webs that determine soil carbon sequestration and primary productivity and how the soil microbiome interacts with abiotic properties and plant-derived resources (Thakur and Geisen, 2019; Geisen et al., 2019). In addition, it has been posed that changes in species diversity of terrestrial decomposers within and across trophic levels can significantly alter leaf-litter decomposition via trophic cascades (Gessner et al., 2010), but this has been studied mainly on lowland ecosystems (Barnes et al., 2014; Cárdenas et al., 2017). Predator-induced changes on prey stoichiometry represent another important effect on the quality of herbivore biomass added to the litter, which may influence plant-litter decomposition (Hawlena et al., 2012); nonetheless this knowledge is non-existent over upland ecosystems.

Other organisms such as bacteria and fungi are remarkable for their symbiotic relationships that increase plant growth and productivity (Juntahum et al., 2020), yet only a few studies have evaluated the impact of microbial interactions on growth and productivity in upland forests (Urgiles et al., 2009). In particular, some studies have suggested that ectomycorrhizal fungi play a central role in slowing down soil carbon cycling (Koide and Wu, 2003; Averill and Hawkes, 2016); however this pattern (known as the Gadgil effect) has been mainly tested on temperate and boreal forests (Fernandez and Kennedy, 2015), and it is unknown to what extent it occurs on tropical mountain ecosystems where fungal diversity has not yet been well-described (Nottingham et al., 2018). Finally, since mycorrhizal fungal mycelium and their associations with fine roots are considered one of the principal precursors of carbon storage in soil, the estimation of annual litter inputs of roots and their associated mycorrhiza may help understand the belowground dynamics of carbon stocks (Lin et al., 2017).

4.4 Carbon cycling assessment

Most of the studies were concentrated on the estimation of carbon stocks, mainly from aboveground as mentioned earlier (Fig. 5a). Nonetheless, it is urgent to better understand the complete carbon cycle with all the components including above- and belowground compartments and their fluxes

to determine how mountain ecosystems will respond to increasing human impacts (Malhi et al., 2011; Girardin et al., 2013b). In this sense, comprehensive predictions about the influence of biotic and abiotic drivers on shifts in carbon stocks and fluxes should be investigated.

Notably, for carbon stocks it is not well-understood what is the role of aboveground necromass as well as fine root necromass is in the contribution to carbon storage. Other than to provide habitat for other plants, animals, and microbes, very little has been calculated about the potential role of dead trees and roots in nutrient and carbon cycling in upland forests (Chambers et al., 2000; Palace et al., 2007; Gurdak et al., 2014). Considering the harsh conditions of mountain ecosystems that may increase mortality rates of trees such as limitation of nutrient uptake (Soethe et al., 2006), strong winds (Sugden, 1986), high ultraviolet light exposure (Flenley, 1992), increasing slopes (Werner and Homeier, 2015), and high precipitation (Schoor and Matson, 2001), necromass seems to be an important input that should be taken into account when analysing carbon storage and release. Specifically, different sizes of necromass can add more detail to these estimations as suggested by Palace et al. (2007).

There is a lack of studies about phenology and this could be important for analysing rhythms of the forest productivity fractions in a long-term sectional analysis (Girardin et al., 2014a). This information would allow better prediction of the effect of seasonality and key ambient variables such as solar radiation, humidity, and temperature in the dynamics of NPP of mountain ecosystems. Furthermore, belowground production has been less studied, and this may complement the analysis about how carbon is allocated and redistributed in the compartments over time. The analysis of production at the ecosystem level (i.e. net ecosystem production) remains poorly investigated because of the lack of simultaneous estimations of above- and belowground carbon production (Fig. 6c). In this regard, it is important to consider that missing components of NPP such as root exudates, leaf and root herbivory, and volatile organic carbon compounds can underestimate the carbon use efficiency and allocation in these ecosystems (Malhi et al., 2011).

As pointed out in the results, fluxes were less studied in carbon cycling despite their importance in linking the compartments with the atmosphere and pedosphere. Although litter decomposition is a pivotal process that concentrates more than 90 % of the aboveground NPP production (Cebrian, 1999; Gessner et al., 2010), the understanding of the mechanisms that modulate this ecological process remains to be explored. In fact, only a minor group of species have been studied (Table B2). It is possible that there are few studies on this flux due to the time it takes to carry out this type of decomposition experiment. For instance, in low-temperature ecosystems such as tropical mountain rainforest of the Andes, less than 50 % of litter material is decomposed within the first 12 months, which suggest that long periods of time are required to obtain a more representative approximation

of the decomposition process in the upland forests (Marian et al., 2017).

