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Smith, Charlotte; Barlow, Jos; Schwartz, Naomi; Healey, John; Young, Paul; Miranda, Leonardo

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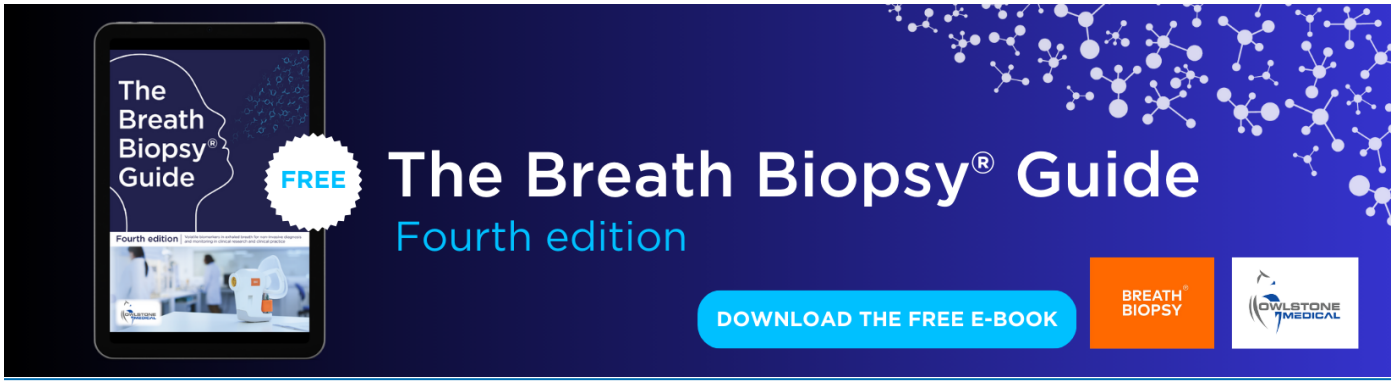

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LETTER

Amazonian secondary forests are greatly reducing fragmentation and edge exposure in old-growth forests

Charlotte C Smith[1,*], **Jos Barlow**[1], **John R Healey**[2], **Leonardo de Sousa Miranda**[1], **Paul J Young**[1,3] and **Naomi B Schwartz**[4]

[1] Lancaster Environment Centre, Lancaster University, Lancaster, United Kingdom
[2] School of Natural Sciences, Bangor University, Bangor, United Kingdom
[3] JBA Risk Management, Broughton, Skipton, United Kingdom
[4] Department of Geography, University of British Columbia, Vancouver, BC, Canada
[*] Author to whom any correspondence should be addressed.

E-mail: Charlottesmith0308@outlook.com

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Supplementary material for this article is available online

Abstract

Restoration of tropical landscapes through the expansion of secondary forests is crucial for climate change mitigation and offers co-benefits for biodiversity. However, the strength of these benefits is influenced by the position of these secondary forests within the landscape. Recovery of both carbon stocks and biodiversity in secondary forests are enhanced by proximity to old-growth forests, and old-growth forests may benefit from secondary forests in return through buffering of edge effects and reduced fragmentation. However, to date there has been no biome-wide assessment of secondary forest location relative to old-growth forests. We mapped Amazonian secondary forests and explored their proximity to old-growth forests of different conditions. We then calculated the extent to which secondary forests buffer old-growth edge forest (<120 m from an edge) and the influence of secondary forests on fragmentation. In 2020, 41.2% of Amazonian secondary forest was directly adjacent to old-growth forest and 94.1% was within a fragment connected to old growth. However, adjacency and connectedness fell to 20.1% and 57.4% respectively when only considering extensive structurally intact old-growth forest. Secondary forests buffered 41.1% of old-growth edge forest and, when acting as corridors, reduced the total number of old-growth fragments by 2 million. Our results reveal the importance of understanding spatial context when examining the potential benefits of increasing secondary forest cover. Improved understanding of the benefits of locating secondary forests next to old-growth forests could support the development of more effective climate change mitigation and restoration strategies.

1. Introduction

Restoration of forests across the globe would make a crucial contribution to achieving global climate change mitigation, with the growth of secondary forests on deforested land in the moist tropics fundamental to success (Cook-Patton *et al* 2020, Strassburg *et al* 2020, Poorter *et al* 2021). Although tropical secondary forests (defined here as forest growing on previously cleared land) store less carbon than old-growth forests, they rapidly remove carbon dioxide from the atmosphere with estimates ranging from 0.89 Mg (Chave *et al* 2020) to 7.6 Mg of carbon per hectare per year (Requena Suarez *et al* 2019). Restoration in tropical regions also offers important co-benefits for the provisioning of other ecosystem services (Matos *et al* 2020), including the preservation of biodiversity (Lennox *et al* 2018), improving water quality (Chavarria *et al* 2021) and regulating water flow (Buytaert *et al* n.d., van Meerveld *et al* 2021).

Understanding where secondary forests exist at present, their temporal dynamics under current policies and practices, and the potential benefits of sustaining or increasing their extent are fundamental to the success of large-scale restoration (Hobbs *et al* 2014). These issues have been addressed in increasing

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detail in recent years, with studies revealing secondary forests extent (Nunes *et al* 2020, Smith *et al* 2021) and carbon offsetting potential (Heinrich *et al* 2021), as well as refining our understanding of secondary forest growth rates under different climate conditions (Poorter *et al* 2016, Elias *et al* 2019) and land-use histories (Jakovac *et al* 2015, Cook-Patton *et al* 2020). Most studies agree that if secondary forests are maintained long-term, they have the potential to store large quantities of carbon and provide habitat for a diverse range of species. With the potential benefits of forest restoration well-established, we must now determine how future restoration efforts can maximise these environmental benefits, especially in terms of forest position (Brancalion *et al* 2019). Understanding the current position of secondary forests at the landscape scale, specifically in relation to old-growth forests (also known as primary forests), could be instrumental in achieving this goal.

1.1. Influence of proximity to old-growth forests on secondary forest recovery

The position of secondary forests within the wider landscape plays a critical role in determining their growth rates and biodiversity (figure 1). Proximity to old-growth forest is advantageous throughout succession, supporting faster forest growth and greater species diversity in the early stages (Jakovac *et al* 2015, Toledo *et al* 2020), as well as providing the diverse seed sources required later (Hawes *et al* 2020). High surrounding forest cover has positive effects on biomass recovery (Martínez-Ramos *et al* 2016, Toledo *et al* 2020), meaning that secondary forests growing in relatively intact forest landscapes are likely to have higher carbon accumulation potential than those in highly deforested landscapes (Chazdon 2003, Bihn *et al* 2010). A key determinant of species richness in secondary forests is whether they are connected to an extensive area of old-growth forest (Mayhew *et al* 2019)—high landscape connectivity accelerates the recovery of seed dispersal mechanisms, particularly for large mammals (Estrada-Villegas *et al* 2023). However, secondary forests are influenced not just by the quantity, but also the quality of surrounding old-growth forest cover. Degraded old-growth forests that have had their composition altered by structural disturbance events (e.g. forest fires, selective logging) are unsuitable as habitat for many forest species (Mestre *et al* 2013, Barlow *et al* 2016, Moura *et al* 2016), while small fragments will not hold many of the large vertebrates that could support the movement of large-seeded plant species into secondary forests (Laurance *et al* 2002, Lees and Peres 2006). Together, these relationships indicate that secondary forests may benefit considerably from proximity to large areas of structurally intact old-growth, whereas development of secondary forests in landscapes with highly fragmented old-growth forest cover or extensive forest disturbance is likely to be limited by lack of seed sources (Matos *et al* 2020).

