Title: Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests

Running head: Recovery of Amazonian secondary forests

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Abstract

Secondary forests (SFs) regenerating on previously deforested land account for large, expanding areas of tropical forest cover. Given that tropical forests rank among Earth's most important reservoirs of carbon and biodiversity, SFs play an increasingly pivotal role in the carbon cycle and as potential habitat for forest biota. Nevertheless, their capacity to regain the biotic attributes of undisturbed primary forests (UPFs) remains poorly understood. Here, we provide a comprehensive assessment of SF recovery, using extensive tropical biodiversity, biomass and environmental datasets. These data, collected in 59 naturally regenerating SFs and 30 co-located UPFs in the eastern Amazon, cover >1,600 large- and small-stemmed plant, bird, and dung beetles species and a suite of forest structure, landscape context, and topoedaphic predictors. After up to 40 years of regeneration, the SFs we surveyed showed a high degree of biodiversity resilience, recovering, on average among taxa, 88% and 85% mean UPF species richness and composition, respectively. Across the first 20 years of succession, the period for which we have accurate SF age data, biomass recovered at 1.2% yr^{-1}, equivalent to a carbon uptake rate of 2.25 Mg ha^{-1} yr^{-1}, while, on average, species richness and composition recovered at 2.6% and 2.3% yr^{-1}, respectively. For all taxonomic groups, biomass was strongly associated with SF species distributions. However, other variables describing habitat complexity – canopy cover and understory stem density – were equally important occurrence predictors for some taxa. Species responses to biomass revealed a successional transition at approximately 75 Mg ha^{-1}, marking the influx of high-conservation-value forest species. Overall, our results show that naturally regenerating SFs can accumulate substantial amounts of carbon and support many forest species. However, given that the surveyed SFs failed to return to a typical UPF state, SFs are not substitutes for UPFs.

1 | INTRODUCTION

Across the tropics, agricultural development and industrialization have resulted in the clearance of primary forests while urbanization has led to the abandonment of marginal agricultural lands (Guariguata & Ostertag, 2001; Wright & Muller-Landau, 2006a; Melo et al., 2013). As a consequence, forests regenerating in previously deforested areas – commonly called secondary forests (SFs) – have become an increasingly prominent feature of tropical landscapes and now account for a majority of remaining forest cover in many regions; for example, all forests in Puerto Rico and Costa Rica are secondary regrowth (Chazdon, 2003; Lugo & Helmeri, 2004), while SFs account for 63% of remaining cover across Southeast Asia (Mukul et al., 2016). Given that the socio-economic forces driving the expansion of SFs are unlikely to abate in the near future (Barlow et al., 2018), SFs are projected to increase in relative and absolute extent (Chazdon et al., 2009; Aide et al., 2012; Chazdon & Guariguata, 2016). Previously labelled 'forests of the future' (Sánchez-Azofeifa et al., 2005; Wright, 2005; Orihuela-Belmonte et al., 2013), SFs have become important forests of the present.

The widespread replacement of relatively undisturbed primary forest (UPF) by SF has profound implications for global climate change and biodiversity conservation. Tropical forests store – principally in the form of plant biomass (Aguiar et al., 2016) – 37% of the planet's terrestrial carbon (U.S. D.O.E., 2010), and deforestation and forest disturbance releases more carbon into the atmosphere than all other sources except fossil fuel combustion (Bonan, 2008; van der Werf et al., 2009; Basham et al., 2016). Tropical forests are also host to two-thirds of all terrestrial species (Dirzo & Raven, 2003). Humanity's ability to mitigate catastrophic climate change and avert extensive species losses therefore depends, in part, on the capacity of SFs to recover the biomass and biota of UPFs. In addition, given that funding for both carbon and biodiversity conservation is far less than needed to meet globally agreed conservation targets (Basham et al., 2016), an understanding of potential synergies and trade-offs between these differing dimensions of SF regrowth is needed to support the design of successful restoration strategies.