Additionally, there are very few studies that incorporate different native plant species to evaluate these processes, for which experiments involving a greater taxonomical and functional variety of plants are required. Considering that litter quality has been posed as one of the main drivers of leaf-litter decomposition (Ristok et al., 2019; Giweta, 2020; Canessa et al., 2021), the inclusion of several species with a broad trait variation that encompasses contrasting ecological strategies (e.g. conservative vs. acquisitive) would allow researchers to parse out different litter types in a comparative axis that provides a representative estimation of the decomposition in these forests (Esquivel et al., 2020; Canessa et al., 2021). Notwithstanding, it is worth highlighting that litter quality is not the only factor that explains decomposition rates, and many other interactive effects of plants, the climate, and soil biota could regulate litter decomposition (Aerts, 1997; Austin et al., 2014). Home-field advantage (Vivanco and Austin, 2008; Veen et al., 2015), substrate–matrix interaction (Freschet et al., 2012), and phenology–substrate match (Pearse et al., 2014) are useful frameworks for exploring the mechanistic underpinning of litter decomposition under different conditions and interactions, thus providing a comprehensive view of the drivers that control decomposition in upland ecosystems. Moreover, other components of the plants such as stems and roots have rarely been subjected to decomposition experiments. Root decomposition is particularly important since upland forests may allocate more root biomass to compensate for low nutrient availability in soils (Leuschner et al., 2007; Moser et al., 2011). Hence, studies focused on root decomposition and turnover may provide important information to understand the contribution of the rhizosphere to belowground carbon storage and how this could be linked to the aboveground compartment.

Soil respiration as well as root, wood, and microbial respiration are essential fluxes that can explain carbon use efficiency of upland forests. There is a growing body of evidence that soil respiration plays a major role in determining a wide range of ecological features ranging from individual plant functioning to the global concentration of atmospheric CO₂ (Chimner, 2004; Liu et al., 2006; Murcia-Rodríguez and Ochoa-Reyes, 2008; Zimmermann et al., 2010b; Giardina et al., 2014). Indeed, respiration of soil organic carbon is considered one of the principal fluxes of CO₂ on terrestrial ecosystems, and hence understanding the drivers that control soil respiration is paramount for predicting future climate change (Averill and Hawkes, 2016). In addition, respiration is an important link to above- and belowground compartments because it is tied to vegetation structure, plant phenology, photosynthetic activity, and fine root and microbial biomass (Rosero et al., 2020; Adachi et al., 2006). Nevertheless, respiration was one of the less studied processes in this review (Fig. 5b), so the knowledge of this flux constitutes an important gap to fill in further studies over upland forests.

4.5 What do we still need to know?

Carbon cycle is a very complex process that involves several properties and interactions between components and can vary importantly in the tropics. However, much that we know comes from altitudinal gradients in the Ecuadorian and Peruvian Andes, but many other ecoregions of the Andean region, African mountains, and southeastern Asia have limited information of different components that integrate the carbon cycle. Important regions including northern South America, rift valleys, Papua New Guinea, and mountains in the Indonesian islands need to be further explored.

Fine root biomass and production are critical to understanding the interaction between above- and belowground compartments which may better integrate the carbon in the biogeochemical cycle. Nevertheless, in this review few studies assessed both compartments concomitantly (18.51%; $n = 25$). It is also unknown how necromass contributes to carbon cycling and how fluxes such as leaf-litter and root decomposition release carbon to the atmosphere as well as incorporate nutrients to the soil systems. With necromass being one of the largest stocks of the total carbon pool in tropical forests (Palace et al., 2007), this component should constitute a future research avenue in carbon cycling. Currently, there is a vigorous debate about whether decomposition affects the increase in carbon emissions or enhances carbon sequestration via plant growth by releasing limited nutrients like nitrogen in very low-resource environments such as mountain forests (Bothwell et al., 2014). Integration of above- and belowground stocks and fluxes is necessary to analyse the response of upland ecosystems to future climate change. However, I found very few studies that simultaneously related the above- and belowground compartments with the fluxes (11.11%; $n = 15$), which is imperative to fully understanding the carbon cycle.

The incorporation of functional traits related to carbon cycling is a missing link that needs to be parsed out in these ecosystems. Information of functional traits from highland mountains is scarce on basic traits such as wood density, foliar traits, and root traits and, even more so for hard traits associated with plant physiology. Gathering this type of information and establishing the relationships between traits from both compartments may shed light on the characteristics that better predict carbon accumulation over these ecosystems.