1.2. Benefits of secondary forest cover for old-growth forest

Secondary forests could provide additional environmental benefits if they help buffer old-growth forests against edge effects (figure 1). Edge effects are a well-documented phenomenon that drastically impact the structure and functioning of a forest (see review by (Laurance *et al* 2002). Field studies have demonstrated that the ecological and physical impacts of edge-effects extend hundreds of metres into a forest (Laurance *et al* 2002), while remote sensing studies have revealed their substantial impact on carbon emissions across large spatial scales (Silva Junior *et al* 2020a). However, these impacts may be mitigated by secondary forest growth adjacent to old-growth forest edges. Secondary forest buffers may significantly reduce edge-related tree mortality (Mesquita *et al* 1999), faunal edge avoidance (Stouffer and Bierregaard 1995) and the intensity of changes in microclimate (Didham and Lawton 1999). However, the benefits of secondary forest buffers are likely to be influenced by the temporal relationship between edge exposure and subsequent regeneration. As much as 90% of edge-induced carbon loss occurs within 5 years of exposure (Silva Junior *et al* 2020a), but it takes time for secondary forests to reach a level of structural development at which they may begin to offer protection from abiotic changes or offer habitat to core-forest species (Laurance *et al* 2002). Nonetheless, landscape-wide increases in the occupancy and abundance of specialist species have been found following regeneration by secondary forests (Rocha *et al* 2018).

Secondary forests may also benefit old-growth forests by increasing fragment connectivity (figure 1, Newmark *et al* 2017). Even small breaks in forest cover can present impassable barriers to some species (Lees and Peres 2009) and fragment isolation has been found to explain more variation in species composition than either forest type or forest age (Mayhew *et al* 2019). By connecting old-growth forest fragments, secondary forests could mitigate isolation effects by supporting the movement of animals between old-growth forest fragments, even if the secondary forest is not necessarily suitable habitat for those species (Newmark *et al* 2017).

As the world's largest remaining expanse of tropical forest, increasing our understanding of the dynamics of regeneration in the Amazon is of critical importance to mitigating climate change. While trends in the location of secondary forests relative to old-growth forests have been demonstrated at regional-scale (Schwartz *et al* 2017a, Smith *et al* 2020, 2021), to date no analyses have directly addressed

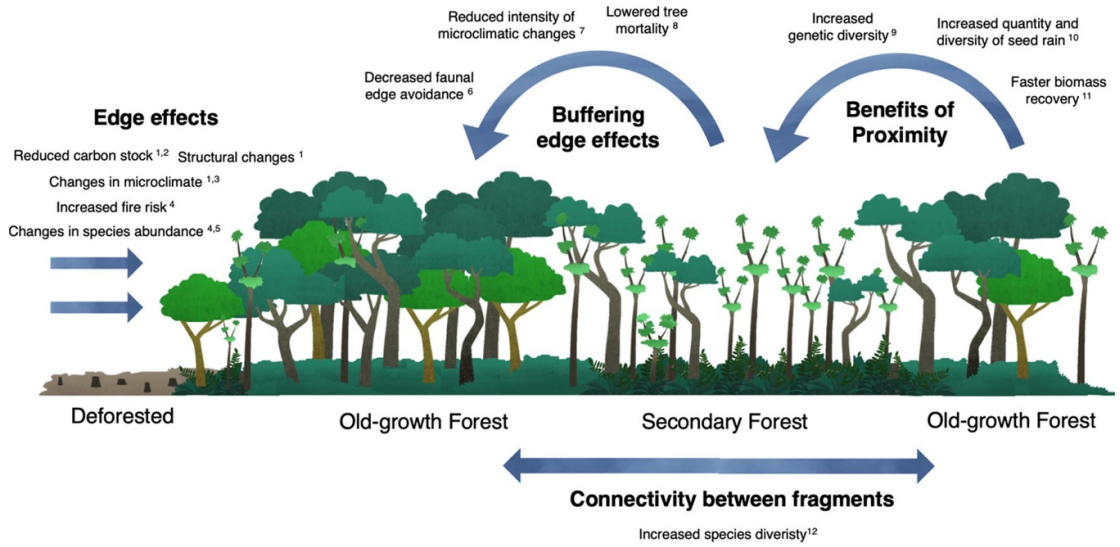

Figure 1. Conceptual diagram of the benefits of secondary forest proximity to old-growth forests. [1] Magnago *et al Functional Ecology* (2017), [2] Silva Junior *et al Science Advances* (2020a), [3] Schwartz *et al Ecological Applications* (2017a), [4] Laurance *et al Conservation Biology* (2002), [5] Pfeifer *et al Nature* (2017), [6] Stouffer & Bierregaard *Ecology* (1995), [7] Didham & Lawton *Biotropica* (1999), [8] Mesquita *et al Biological Conservation* (1999), [9] Senzen *et al Ecology* (2007), [10] Cramer *et al Biological Conservation* (2007), [11] Martínez-Ramos *et al Biotropica* (2016), [12] Mayhew *et al Biotropica* (2019).

this issue at landscape-scale for the entire biome. Here, we conduct the first Amazon-wide assessment of the location of secondary forests in relation to old-growth forests. We explore the positioning of secondary forests within the landscape, asking (1) where are secondary forests located in relation to old-growth forests of different quality? (2) What extent of old-growth forest edges are buffered by secondary forests? And (3) how does secondary forest affect connectivity between old-growth forest fragments? We also investigate the exposure time of old-growth edge forest, as well as the age of secondary forests acting as buffers or connecting fragments, to provide insights into the potential benefits of their proximity. Enhancing our understanding of the spatial and temporal relationships between old-growth edges and secondary forests would help to refine our estimates of edge-related carbon emissions and habitat loss and could aid in the design and prioritisation restoration programmes.

The article is based on chapter 4 of the lead author's doctoral thesis (see Smith 2022).

2. Methods

2.1. Study area

The Amazon biome spans 6.7 million km^2 and is the largest remaining expanse of tropical forest on earth. This study focuses on upland *terra firme* forests (92% of total forest cover), as wetland forests are very different structurally and in their species assemblages. Any pixels classified as wetland by (Hess *et al* 2015) or (Gumbricht *et al* 2017) are excluded from our forest classes.

2.2. Mapping forest cover

We assessed old-growth and secondary forest cover in the Amazon biome in 2020 using the MapBiomas Amazonia Collection 3.0 dataset (MapBiomas 2021), which provides annual 30 m resolution land cover maps from 1985 to 2020. We reduced the MapBiomas schema to two classes (forest and non-forest) and then applied a change detection algorithm to identify which forest pixels were secondary forests. Following the method of (Smith *et al* 2021), any pixel (900 m^2) in the 'forest' class in the first year of the time series (1985) was considered old-growth forest until it transitioned to 'non-forest'. Pixels that transitioned from 'non-forest' to 'forest' were labelled as secondary forest. Secondary forest age was measured as the number of consecutive years a pixel was labelled as secondary forest. Monoculture tree planting is classified as agricultural land use in the original MapBiomas schema and has been excluded from the forest mask used in this study.