While the structural features of a forest, including plant biomass, often approach values typical of UPF in under a century of secondary succession (Guariguata & Ostertag, 2001; Feldpausch et al., 2005; Fountain-Jones et al., 2015), biotic recovery is subject to much greater uncertainty and debate (Gardner et al., 2006; Wright & Muller-Landau, 2006b; Whitworth et al., 2016). Estimates of the time required for SFs to regain the species richness of UPFs range from decades to centuries (Dunn, 2004; Martin et al., 2013; Whitworth et al., 2016). The rate at which the species composition of SF converges to that of UPF is even less certain, with estimates of recovery timescales ranging anywhere from decades to millennia (Chazdon, 2008; Letcher & Chazdon, 2009). Indeed, some findings suggest that SFs will inevitably contain a severely impoverished subset of primary forest specialists and thus lack the capacity to return to a pre-disturbance state (Kettle, 2012; Moura et al., 2014; Jakovac et al., 2016). And, although large-scale studies have revealed a high degree of congruence between carbon and biodiversity in the tropics (Strassburg et al., 2010; Cavanaugh et al., 2014), evidence regarding the nature of the biomass-biodiversity recovery relationship in regenerating secondary forests is both conflicting and extremely limited (Martin et al., 2013; Gilroy et al., 2014).

Patterns of biotic recovery during secondary succession are not expected to be consistent, and will vary along broad geographical, temperature and soil fertility gradients (Nichols et al., 2007; Wright & Fridley, 2010) and as a consequence of stochastic events, such as chance dispersal (Chazdon, 2008; Norden et al., 2015). Nonetheless, the starkly differing findings that emerge from previous research may also be strongly influenced by a variety of methodological limitations. These limitations can be grouped into four main categories: (i) *Site selection bias*: Most SF analyses focus on sites that have only recently begun regenerating (Dent & Wright, 2009). Extrapolations of recovery prospects from the earliest stages of succession may miss important later-stage shifts in regeneration pathways (Whitworth et al., 2016); (ii) *Taxonomic Sampling bias*: Many studies infer the biodiversity value of SFs by sampling a single taxonomic group (Dunn, 2004). In fact, almost three-quarters of all studies focus solely on woody vege-tation (Quesada et al., 2009). Whether the successional dynamics of large-stemmed plants can serve as a dependable proxy for all SF biodiversity remains relatively unexplored (Hilje & Aide, 2012); (iii) *Insufficient sampling effort*: To accurately determine SF recovery rates requires: (a)

sufficient replication at all stages of regeneration and (b) a sufficient sample of co-located UPFs to provide a meaningful recovery baseline. Few studies apply such sampling effort (Barlow et al., 2007); (iv) *Bifurcation of scale*: The scale at which SF research is conducted is largely split between (a) macroscale meta-analyses spanning thousands of kilometers, which rely on coarse-grained data and, therefore, likely fail to capture important inter- and intra-regional variability (Gardner et al., 2013), and (b) microscale intensive studies of plots covering only a few tens of kilometers (Barlow et al., 2007; Peres et al., 2010).

We seek to address these limitations by undertaking a detailed mesoscale assessment of the recovery of SFs spanning 800 kilometers of the Brazilian Amazon (Figure 1). Brazil contains the largest remaining expanse of tropical forests, with over 60%of the Amazon rainforest lying within its borders (FAO, 2010). As in other tropical regions, agricultural abandonment on deforested land has led to a proliferation of SFs across Brazil: in the last three decades, the area of the Brazilian Amazon occupied by regenerating secondary forests increased fivefold, from less than 3 million ha in 1980 to over 15 million ha in 2012 (Aguiar et al., 2016; Jakovac et al., 2016). Moreover, as part of the Bonn Challenge, Initiative 20 x 20, and its Forest Code law, Brazil is committed to the restoration of an additional 12 million ha of forest by 2030 (Chazdon et al., 2016; Crouzeilles et al., 2016; Mukul et al., 2016). Despite these bold commitments, there is significant uncertainty regarding restoration priorities and the extent to which SFs are able to meet legally mandated minimum ecological standards (de Souza et al., 2016).

We surveyed 59 forests undergoing natural regeneration following agricultural abandonment, along with 30 UPF reference sites, in two deforestation frontier regions of the eastern Amazon. Alongside large-stemmed plants, the most commonly sampled group in SF studies, we sampled scarabaeine dung beetles, birds, and small-stemmed plants. Each of these groups plays a key functional role in secondary succession – through, for example, primary or secondary seed dispersal, control of herbivorous insects, and nutrient cycling – and together provide a powerful and complementary set of bioindicators of ecosystem-wide change (Guariguata et al., 1997; Gardner et al., 2008; Reid et al., 2012; Moura et al., 2013; Audino et al., 2014). To investigate the drivers of succession in regenerating forests, we also measured a suite of forest structure,

current and historical landscape context and topoedaphic environmental variables at the plot and landscape scales. These data provide one of the most comprehensive assessments of tropical SFs to date, and we used them to address five questions: (i) Have our SFs regained the biomass and biodiversity typical of UPFs? (ii) How do species richness and composition recover in regenerating forests relative to biomass? (iii) At what rates do biomass and biodiversity recover towards a UPF state? (iv) Will managing SFs for carbon necessarily protect biodiversity, or are patterns of species occurrence driven by factors other than biomass? (v) Are there thresholds in species' responses to biomass that can help guide forest management decisions?