Future analysis of the carbon cycle needs to explore ecological gradients such as nutrient resources and successional gradients. In the former, the relations with nutrient cycling would be important to know for how enrichment conditions of several soil elements sustain forest productivity in each compartment but also in their fluxes. This is important considering the extensive agricultural activities performed in mountain ecosystems in which there is an intense use of fertilizers and agrochemicals on the soil, yet very little is known about the impacts on carbon cycling. In the case of successional gradients, despite some studies having suggested that

secondary forests can rapidly recover their species richness promoting carbon storage and sequestration (Rozendaal et al., 2019), these models have been generally performed on lowland ecosystems, and it is not well-established if the same pattern occurs in the upland region.

Admittedly, the influence of biotic interactions on every single component of the carbon cycle is still unexplored. All the organisms associated with plants from microbial communities to large terrestrial predators may have subsequent effects on carbon storage and release, but we have no knowledge about the functional role of many of these species. This is worth mentioning because biotic interactions can maintain several functions and we do not know to what extent the loss of species and interactions may impact litterfall, biomass, production, decomposition, or respiration.

Ultimately, as a conservation strategy to mitigate global warming, the monitoring of upland regions and the establishment of their connectivity to the lowlands have been suggested (Malhi et al., 2010). Therefore, the assessment of every component pointed out in this review may lead us to an in-depth understanding of the biogeochemical cycle, and for this the long-term monitoring is critical, especially in the upland regions where ecosystem dynamics are generally slowed down. Indeed, more complete information on ecological properties of these ecosystems comes from longitudinal studies conducted in permanent plots in many of the aforementioned sites. In line with this, the combination of different research networks at a regional or global scale as well as open data science can contribute to unveiling general patterns of carbon balance as previous studies have demonstrated (e.g. Duque et al., 2021; Powers et al., 2009; Wall et al., 2008).

5 Conclusions

The take-home lessons of this review can be described as follows. (1) There were differential patterns in the number of publications about the carbon cycle over high-mountain tropical forests where biomes and ecoregions from the Neotropics were studied to a greater extent (especially in the Andes). This brings attention to the need to explore many other ecoregions to have a big picture about the carbon cycling in the tropical uplands. (2) Elevational gradient was the topic most studied, but other critical aspects such as successional gradient, landscape management, diversity–productivity relationship, functional-trait-based approach, faunal and microbial effect, trophic cascades, Gadgil effect, and fire ecology require more attention for a comprehensive understanding of the carbon cycle. (3) The estimation of aboveground and soil carbon stocks was the component most quantified, while fluxes such as litterfall, respiration, and litter decomposition comprised a quarter of the studies. (4) The inclusion of several litter species and origins other than leaves (i.e. roots and stems) in decomposition experiments as well as theoretical frameworks including home-field advantage, substrate–matrix interaction, and phenology–substrate match may provide useful information and explanatory mechanisms that help disentangle the complex process of litter decomposition over these ecosystems. (5) Despite respiration being a paramount link that is closely tied to above- and below-ground compartments, this flux was less studied in this review and, therefore, constitutes one important gap to study in future research. (6) Finally, to better understand the carbon cycle, knowledge of its main fluxes is necessary in climate change mitigation plans, which is seen as one of the main threats to ecosystem functioning in the coming years.