As the MapBiomas time series begins in 1985, any secondary forest that began growing before this date is classified as old-growth forest and the maximum age of secondary forests detectable with this method is 34 years. As such, our method may be overestimating old-growth forest extent and underestimating secondary forest extent. However, we believe the impact of this on our results to be small as secondary forests typically have low residence times and high turnover rates (Schwartz *et al* 2020, Smith *et al* 2020), so it is unlikely that much of the pre-1985 secondary forest remains in 2020. Furthermore, as the earliest reliable satellite imagery covering the whole Amazon is from 1985, MapBiomas provides the best available map of historic forest cover.

2.3. Assessing old-growth forest quality

We created three classes of old-growth forest quality based on structural disturbance (see definition from Bullock *et al* 2020) and fragment size: (1) any old-growth forest, (2) structurally-intact old-growth forest, and (3) extensive (>50 km^2), structurally-intact old-growth forest. These classes are intended primarily as a proxy for the availability of faunal seed dispersers and seed rain diversity, based on evidence showing that disturbance or fragmentation in old-growth forests alters seed-dispersal processes (e.g. Cordeiro and Howe 2003, Liu *et al* 2019, Hawes *et al* 2020).

Bullock *et al* (2020) provide a spatially explicit dataset of forest degradation from 1995 to 2017. They defined degradation (distinct from deforestation) as a natural or anthropogenic disturbance that does not change a pixel's land cover category—including fire, windthrow, selective logging, and damage to standing forests during expansion of roads or other development. We resampled the condensed Bullock *et al* (2020) dataset to align with MapBiomas, then identified structurally-intact old-growth forest as those pixels that had not experienced a disturbance event in the last 10 years (relative to 2020). We selected a 10 year threshold as forests recover over time (Rutishauser *et al* 2015, Silva *et al* 2018) and some species may eventually be able to return if further disturbance events are avoided (Mestre *et al* 2013, Mollinari *et al* 2019). While the (Bullock *et al* 2020) dataset is the most recent map of forest degradation currently available for the Amazon, there are two limitations to its use in this study that may mean we are underestimating the extent of structural disturbance. First, it does not extend to our study year (2020) so we cannot account for the three most recent years of structural disturbance. Second, (Bullock *et al* 2020) conducted their analysis for the Amazon EcoRegion as defined by (Olson *et al* 2001), which means a small portion of our study area (the RAISG-defined Amazon biome) is not included.

We measured the size of forest fragments in our 2020 land cover map as the number of contiguous pixels classified as each forest type. Fragment size was calculated using the Accounting tool from the Guidos Toolbox software. We applied 8-way connectivity and identified 'extensive' forest as those fragments over 50 km^2.

2.4. Assessing the proximity of secondary forests to old-growth forests

2.4.1. Distance to nearest old-growth forest

We calculated the distance between secondary forests and their closest old-growth forest fragment using the Guidos Toolbox Distance tool. We applied the tool to a binary map of old-growth forest cover to calculate the Euclidean distance from every secondary forest pixel to the nearest old-growth forest edge. We repeated this analysis for the three classes of old-growth forest cover defined above: any, structurally intact, and extensive structurally intact. We identified secondary forest that was directly adjacent to old growth forest (i.e. a secondary forest pixel occurring next to an old-growth pixel) as those pixels less than one pixel width (30 m) from an old-growth forest edge.

To identify secondary forest that was within a fragment connected to old-growth forest (i.e. via a chain of contiguous secondary forest pixels) we used the Python package pylandstats to label individual forest fragments in a binary map of all forest (i.e. forest = 1, non-forest = 0). We then intersected this with our land cover map to identify which 'all forest' fragments contained both old-growth forest and secondary forest. Secondary forests within a mixed fragment where then marked as being connected to old-growth forest (figure S1). We repeated this analysis for our three old-growth forest classes.

2.4.2. Landscape context

We measured the landscape context of secondary forests as the proportion of the surrounding landscape that was occupied by each old-growth forest class. This analysis was conducted using the Guidos Toolbox Landscape Mosaic tool for a 0.99 km radius, the nearest value to 1 km available for 30 m pixels. For each secondary forest pixel, this tool provided the percentage of the surrounding landscape classified as old-growth forest (to the nearest 10%).

2.5. Identifying and analysing old-growth edge forest

To map old-growth edge forest, we calculated the Euclidean distance from every old-growth pixel to the nearest old-growth forest edge using the Guidos Toolbox Distance tool. Any pixel within 120 m of an edge was marked as edge forest. The most intense edge effects occur within 100 m of an edge (Laurance *et al* 2002); 120 m is the closest distance beyond this that is measurable using 30 m resolution pixels. In cases where a forest fragment is less than 120 m in width, the entire fragment is considered edge forest, as all forest within the fragment would be subject to edge effects. We repeated this analysis for all forest cover (old-growth and secondary forest combined). Any old-growth forest pixels that were no longer in the edge zone after the inclusion of secondary forests were identified as buffered edge forest, while those that remained within the edge zone were considered exposed edge forest. We conducted this analysis for every year in the time series to produce annual maps of edge forest exposure (1986–2020). Old-growth edge forest present in 1985 was excluded from the analysis as we could not determine its age or duration of exposure. Excluding this edge forest also served to remove natural edges from our analysis. This method

is similar to that of Silva Junior *et al* (2020a); differences in results can be attributed to the longer timeseries used in our study. We repeated our analysis for three secondary forest age classes (any, >5 years old, >15 years old).

From our annual maps of forest edges, we calculated the age of old-growth edge forests in 2020 as the total number of years since a pixel was within the edge zone. We randomly sampled the exposed and buffered edge ages and used the Wilcoxon rank sum test to assess whether the samples were drawn from different distributions. We repeated this process 10 000 times and recorded the mean *p*-value. We undertook these analyses with a variety of sample sizes. However, results were insensitive to sample size (table S2) and we report results for $n = 1000$. We also used our annual edge maps to calculate the total number of years each pixel of edge forest was classified as exposed or buffered.

To explore the spatial relationship between old-growth forest cover and edge buffering, we divided the Amazon biome into a regular grid of ~58.9 km^2 cells (65 536 pixels; pixel size: 0.0009 km^2; size determined by computational efficiency). For each grid cell, we calculated the percentage of land cover that was occupied by old-growth forest and the percentage of old-growth forest edges that were buffered by secondary forest. Cells with >99.9% of pixels with a land cover classification of 'other' (i.e. where less than 0.1% of the cell area is capable of being forest) and cells where no forest edges are present were excluded from the grid level analysis. We then applied Spearman's rank-order correlation to a sample of grid cells to test the association between old-growth forest cover and buffering by secondary forests. To enhance the dispersal of selected grid cells across the study area, we used stratified sampling with replacement such that 25% of pixels were situated in each quadrant of the Amazon biome, while within-quadrant selection was random. We repeated this process 10 000 times, recording the mean correlation coefficient. We undertook these analyses with a variety of sample sizes. However, results were insensitive to sample size (table S1) and we report results for $n = 1{,}000$.