2 | MATERIALS AND METHODS

2.1 | Study regions and context

Our study focused on the Brazilian municipalities of Paragominas (PGM) and Santarém-Belterra (hereafter Santarém (STM)), located in the eastern Amazonian state of Pará (Figure 1). Although differing in their histories of human colonization (Gardner et al., 2013), both regions have suffered considerable landscape disturbance. PGM sits within Brazil's 'arc of deforestation,' which spans the eastern and south-eastern edges of the Amazon (Figure 1a & b). It has lost almost half of its primary forests, and 57% of its remnant cover is fragmented (INPE, 2013; Supporting information). STM lies in the region of deforestation at the confluence of the Amazon and Tapajós rivers. While less disturbed than PGM, STM has lost almost 30% of its primary forests and half of that which remains is fragmented. Both regions contain large areas of naturally regenerating SF – 21.9% and 14.0% of remaining forest cover in PGM and STM, respectively, was SF at the time of our study (INPE, 2013; Figure 1d & e) – spanning a gradient from newly regenerating sites to those with levels of plant biomass approaching regional UPF averages.

Ranked, respectively, in the 5th and 4th deciles for historic municipality-level deforestation, PGM and STM have levels of landscape disturbance typical of the Brazilian Amazon. They also exhibit many characteristics shared across the eastern Amazon, such as expanding mech-

anized agriculture, extensive cattle pastures, and a highly mobile population of mostly small-holder farmers (Gardner et al., 2013). Consequently, PGM and STM are prime locations for understanding the potential for SF regrowth in deforestation frontier areas across the region.

2.2 | Experimental design

We divided PGM and STM into third- and fourth-order catchments using a 90-m digital elevation model and the Soil and Water Assessment Tool for ArcGIS 9.3. Eighteen study catchments, ranging in size from approximately 3,200 ha to 6,100 ha (mean size ≈ 4,700 ha), were allocated to each region. Within catchments, study plots (10 x 300 m; Figure 1f) were distributed according to a stratified random sampling design. Plots were allocated in proportion to forest and non-forest cover at an approximate density of 1 per 400 ha, were located on *terra firme*, and, to minimize spatial autocorrelation, were separated by at least 1.5 km.

Land-use maps of catchments were made by supervised classification of 30-m spatial resolution Landsat time-series images from 1988 to 2010 and field assessments of forest condition made in 2010-11. We defined primary forests as areas under permanent forest cover. Undisturbed primary forests (UPFs; n = 30, 13 in PGM and 17 in STM; Figure 1) were then defined as primary forests that showed no evidence of disturbance, such as fire scars, charcoal, or logging debris. Secondary forests (SFs) were defined as forests regenerating after complete removal of native vegetation (Corlett, 1994; Putz & Redford, 2010). Where vegetation removal was suspected to have occurred before the start of the time series, we concluded that a site was SF if visual inspection of the earliest Landsat image unambiguously indicated early-stage SF regrowth. This resulted in 59 SF sites (20 in PGM, 39 in STM): 15 between 1 and 10 years old, 19 between 11 and 20 years old, and a further 25 that we could specify only as greater than 20 years old (Figures 1 & S1). Given that high rates of deforestation in both regions only commenced following the construction of the Cuiabá-Santarém Highway and paving of the Belém-Brasília Highway in the 1970s, it is unlikely, however, that any of our SF sites are more than 40 years old, and we use this as the probable upper-bound on regeneration age. These secondary forests span a broad gradient of land-use contexts. They range from 28 m to over 3

km from the nearest primary forest edge (median value = 313 m) and contain between 0 and 96% UPF in a 1-km buffer around the site centroid (median value = 11%).