Appendix A

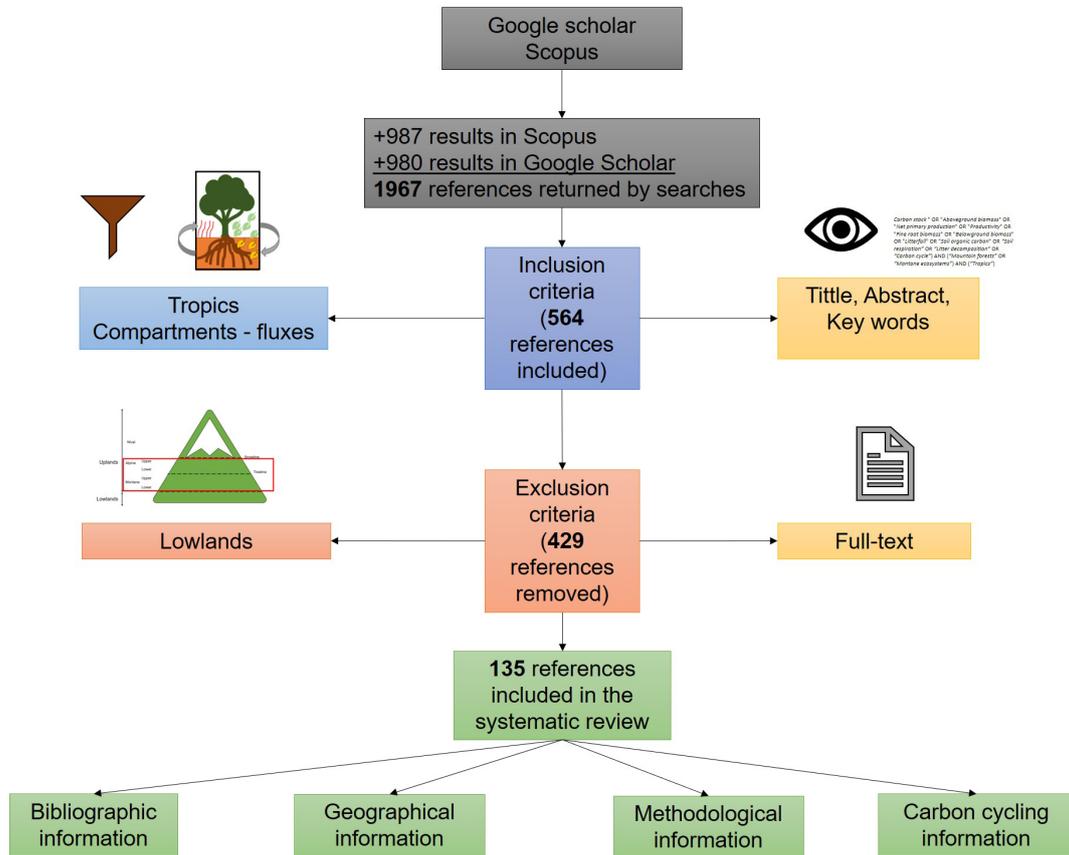


Figure A1. Procedure for selecting the studies in the systematic review of the carbon cycle in tropical upland ecosystems. Grey boxes indicate results from databases. Blue and red boxes represent the inclusion and exclusion criteria, respectively, and orange boxes show what components of the paper analysed those criteria. Green boxes indicate how the selected studies where scrutinized.

Appendix B

Table B1. Continued.

Table B1. List of references selected in the systematic review of the carbon cycle in tropical upland ecosystems.

1	Aiba et al. (2005)	14	Chiti et al. (2018)
2	Aiba et al. (2007)	15	Cizungu et al. (2014)
3	Álvarez-Arteaga et al. (2013)	16	Clark et al. (2016)
4	Alvarez et al. (2012)	17	Clark et al. (2017)
5	Allvarez-Dávila et al. (2017)	18	Clark et al. (2015)
6	Asbjornsen et al. (2005)	19	Clerici et al. (2016)
7	Asrat et al. (2020)	20	Coûteaux et al. (2002)
8	Bothwell et al. (2014)	21	Culmsee et al. (2010)
9	Bruijnzeel et al. (2011)	22	Cuni-Sanchez et al. (2017)
10	Butenschoen et al. (2014)	23	Dalling et al. (2016)
11	Calderón-Loor et al. (2020)	24	de la Cruz-Amo et al. (2020)
12	Chimner (2004)	25	Dielman et al. (2013)
13	Chimner and Karberg (2008)	26	Esquivel et al. (2020)
		27	Fahey et al. (2016)
		28	Farley et al. (2004)
		29	Farley et al. (2013)
		30	Fehse et al. (2002)

Table B1. Continued.