2.6. Measuring changes to connectivity

We measure the influence of secondary forests on old-growth forest connectivity by calculating the change in the number of isolated fragments and fragment size. First, we used the Guidos Toolbox Accounting tool to identify individual old-growth forest fragments and determined their area. To measure the effect of secondary forests on fragmentation, we repeated this analysis for three secondary forest age thresholds (all secondary forest, secondary forests >5 years old, and secondary forests >15 years old) and four minimum secondary forest bridge widths (0 m, 60 m, 120 m, 240 m). To identify secondary forest bridges meeting each minimum width threshold, we calculated the Euclidean distance from every secondary forest pixel to the nearest forest edge using the Guidos Toolbox Distance tool. To test for differences in median fragment size resulting from secondary forest bridges of different ages and width, we randomly sampled fragments and used the Kruskall–Wallis *H*-test. We repeated this process 10 000 times and recorded the mean *p*-value. We undertook these analyses with a variety of sample sizes. However, results were insensitive to sample size (tables S3 and S4) and we report results for $n = 1{,}000$.

In this analysis we used age thresholds rather than discrete age classes, as species that are sensitive to secondary forest age will typically have a lower age tolerance limit but not an upper age limit—meaning if a species can move through a 5 year-old secondary forests, it can also make use of any secondary forest that is older than that threshold.

3. Results

3.1. Where are secondary forests located in relation to old-growth forests of different quality?

In 2020, there was 189 451 km^2 of secondary forest in the Amazon biome (figure 2); found in more than 5.3 million spatially discrete patches that ranged in size from 4500 m^2 (the smallest area detectable by our analysis) to 125 km^2. 41.2% of all secondary forest (78 059 km^2) was directly adjacent to an old-growth forest, while 94.1% of secondary forest was within a fragment connected to an old-growth forest fragment (the latter includes the former as directly adjacent secondary forest is also within a connect fragment). These figures were only slightly lower when we restricted our assessment to structurally-intact old-growth forests, with 33.2% of secondary forest directly adjacent and 92.6% within a connected fragment. However, the proximity measures were much lower when we restricted our assessment to extensive, structurally-intact old-growth forest, with only 20.1% of secondary directly adjacent and 57.4% within a connected fragment.

The median (inter-quartile range; IQR) distance of secondary forest pixels to old-growth forest was 30 m (30–120), 60 m (30–210), and 1110 m (30–8010) when we compared to any old-growth forest, structurally-intact old-growth forest, or extensive structurally intact old-growth forest, respectively (figure 2). Across the biome, less than half of all secondary forests were within 1 km of extensive, structurally-intact old-growth forest (48.9%; 92 674 km^2), but the majority were within 1 km for any old-growth forest or structurally-intact old-growth forest (98.6% and 96.8% respectively; figure 2(C)).

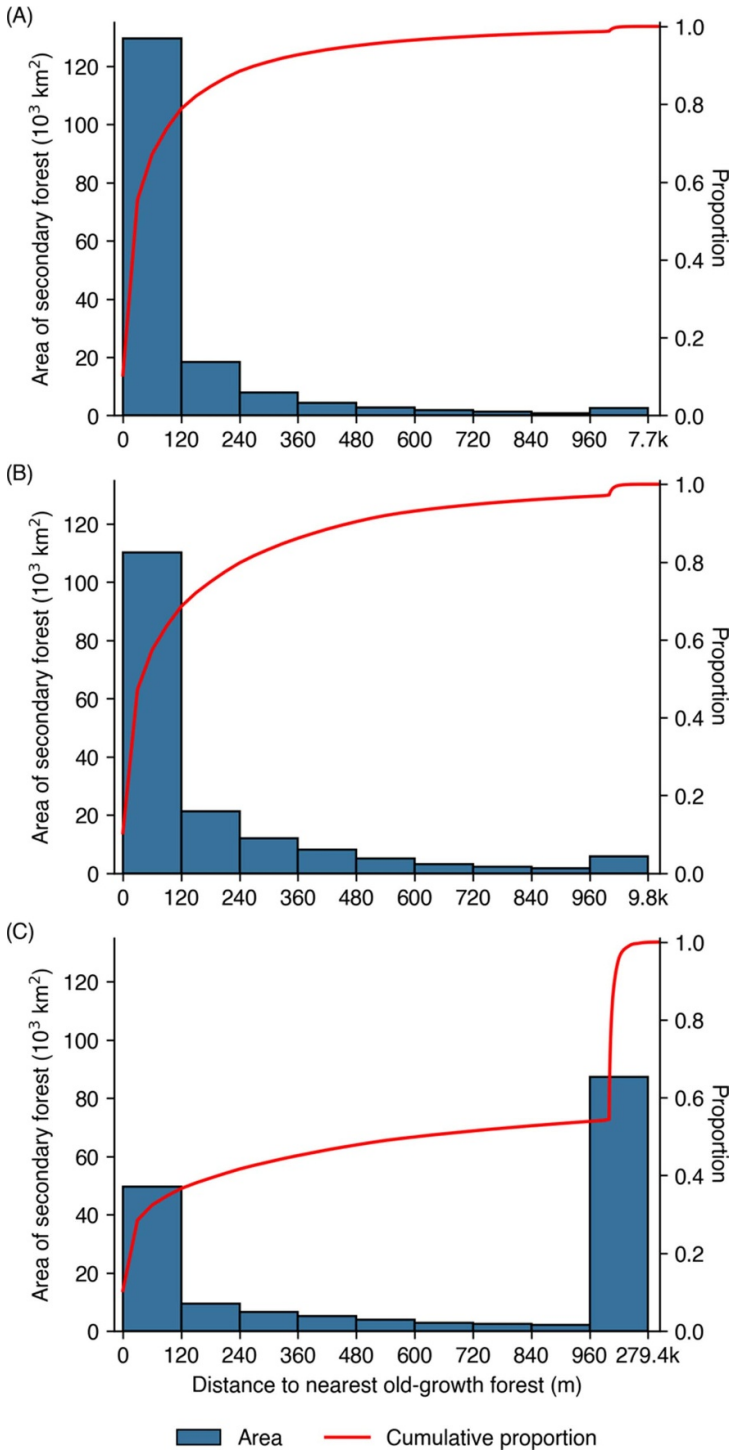

Figure 2. The distance from secondary forests to old-growth forests in the Amazon biome in 2020. The distance from the centre of a secondary forest pixel to the centre of the nearest pixel of (A) any old-growth forest, (B) structurally intact old-growth forest, and (C) extensive (>50 km^2) structurally intact old-growth forest. The cumulative proportion of all secondary forests is indicated by the red line. For each old-growth forests class, the secondary forests pixels more than 960 m from an old-growth forest are grouped into the final bar.

Less than half of secondary forest pixels (45.5%; 85 759 km^2) had >50% old-growth forest in the surrounding landscape (0.99 km radius) and 21.7% (40 907 km^2) had <10% surrounding old-growth forest cover. Restricting the analysis to structurally intact old-growth forest, 33.0% (62 604 km^2) of secondary forests had >50% surrounding old-growth forest cover, while 30.8% (58 271 km^2) had <10% surrounding old-growth forest cover. With further restriction to extensive structurally intact old-growth forest, only 23.0% (43 545 km^2) of secondary forests had >50% surrounding old-growth forest cover, and 63.2% (119 666 km^2) had <10% surrounding old-growth forest cover.