2.3 | Biodiversity surveys

Biodiversity surveys were conducted in PGM between July 2010 and June 2011 and in STM between June 2010 and May 2011. We sampled dung beetles using pitfall traps, measuring 14 cm in radius and 9 cm in height. Traps were baited with 50 g of dung and half-filled with a killing and preservation solution. Traps were placed at the vertices of a 3 m equilateral triangle at three locations spanning the study plot (0, 150 and 300 m; Figure 1f) and were left for 48 hours before inspection. We sampled birds using two repeat surveys of 15-minute point counts at three locations spanning the study plot (0, 150 and 300 m; Figure 1f). Sampling was undertaken between 15 min before dawn and 09:30. We sampled all live trees, palms, and lianas ≥ 2 cm diameter at breast height (DBH). Large-stemmed plants (DBH ≥ 10 cm) were sampled in a 250×10 m strip of the study plot (Figure 1f). Small-stemmed plants (2 cm $\leq$ DBH < 10 cm) were sampled in five 5×20 m subplots (Figure 1f). All plants were identified to species level by local parabotinists (see Gardner et al. (2013) for further details of the biodiversity sampling procedures).

2.4 | Measurement of environmental variables

At each site, we measured a suite of forest structure, landscape context and topoedaphic variables (Figure S2). We used four variables to describe forest structure: (i) above-ground biomass density within the study plot (hereafter biomass), (ii) plot canopy cover (canopy cover), and the density of (iii) understory stems (understory stem density) and (iv) lianas (liana density) within the study plot. Biomass was estimated using all sampled plants ≥ 2 cm DBH. The biomass of each sampled plant was estimated using allometric equations, and the site value was found by summing over all plants and scaling by plot area (see Berenguer et al. (2014) for further details of the biomass estimation procedure). Canopy cover was estimated by applying gap fraction analysis to hemispherical photos taken systematically at five sampling locations along the plot

(25, 75, 125, 175, 225 m). Understory stem and liana densities were estimated by counting, respectively, all live plants and lianas ≥ 2 cm DBH in the five 5 × 20 m study subplots and scaling by plot area.

We used three variables to describe a site's landscape context: (i) the percentage of primary and secondary forest >10 years old in a 1-km buffer around the study plot centroid (forest cover), (ii) land-use intensity in a 500-m buffer around the study plot centroid (LUI), and (iii) the mean nearest-neighbour distance of all site pixels to a primary or > 10-year-old secondary-forest edge (edge distance). Forest cover and edge distance were calculated using the 2010 land-use map. LUI measures the mean time since deforestation of all pixels in the buffer and was calculated using the land-use maps across the whole time series (Ferraz et al., 2009).

We used three variables to describe a site's topoedaphic state: (i) soil clay content and the mean (ii) slope (slope) and (iii) elevation (elevation) of all pixels in a 100-m buffer around the study plot centroid. Soil clay content was estimated as the mean value from five 30-cm-deep soil profiles spanning the study plot (25, 75, 125, 175, 225 m) using the densimeter method (Camargo et al., 2009). Slope and elevation were derived from a digital elevation model at 90-m spatial resolution from the Shuttle Radar Topographic Mission dataset.

2.5 | Data analyses

To ensure that our evaluations of SF biodiversity recovery were not confounded by non-forest species, we applied a classification filter to our species dataset, leaving 1,348 species characteristic of forests from the 1,638 that we found (Supporting information). We then calculated SF and UPF species richness as the observed richness weighted by species conservation importance, where conservation importance was defined by wood density for plants and geographic range size for birds (Supporting information). Given the lack of information linking dung beetle life-history traits to conservation value, we assumed all dung beetle species had equal conservation importance. We used the Sørensen similarity index to determine the compositional similarity of an SF to UPF (Oksanen et al., 2017). For each SF, we first calculated its pairwise

compositional similarity to each UPF. SF compositional similarity to UPF was then taken to be the mean of the pairwise similarity values.

We took two approaches to measuring SF recovery. First, we defined a continuous successional gradient based on biomass to map biodiversity levels as a function of forest regeneration. We took this approach, rather than measuring succession by age-since-abandonment, because a substantial proportion of our sites (42%) have been regenerating for more than 20 years, longer than the duration of high-resolution Landsat TM satellite imaging. As such, their age cannot be estimated accurately. Moreover, given that SF stands of the same age can display drastically different biotic and abiotic attributes, fallow age can be a poor measure of successional development (van Breugel et al., 2006). Characterizing successional state by forest structure can be a more accurate approach (Arroyo-Mora et al., 2005; Chazdon et al., 2007; Lebrija-Trejos et al., 2011) because it removes the potentially confounding effects of within-plot environmental variation arising from, for example, historical land-use differences and topoedaphic variation (Arroyo-Mora et al., 2005; Kalacska et al., 2005). Second, recognizing the practical importance of understanding the rate of secondary succession, we used the subset of our sites with known regeneration ages to measure how quickly biomass and biodiversity recover during the first 20 years of succession.