31	Fisher et al. (2013)
32	Fox et al. (2010)
33	Gebeyehu et al. (2019)
34	Giadina et al. (2014)
35	Gibbon et al. (2010)
36	Girardin et al. (2014b)
37	Girardin et al. (2013a)
38	Girardin et al. (2013b)
39	Girardin et al. (2010)
40	Girardin et al. (2014a)
41	González-Jarmillo et al. (2018)
42	Graefe et al. (2008a)
43	Graefe et al. (2008b)
44	Guillozet et al. (2015)
45	Gurdak et al. (2014)
46	Heitkamp et al. (2014)
47	Hobbie (2000)
48	Homeier and Leuschner (2021)
49	Homeier et al. (2021)
50	Homeier et al. (2010)
51	Illig et al. (2008)
52	Kitayama et al. (2000)
53	Kitayama and Aiba (2002)
54	Kübler et al. (2020)
55	Lemenih and Itanna (2004)
56	León et al. (2011)
57	Leuschner et al. (2007)
58	Leuschner et al. (2013)
59	Litton et al. (2020)
60	Litton et al. (2011)
61	Malhi et al. (2017)
62	Marian et al. (2017)
63	Marian et al. (2018)
64	Marthews et al. (2012)
65	Moser et al. (2010)
66	Moser et al. (2011)
67	Moser et al. (2008)
68	Moser et al. (2007)
69	Murcia-Rodríguez and Ochoa-Reyes (2008)
70	Murcia-Rodríguez et al. (2012)
71	Nierop et al. (2007)
72	Nottingham et al. (2012)
73	Nyirambangutse et al. (2017)
74	Oliveras et al. (2014)
75	Peña et al. (2010)
76	Phillips et al. (2019)
77	Phillips et al. (2016)
78	Pinos et al. (2017)
79	Ponette-González et al. (2016)
80	Powers et al. (2009)
81	Quichimbo et al. (2017)
82	Raich et al. (2006)
83	Ramírez-Correa et al. (2007)
84	Ramos Scharrón et al. (2012)
85	Rapp et al. (2012)

Table B1. Continued.

86	Röderstein et al. (2005)
87	Rodríguez-Alarcón et al. (2018)
88	Román-Cuesta et al. (2011)
89	Romero-Torres and Varela-Ramírez (2011)
90	Rosero et al. (2020)
91	Salinas et al. (2011)
92	Schawe et al. (2007)
93	Schuur (2001)
94	Schuur and Matson (2001)
95	Scowcroft et al. (2000)
96	Segnini et al. (2011)
97	Selmants et al. (2014)
98	Selmants et al. (2016)
99	Shirima et al. (2015)
100	Simegn and Soromessa (2015)
101	Soethe et al. (2007)
102	Soethe et al. (2006)
103	Soethe et al. (2008)
104	Spracklen and Righelato (2014)
105	Spracklen and Righelato (2016)
106	Suárez and Medina (2001)
107	Taddese et al. (2020)
108	Tonneijck and Jongmans (2008)
109	Tonneijck et al. (2010)
110	Unger et al. (2012)
111	Varela et al. (2003)
112	Varela et al. (2007)
113	Vázquez et al. (2014)
114	Velescu et al. (2016)
115	Wall et al. (2008)
116	Wanyama et al. (2019)
117	Werner and Homeier (2015)
118	Whitaker et al. (2014)
119	Wilcke et al. (2008)
120	Wilcke et al. (2005)
121	Wilcke et al. (2002)
122	Wittich et al. (2012)
123	Wolf et al. (2011)
124	Yepes et al. (2016)
125	Yepes et al. (2015)
126	Yimer et al. (2006)
127	Zach et al. (2010)
128	Zach et al. (2008)
129	Zapata-Duque et al. (2007)
130	Zimmermann et al. (2010a)
131	Zimmermann et al. (2012)
132	Zimmermann et al. (2010b)
133	Zimmermann et al. (2009a)
134	Zimmermann et al. (2009b)
135	Zúñiga-Escobar et al. (2013)

Table B2. Species studied in litter decomposition experiments conducted in tropical upland ecosystems.

Litter species	Time harvesting	Site	Elevation range (m)	Reference
<i>Acalypha communis</i>	10 times (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 months)	Costa Rica	2150–2950	Esquivel et al. (2020)
<i>Hyeronima oblonga</i>	10 times (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 months)	Costa Rica	2150–2950	Esquivel et al. (2020)
<i>Alchornea latifolia</i>	10 times (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 months)	Costa Rica	2150–2950	Esquivel et al. (2020)
<i>Quercus bumelioides</i>	10 times (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 months)	Costa Rica	2150–2950	Esquivel et al. (2020)
<i>Jarava ichu</i>	10 times (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 months)	Costa Rica	2150–2950	Esquivel et al. (2020)
<i>Minuartia guianensis</i>	10 times (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 months)	Costa Rica	2150–2950	Esquivel et al. (2020)
<i>Magnolia sororum</i>	10 times (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 months)	Costa Rica	2150–2950	Esquivel et al. (2020)
<i>Vochysia allenii</i>	10 times (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 months)	Costa Rica	2150–2950	Esquivel et al. (2020)
<i>Pourouma bicolor</i>	10 times (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 months)	Costa Rica	2150–2950	Esquivel et al. (2020)
<i>Carapa guianensis</i>	10 times (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 months)	Costa Rica	2150–2950	Esquivel et al. (2020)
<i>Polylepis reticulata</i>	7 times (30, 60, 90, 150, 210, 300, 365 months)	Peru	3735–3930	Pinos et al. (2017)
<i>Puteria</i> sp.	5 times (6, 12, 24, 36, 48 months)	Ecuador	1000–3000	Marian et al. (2017)
<i>Cavendishia</i> sp.	5 times (6, 12, 24, 36, 48 months)	Ecuador	1000–3000	Marian et al. (2017)
<i>Mollinedia</i> sp.	5 times (6, 12, 24, 36, 48 months)	Ecuador	1000–3000	Marian et al. (2017)

Table B2. Continued.