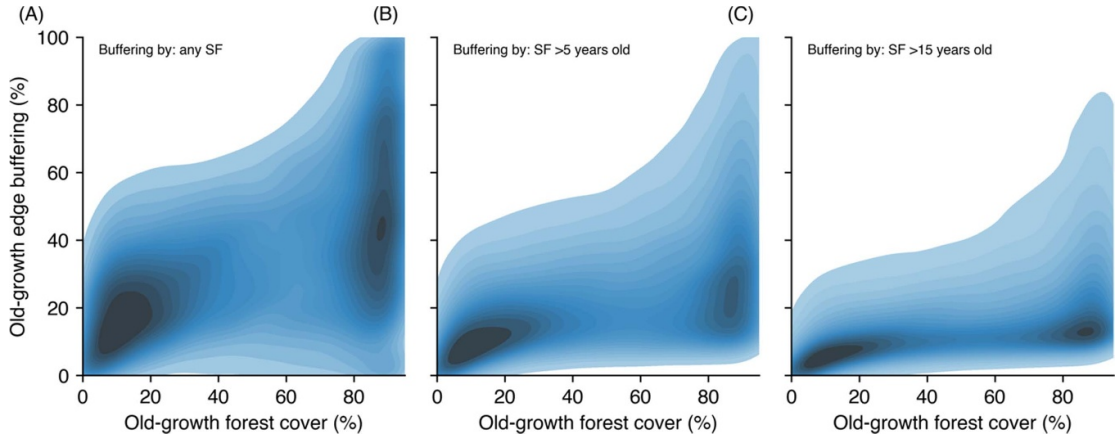

Figure 3. The spatial relationship between old-growth forest cover and old-growth forest edge buffering in the Amazon. The kernel density estimation of old-growth edge forest buffering is shown relative to old-growth forest cover, for buffering by secondary forest of (a) any age, (b) >5 years old, and (c) >15 years old. The percentage of old-growth forest cover and edge buffering were calculated across an ~58.9 km^2 regular grid.

3.2. What extent of old-growth forest edges are buffered by secondary forests?

In 2020, 6.4% (348 903 km^2) of old-growth forest in the Amazon biome was within 120 m of an anthropogenic edge created after 1985. However, 41.1% (143 392 km^2) of this old-growth edge forest was buffered by secondary forests (figure 4(A)). The extent of buffering reduced to 32.2% (112 448 km^2) when restricted to secondary forests more than 5 years old, and 22.9% (79 902 km^2) for secondary forests more than 15 years old.

The proportion of buffered edges varied spatially with old-growth forest cover, with less buffering in areas with low old-growth forest cover ($p \leqslant 0.01$; table). This trend was less pronounced when restricting buffering to secondary forests of $\geqslant$5 years or $\geqslant$15 years old (figure 3). In highly deforested landscapes (<20% forest cover remaining), the mean $\pm$ SD percentage of buffered edge forest was 24.6 $\pm$ 17.5%, while in more intact regions (>80% forest cover remaining) it was 50.4 $\pm$ 27.7%.

The median age (years since a pixel became an edge forest) of edge forest present in 2020 was 19 years (IQR, 8–27; also see (Silva Junior *et al* 2020a), but buffered edge forest was typically older (23 years, 15–29) than exposed edge forest (14 years, 4–24; Wilcoxon rank sum: $W = 9.81$, $p \leqslant 0.01$). One-year old edge forest (i.e. edge created in 2020) was almost double the extent of any other annual age class (1 year-old: 25 769 km^2; older edge classes: 6472–15 114 km$^{2;}$ figure 4(A)). Edges had a median (IQR) exposure time of 6 years (2–14) and over a third (36.9%) of edges had never been buffered by secondary forest (figure 4(C)). Where edges were buffered, on average, this occurred within 3 years (2–5) of creation.

Of the 681 027 km^2 of old-growth forest that became edge forest during our time series (1986–2020), almost half (48.8%) was subsequently deforested by 2020. The median (IQR) time between becoming edge forest and being deforested was 4 years (2–9), with buffered edge forests typically older (median, IQR; 9 years, 6–15) at clearance than exposed edge forest (4 years, 1–8; figure 4(B)).

3.3. How does secondary forest affect connectivity between old-growth forest fragments?

In 2020, there were 3.3 million old-growth forest fragments in the Amazon biome (figure 5), with a median (IQR) fragment size of 4500 m^2 (1800–13 500; (figure 6(A)). Allowing any secondary forest to act as a bridge between old-growth fragments reduced the total to 1.3 million fragments (excluding those comprised of only secondary forest; figure 5), almost doubled the median (IQR) fragment area (8100 m^2, 3600–26 100; the area of old-growth forest within a mixed-forest fragment), and reduced the area of old-growth forest in small fragments (<50 km^2) by 31.2% (77 456 km^2; figures 6(A) and (B)). When applying a minimum age (of either 5 or 15 years) for secondary forest bridges, the effect of secondary forest on fragmentation was reduced but still pronounced (figure 6; Kruskal–Wallis: $H = 104.48$, $p = \leqslant 0.01$). Applying a minimum width to secondary forest bridges created a similar pattern—increasing minimum bridge width resulted in more fragments and smaller median fragment size (figures 6(C) and (D)); Kruskal–Wallis: $H = 25.86$, $p = \leqslant 0.01$).

4. Discussion

We have expanded upon recent research on secondary forest extent (Smith *et al* 2020, 2021, Nunes *et al* 2020,