We used Bayesian piecewise-linear spline models and Markov Chain Monte Carlo (MCMC; Lunn et al. 2009) simulations to produce smoothed curvilinear relationships between variables (full model details can be found in the Supporting information). In each simulation, we allowed between zero and three change-points for the linear splines and used marginal likelihoods to weight different models. This simulation approach returned model-averaged parameter estimates and 95% credible intervals for those estimates. All models included region-specific intercepts, which account for differences among regions; catchment-level random effects, which account for expected similarities between study plots in the same catchment; and similarity models included a geographic distance parameter that accounts for finer-scale autocorrelation evident for species composition. No residual autocorrelation was evident for any model. This modeling approach allowed us to investigate a variety of ecologically plausible successional

dynamics, such as linear responses, mid-succession peaks, and abrupt, discontinuous changes in recovery pathways as regenerating ecosystems rapidly transition from one state to another.

Next, we used Random Forest (RF) models to investigate the strength of association between SF biodiversity patterns and the forest structure, landscape context, and topoedaphic environmental variables. RF is a machine learning tree ensemble model used for regression and classification analyses (Ellis et al., 2012). It is particularly suited to the analysis of community change along environmental gradients because it allows for nonlinear responses and is insensitive to multi-collinearity, features typical of ecological data (Oppel et al., 2009). We assessed the importance of an environmental variable by its power to predict species occurrences along the gradient, as measured by the cross-validated area under the curve (AUC_{cv}) of relative operating characteristics (Pearce & Ferrier, 2000; Supporting information). Species present in at least three study plots and with a summed $AUC_{cv} > 0.6$ over all environmental variables were classified as well-modeled and were included in the analyses (Barlow et al., 2016). Variable importance was then measured as the variable's mean AUC_{cv} over all well-modeled species. We determined the significance of differences in the mean importance of the environmental variables using linear-mixed models with species-level random effects and used Tukey's range test for multiple pair-wise comparisons of variable mean importance.

Last, we mapped species responses to biomass. We used RF to calculate the relative odds of detecting each well-modeled species along the biomass gradient holding all other environmental variables constant at their mean values (Barlow et al., 2016). We then used Latent Trajectory Analysis (LTA), an extension of linear-mixed models that groups responses into homogeneous classes (Proust-Lima et al., 2017), to determine the main types of biomass response. We fitted models with up to five response classes and selected that with the lowest Bayesian Information Criterion score. For each LTA-defined response class, we assessed if there was evidence of thresholds in its species responses to biomass, using a Bayesian multi-species change-point model and MCMC simulations (full model details can be found in the Supporting information). Focusing on birds – the species group with the most clearly defined taxonomy and with the most reliable data – we then investigated if species responses to biomass revealed by the RF

and LTA analyses were associated with changes in species conservation importance. To do so, we defined a biomass preference measure, a high/low value of which means that a species is disproportionately likely to be observed in high/low biomass forests (Supporting information). For each LTA-defined class, we calculated species mean biomass preference and geographic range size, and used linear models weighted by class size to test for significant relationships.

3 | RESULTS

3.1 | Recovery of and relationship between biomass and biodiversity

The SFs we surveyed did not return to an average UPF state (Figure 2). However, they did recover substantial UPF biodiversity. For large-stemmed plants, small-stemmed plants, birds and dung beetles, respectively, species richness recovered up to 91%, 85%, 100% and 76% of the UPF mean, while compositional similarity to UPF recovered up to 76%, 84%, 104% and 77% of the mean similarity among the UPFs.

Along the biomass gradient, the recovery of species richness and compositional similarity to UPF was similar for each taxonomic group (Figure 2). Where there were differences, the recovery of richness outpaced that of species composition. However, these differences did not reach statistical significance (the 95% credible intervals overlapped; Figure S3) and were limited to earlier stages of succession. For example, with biomass levels at 50 Mg ha^{-1}, birds had recovered 44% of the mean richness (Figure 2c) of UPFs but only 32% of mean UPF species composition (Figure 2f).

The biomass-biodiversity recovery relationship displayed marked differences among taxa. For large-stemmed plants, biomass and biodiversity were tightly coupled at all stages of succession (Figure 2a & e). For the other groups, biomass substantially underestimated biodiversity levels until the later stages of succession. This underestimation was a function of two different recovery trajectories. Biodiversity was low in newly regenerating sites for small-stemmed plants dung beetles (Figure 2b, d, f & h) , increased markedly during early succession, before

reaching a change-point during mid-succession beyond which the rate of recovery slowed considerably. By contrast, birds presented a unique response, with higher biodiversity (especially species richness) in newly regenerating sites and a moderate recovery rate (Figure 2c & g).