Litter species	Time harvesting	Site	Elevation range (m)	Reference
<i>Graffenrieda emarginata</i>	5 times (6, 12, 24, 36, 48 months)	Ecuador	1000–3000	Marian et al. (2017)
	3 times (6, 12, 24 months)	Ecuador	2000	Butenschoen et al. (2014)
	3 times (2, 6, 12 months)	Ecuador	1850–2280	Illig et al. (2008)
<i>Clusia</i> sp.	5 times (6, 12, 24, 36, 48 months)	Ecuador	1000–3000	Marian et al. (2017)
<i>Hediosmum</i> sp.	5 times (6, 12, 24, 36, 48 months)	Ecuador	1000–3000	Marian et al. (2017)
<i>Metrosideros polymorpha</i>	3 times (1, 3, 6 months)	Hawaii	800–1600	Bothwell et al. (2014)
	6 times (1, 6, 12, 18, 24, 30 months)	Hawaii	800–2410	Hobbie et al. (2000)
	8 times (1, 3, 6, 12, 18, 24, 30, 36 months)	Hawaii	410–1780	Scowcroft et al. (2000)
	5 times (1, 3, 6, 9, 15 months)	Hawaii	1270–1370	Schurr (2001)
<i>Clusia alata</i>	7 times (7, 14, 28, 56, 112, 224, 448 d)	Peru	2720–3025	Salinas et al. (2011)
<i>Nectandra longifolia</i>	7 times (7, 14, 28, 56, 112, 224, 448 d)	Peru	2720–3025	Salinas et al. (2011)
<i>Weinmannia bangii</i>	7 times (7, 14, 28, 56, 112, 224, 448 d)	Peru	2720–3025	Salinas et al. (2011)
<i>Weinmannia crassifolia</i>	7 times (7, 14, 28, 56, 112, 224, 448 d)	Peru	2720–3025	Salinas et al. (2011)
<i>Hesperomeles ferruginea</i>	7 times (7, 14, 28, 56, 112, 224, 448 d)	Peru	2720–3025	Salinas et al. (2011)
<i>Myrcia pubescens</i>	3 times (6, 12, 24 months)	Ecuador	2000	Butenschoen et al. (2014)
<i>Dictyocaryum lamarckianum</i>	3 times (6, 12, 24 months)	Ecuador	2000	Butenschoen et al. (2014)
<i>Cavendisha zamorensis</i>	3 times (6, 12, 24 months)	Ecuador	2000	Butenschoen et al. (2014)
<i>Clusia</i> spp.	3 times (6, 12, 24 months)	Ecuador	2000	Butenschoen et al. (2014)
<i>Cecropia andina</i>	3 times (6, 12, 24 months)	Ecuador	2000	Butenschoen et al. (2014)
<i>Purdiaea nutans</i>	3 times (2, 6, 12 months)	Ecuador	1850–2280	Illig et al. (2008)
<i>Parinari excelsa</i>	5 times (31, 61, 92, 189, 316 d)	Rwanda	1854–1934	Cizungu et al. (2014)
<i>Cleistanthus polystachyus</i>	5 times (31, 61, 92, 189, 316 d)	Rwanda	1854–1934	Cizungu et al. (2014)
<i>Carapa grandiflora</i>	5 times (31, 61, 92, 189, 316 d)	Rwanda	1854–1934	Cizungu et al. (2014)
<i>Eucalyptus saligna</i>	5 times (31, 61, 92, 189, 316 d)	Rwanda	1854–1934	Cizungu et al. (2014)
<i>Eucalyptus maidenii</i>	5 times (31, 61, 92, 189, 316 d)	Rwanda	1854–1934	Cizungu et al. (2014)

Code availability. There is no underlying code to be made available.

Data availability. All data used are either presented or referred to in the text and are based on the 135 studies listed in Table B1.

Competing interests. The contact author has declared that there are no competing interests.

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