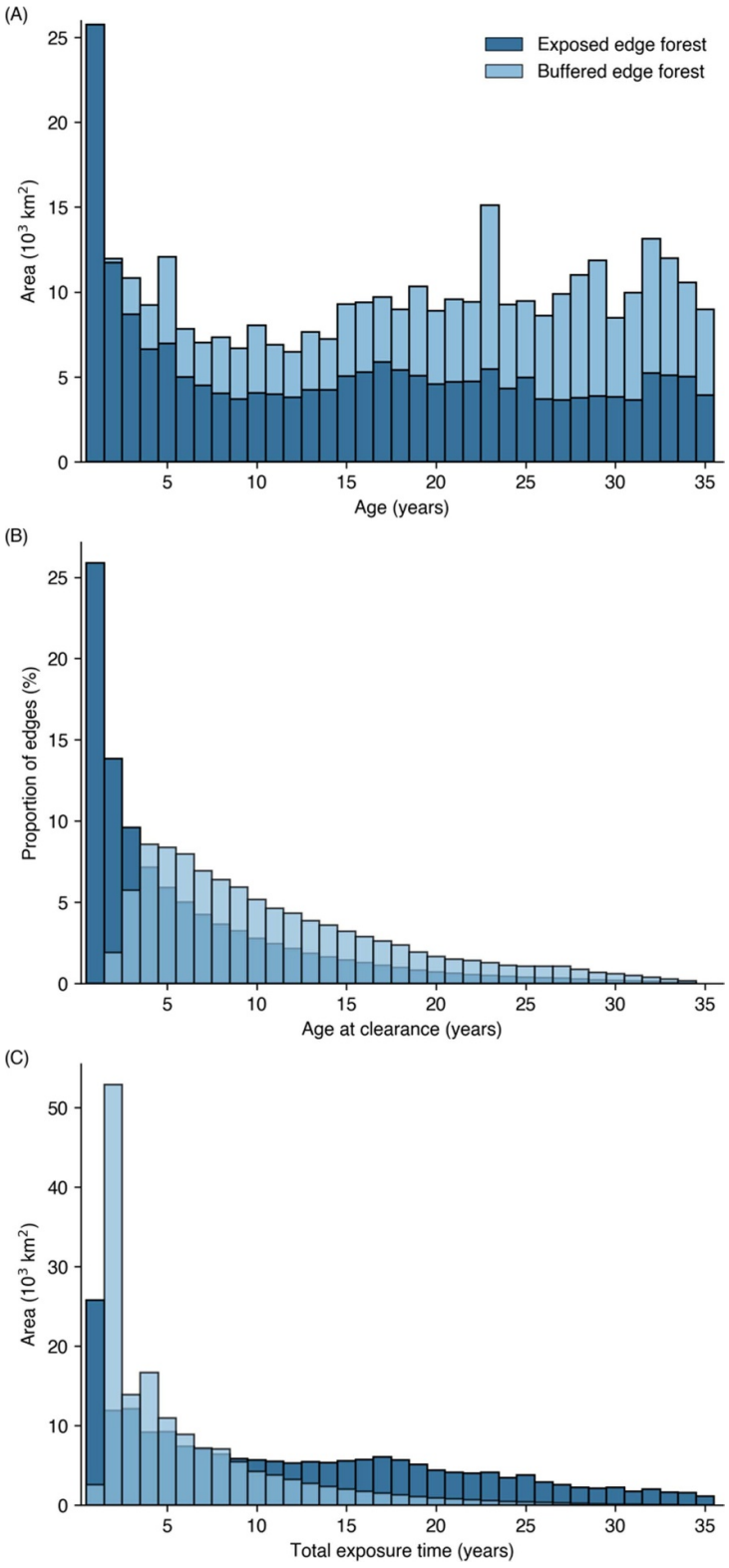

Figure 4. The distribution, age, and exposure time of old-growth forest edges in the Amazon in 2020. (A) The area of old-growth forest within 120 m of anthropogenic edges created between 1986 and 2020, for edge forest adjacent to non-forest landcover (exposed; dark blue) and edge forest buffered by secondary forests (light blue). (B) The proportion of exposed (dark) and buffered (light) edge forest cleared before 2020 that was a given age at clearance. (C) The area of exposed (dark) and buffered (light) edge forest with different durations of exposure (total time in years that a pixel was classified as an exposed edge). Panel (A) presents a stacked bar, while panels (B) and (C) are overlapping.

Silva Junior *et al* 2020b) to conduct the first Amazon-wide assessment of the location of secondary forests in relation to old-growth forests. We find that the co-location of secondary and old-growth forests has the potential to bring strong benefits to both forest types and explore these in detail here.

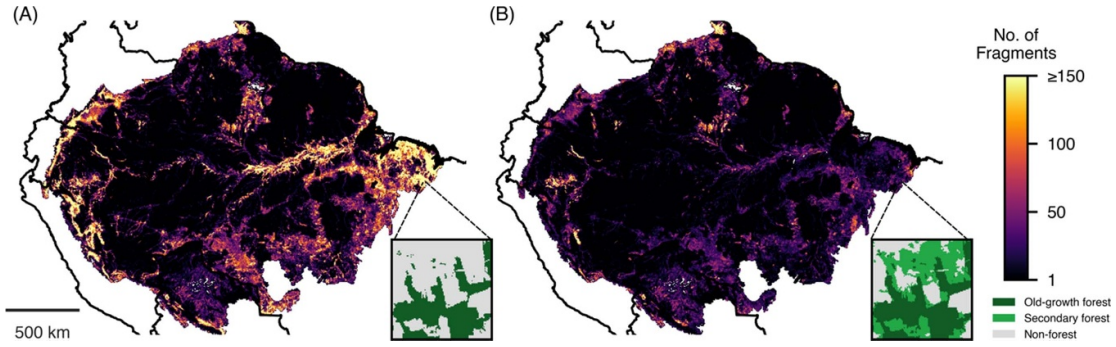

Figure 5. A comparison of old-growth forest fragmentation with and without connectivity by secondary forests across the Amazon biome in 2020. The number of old-growth forest fragments in the Amazon when considering (A) only old-growth forest and (B) when allowing secondary forest to connect fragments. Data is presented across a ∼56.2 km^2 grid. Fragment count was calculated as the number of fragments intersecting each grid cell. The insets show old-growth forest fragments (dark green) in the same landscape with and without connectivity by secondary forests (light green).

4.1. Conserving old-growth forest extent and integrity could support secondary forest succession

In 2020, almost half of Amazonian secondary forest was growing directly adjacent to old-growth forest. This is potentially beneficial news for forest recovery potential, as, all else being equal, restoration success is highly associated with remaining forest cover, (Crouzeilles *et al* 2019) and proximity to old growth supports the recovery of high biomass and high diversity ecosystems (Jakovac *et al* 2015, Mayhew *et al* 2019). These advantages span the successional life of a secondary forest, supporting both the early (Toledo *et al* 2020) and later stages of succession, when they provide the diverse seed sources required to establish resilient secondary forests (Martínez-Ramos *et al* 2016, Hawes *et al* 2020).

Our results show that the proximity metrics are sensitive to changing the extent and intactness of old-growth forest fragments, with secondary forest adjacency declining by as much as 64%. These findings highlight an important research gap, as it is not clear how old-growth condition or extent affect the spill over of benefits to adjacent secondary forests. As old-growth forests become increasingly fragmented (Montibeller *et al* 2020, Fischer *et al* 2021) and structural disturbance continues to spread (Bullock *et al* 2020, Matricardi *et al* 2020), furthering our understanding of these relationships will be integral to designing effective restoration programmes, especially in landscapes where there is little old-growth forest remaining (Crouzeilles *et al* 2019).

4.2. The potential impact of buffering by secondary forests on old-growth forest condition

The proximity of secondary forests to old-growth forests indicates they could have a substantial role in mitigating edge effects: 43.1% of old-growth edge forests were buffered by secondary forests. However, there is scope for improvement, as over half (56.9%) of all old-growth edge forests are not buffered. We found opportunities for increasing edge buffering across the Amazon, with less than half of edge forests buffered in over two-thirds of landscapes (68.8%; figure 3). These opportunities are currently greatest in highly deforested landscapes, suggesting that policy measures aiming to encouraged restoration on private lands would benefit from incentivising buffering. There are opportunities too in high forest cover landscapes, where existing buffers are dominated by young secondary forests (figure 3). Incentivising secondary forest permanence could prevent major loss of carbon stocks from old-growth forest along newly-created edges (Silva Junior *et al* 2020a) and aid in preventing old-growth deforestation (Wang *et al* 2020).

Loss of carbon stocks in exposed edge forest is rapid, with declines of over 20% within 1 year of edge creation (Silva Junior *et al* 2020a). Based on the edge exposure times found in this study and the 15 year carbon stock decay curve reported by (Silva Junior *et al* 2020a), as much as 33.4% of the carbon stock in old-growth edge forests (⩽15 years old) may have already been lost. The role of secondary forests as buffers is also relevant for biodiversity conservation. Changes in microclimate and structure at forest edges (Laurance *et al* 2002) mean that for many species, the amount of forest interior habitat available in landscapes with highly fragmented forest is considerably smaller than the total forest cover. Our findings show that across the biome 6.4% of remaining old-growth forest cover is within 120 m of an edge, meaning core-forest species that avoid edges, (e.g. as reported by Pfeifer *et al* 2017), may have lost as much as 348 903 km^2 of habitat in addition to that already lost to deforestation. However, if the secondary forest that borders almost half of that old-growth forest edge can mitigate microclimatic changes, it could be playing

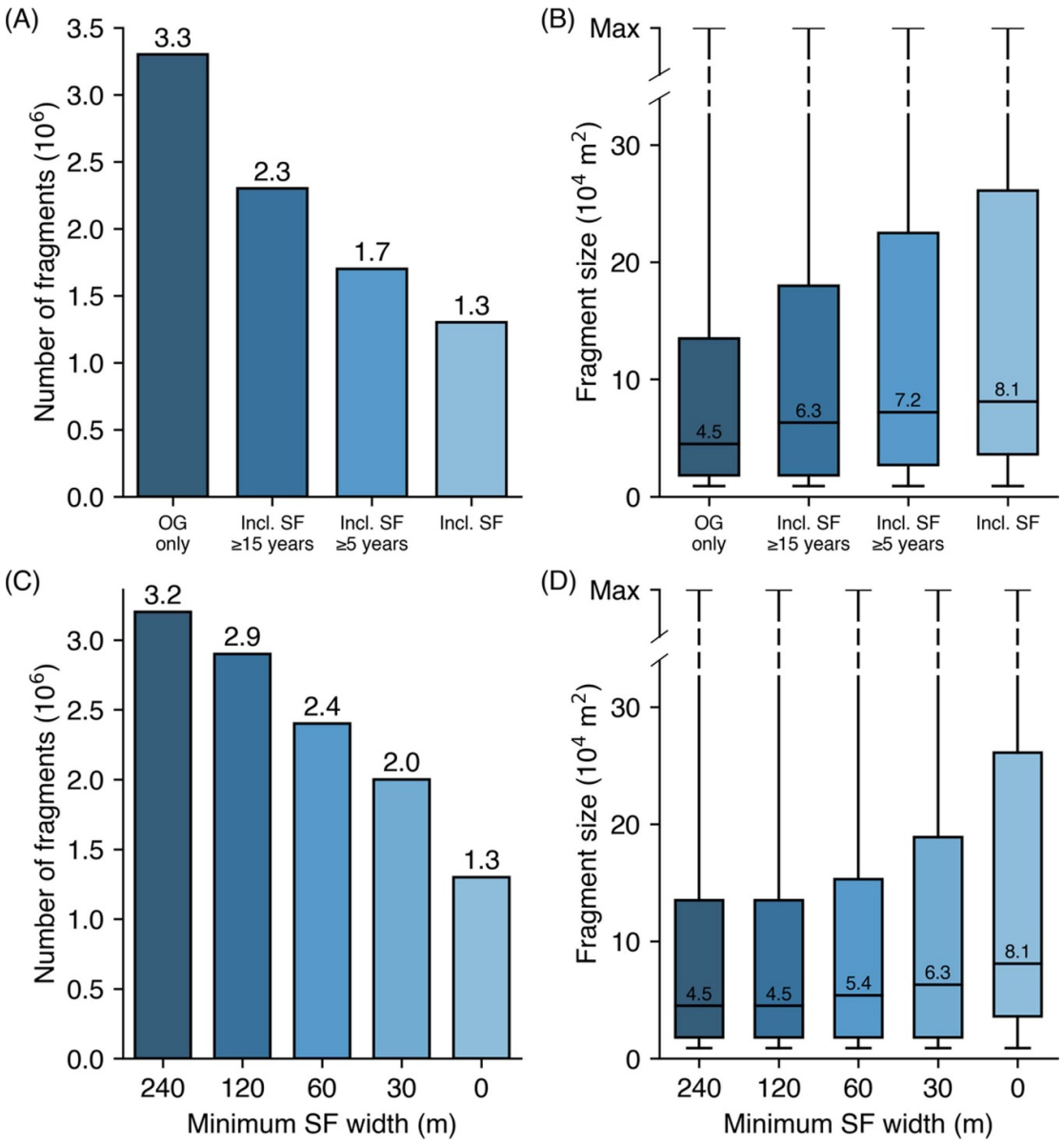

Figure 6. Old-growth forest fragmentation in the Amazon in 2020. The (A), (C) total number and (B), (D) size distribution of old-growth forest fragments for old-growth forest cover only (OG) and when including bridges of secondary forest (SF) of different (A), (B) ages (⩾15 years old, ⩾5 years, and all ages) and (C), (D) minimum widths. For old-growth forest fragments connected by secondary forest bridges, size was measured as the total area of old-growth forest within the mixed-forest fragment. Fragments consisting of only secondary forest were excluded. The total number of fragments and the median area for each group are annotated. The error bars show the full range of fragment sizes, with the maximum fragment size for each group being ∼137 000 km^2.

an important role in increasing habitat availability for forest-specialist species.

The potential benefits of secondary forests as buffers for old-growth forest edges are numerous and include reduced edge-related tree mortality (Mesquita *et al* 1999). However, more research is needed to quantify the scale of these effects, and the underlying mechanisms that drive them. With 63% of old-growth edge forests in 2020 having been buffered at some point during the study period, an important question is whether secondary forest buffering simply prevents further degradation or enables old-growth edge forests to recover some of their ecological integrity. Equally, the increase in height, leaf area, and canopy complexity of secondary forests during succession (Pena-Claros 2003, Feldpausch *et al* 2005) suggests that the age of a secondary forest would strongly influence its effectiveness as a buffer. Given that the proportion of buffered edge forest drops from 41% to 22% when restricting buffers to secondary forests ⩾ 15 years-old, the impacts of an age-related relationship could be substantial. The effectiveness of a secondary forest buffer in mitigating different edge effects in old-growth forest could also vary with its width (Laurance *et al* 2002). However, we lack sufficient data to demonstrate the form of these relationships, or identify thresholds that could be used to guide management. A more comprehensive

understanding of how secondary forests influence old-growth edge forest could help improve estimates of carbon emissions and guide conservation planning for some of the world's most vulnerable species.

4.3. Secondary forests reduce old-growth forest fragmentation

The considerable reduction in old-growth fragment isolation resulting from secondary forest bridges further demonstrates that the value of secondary forests extends far beyond their ∼189 451 km^2 extent. The connectivity provided by secondary forests could enable movement of organisms between old-growth forest fragments, maintaining or restoring genetic diversity and alleviating the extinction risk where fragments that are too small to support long-term viable populations (Metzger *et al* 2009, Newmark *et al* 2017).

However, the value of secondary forests for connectivity remains very uncertain, and future research needs to quantify the parameters of viable secondary forest bridges. For example, species differ in their ability to move through secondary forests of different ages (Powell *et al* 2013, 2015). Our analysis suggests this is a key criterion at the landscape level, as there were an additional ∼400 000 isolated fragments of old-growth forest when we restricted bridges to secondary forests $\geqslant$ 5 years old. The width and length of a secondary forest are also likely to be important in determining its functionality as a bridge. The width of a secondary forest bridge is important as edge effects alter abiotic conditions (Laurance *et al* 2002), especially in very narrow bridges that may suffer from additive edge effects (Porensky and Young 2013). Secondary forest bridge length, although not quantified in the present study, may also be important as some species may have maximum dispersal distances that they will not move beyond (Powell *et al* 2015). Our study evaluates the effect of secondary forests on direct connectivity, however, secondary forests may also provide indirect connectivity by acting as stepping-stones for species that are able to cross gaps (Urban and Keitt 2001, Anon 2007) . As species differ in their ability to cross gaps (Lees and Peres 2009), assessing how secondary forests affect the distance between old-growth forest fragments may also be an important metric to consider when quantifying the value of secondary forests.

4.4. Improving the accuracy of methods used to record spatial and temporal shifts in secondary forests

In satellite imagery, pixels at the intersection of different land cover types may contain a mixture of land covers and are therefore prone to temporal variation in classification. Our method of identifying secondary forests through change detection means that if a mixed pixel was misclassified as undergoing deforestation, it would subsequently be classed as secondary forest by our algorithm if it appeared to 'return' to a forested state in future years. As such, it is possible that some of our adjacent secondary forest pixels may be a misclassification of exposed old-growth edge forest, which would lead to an overestimation of the extent of secondary forest and its role in buffering edge forest. The sharp increase in buffered edge forest in 1998 and 2016 also suggests that some degradation from fire may have been misclassified as deforestation during the 1997–1998 and 2015–2016 El Niño events—which would result in degraded forest being counted as secondary forest (e.g. Lapola *et al* 2023). However, the impact of such misclassifications on our results is likely to be limited as the MapBiomas dataset undergoes a rigorous validation process (MapBiomas 2021). Nonetheless, further work will benefit from improved assessments of land use change at forest edges.

4.5. Implementation challenges

Expanding Amazonian forest restoration is essential for achieving global targets on climate change mitigation and biodiversity conservation (Barlow *et al* 2021). Our assessment of the co-location of secondary and old-growth forests provides important insights for large-scale restoration success.

First, the substantial reductions in the edge buffering and connectivity achieved by secondary forests when restricting our analysis by secondary forest age highlight the importance of considering secondary forest permanence, and moving away from the high-turn-over, low-residency-time regime that currently dominates Amazonia's secondary forests (Schwartz *et al* 2017b, Nunes *et al* 2020, Smith *et al* 2020). Unfortunately, with Amazonian deforestation on the rise in recent years (PRODES 2021, Smith *et al* 2021), even just maintaining the existing extent of secondary forests will be a major challenge.

Second, for secondary forests to play a decisive role in avoiding the rapid loss of carbon stocks in old-growth edge forest (Silva Junior *et al* 2020a), they need to establish soon after deforestation, at the newest edges. Unfortunately, this is likely to be difficult to achieve in practice, as new edges are created in regions of active deforestation where forest loss rather than land abandonment dominates (Smith *et al* 2021). Furthermore, regions of active deforestation are characterised by low levels of governance and inadequate land tenure arrangements (Geist and Lambin 2002); the opposite of what is required for encouraging restoration (Barlow *et al* 2022). However, in regions where deforestation has been stopped, and governance is reinstated, incentivising natural regeneration along edges would be a sensible strategy (Chazdon and Guariguata 2016).

Such incentives would offer win–win for conservation, particularly in highly deforested regions: providing additional habitat and improving the quality of adjacent forest while also preserving carbon stocks. Nonetheless, the development of any future incentive programmes must also carefully consider local socio-economic factors, as these are critical in determining the success or failure of incentivised restoration (Tedesco *et al* 2023).

Third, we show that even existing secondary forests have the potential to make an important difference to landscape connectivity, helping maintain species diversity and viable long-term populations in old-growth fragments (Michalski and Peres 2007) (Mayhew *et al* 2019). This could be particularly advantageous for critically endangered species, such as the Ka'apor capuchin monkey (*Cebus kaapori*), that are able to use secondary forest, (de Oliveira *et al* 2014). Future restoration—such as the state of Pará's Plan for the Amazon Now—could enhance the connectivity benefits of secondary forests in highly disturbed landscape seven further by incorporating large-scale systematic conservation into the planning process. However, it may be that simpler approaches are also effective: for example, studies simulating the ideal approach to restoration have shown that starting close to remaining old-growth fragments is an efficient method of improving functional connectivity (Tambosi *et al* 2014, Miranda *et al* 2021). This is not only a simple rule to apply to any landscape, it also maximises the chances of successful restoration and the potential benefits for buffering old growth forest edges.

4.6. Caveats and future research directions

Although our definition of secondary forest encompasses both restoration initiatives and natural regeneration, currently the vast majority of Amazonian secondary forest is natural regeneration. As an example, one of the most famous assisted regeneration schemes to date—Rede de Sementes do Xingu—has restored only 5000 ha of forest in a decade, a tiny proportion of all secondary vegetation (Barlow *et al* 2021). Nonetheless, the concepts surrounding proximity to old-growth forest can be applied equally to both types of secondary forest.

Our exploration of the spatial relationship between old growth and secondary forests is intended to highlight the potential importance of this rarely considered relationship, acting as an catalyst to encourage., more research that addresses the potential benefits. In particular, field and remote sensing studies are required to understand the importance of old-growth forest size, condition and proximity for secondary forest recovery; how that relationship changes over time, and if old-growth forest are most important at a particular stage. We also highlight the need for more research on the potential benefits of secondary forests as buffers of old growth edges, exploring how this is mediated by secondary forest widths and ages. Advancing these research areas will not only improve our understanding of restoration strategies, it will also help refine estimates of forest carbon stocks and habitat provision for tropical forest biodiversity.

5. Conclusion

Forest restoration is undoubtedly a valuable conservation tool (Chazdon and Guariguata 2016, Chazdon and Brancalion 2019) and in this study we have shown that it may also already be providing substantial benefits to deforested landscapes across the tropics. However, we also highlight (Crouzeilles *et al* 2020) the potential benefits of aligning restoration activities with the location of old-growth forests. Doing so could generate important co-benefits by both increasing recovery rates in regenerating secondary forests and improving conservation of biodiversity and carbon stocks in remaining old-growth forest. Meanwhile, more research is needed to improve our understanding of the mechanisms driving variation in forest recovery and the potential benefits of secondary forest as buffers so that we can refine current estimates of forest carbon stocks and habitat provision.

Data availability statement

No new data were created or analysed in this study.

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ORCID iDs

Charlotte C Smith https://orcid.org/0000-0001-8166-3938
John R Healey https://orcid.org/0000-0002-5398-2293
Leonardo de Sousa Miranda https://orcid.org/0000-0001-6427-8157
Paul J Young https://orcid.org/0000-0002-5608-8887

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