Biomass recovered linearly with time across the first 20 years of secondary regeneration (Figure 3). Reaching 24% of the UPF mean, equivalent to 90 Mg ha^{-1}, biomass recovered at 1.2% yr^{-1}. This equals a net carbon uptake of 2.25 Mg ha^{-1} yr^{-1}. Consistent with the biomass-biodiversity relationships (Figure 2), biodiversity levels recovered quicker than biomass in the first 20 years of succession, and there were no significant differences in the recovery of species richness and compositional similarity to UPF (Figure S4). Respectively, large-stemmed plants, small-stemmed plants, birds and dung beetles recovered the species richness of UPF at a mean rate of 1.6%, 2.6%, 2.6% and 3.6% yr^{-1} and recovered the species composition of UPF at a mean rate of 1.4%, 2.1%, 2.4% and 3.4% yr^{-1}.

3.2 | The association between environmental variables and species distributions

Biomass was among the most strongly associated environmental variables with species occurrences in SFs for all taxonomic groups (Figure 4). However, for all groups except large-stemmed plants, other forest structure variables, independent of biomass, were as strongly associated. Canopy cover was among the most important predictors for small-stemmed plants, birds and dung beetles, while liana and understory stem density were important predictors for small-stemmed plants. In our study sites, landscape context and topoedaphic variables were, in general, less important predictors of species occurrences than forest structure variables.

3.3 | Species' associations with biomass

The association of birds and large- and small-stemmed plants species with biomass were remarkably similar, with four response classes that displayed analogous successional change (Figure 5a-c). The small number of species that dominated in low-biomass forests (purple lines)

quickly declined during early succession, reaching a change-point beyond which their odds of occurrence remained low. These species were replaced by two species classes, one (green lines) that had very low odds of occurrence during the early phases of succession before increasing substantially at higher levels of biomass, and another (blue lines) that increased steadily from low-biomass sites until reaching a late-succession deceleration. The main difference between these taxa was in the species class least sensitive to biomass (orange lines). For birds, this species-rich group had relatively high odds of occurrence in low-biomass forests, which likely accounts for the high avifauna richness in these forests (Figure 2c).

This biomass-associated change in bird community structure was reflected in species conservation importance (Figure 6). Specifically, species likely to be found in the highest biomass SFs (i.e. those with the highest biomass preference) had a 48% lower mean geographic range size, and thus substantially higher conservation importance, than those found in low-biomass forests.

Dung beetle associations with biomass were similar to the other taxa, but with important differences (Figure 5d). Biomass-poor forests were dominated by a relatively diverse community of dung beetle species (orange line). This class was exceptionally sensitive to biomass, however, displaying a decrease in odds occurrence of approximately 75% within the first 20 Mg ha^{-1} increase. These dung beetle species were replaced by two classes of species, one (blue line) that, although it increased during early succession, was insensitive to higher biomass, and another (green line) that, as with the other taxa, increased steadily along the gradient before reaching a late-stage deceleration. This precipitous shift in the dung beetle community structure explains the accelerated recovery of dung beetle species composition (Figure 2h).

Taken together, species' biomass associations suggest three successional transitions (Figure 5): an early succession transition at around 50 Mg ha^{-1} of biomass by which point low-biomass-favoring dung beetles and birds reach close to their occurrence minima; a mid-succession transition at around 75 Mg ha^{-1} of biomass, marking the influx of forest vegetation and birds; and a late succession transition at around 150 Mg ha^{-1} of biomass where the increase in the most species-rich class of forest species subsides.

4 | DISCUSSION

Studies of forest regeneration on abandoned agricultural land have produced a wide array of results and much debate. Most pessimistically, due to the impoverished biodiversity of some secondary forests (SFs), several authors have concluded that primary forests are irreplaceable (e.g. Barlow et al., 2007; Gibson et al., 2011; Crouzeilles et al., 2016). In contrast, other researchers have found that regenerating forests can quickly attain the structure, function, and biodiversity of primary forests (e.g. Dunn, 2004; Letcher & Chazdon, 2009; Basham et al., 2016). The results of our study, which represents one of the most comprehensive assessments of SFs to date, lie between these extremes. Among diverse floral and faunal taxonomic groups, in two biogeographically distinct regions of the eastern Amazon, we show that SFs undergoing natural regeneration can regain substantial, encouraging proportions of the biomass and biodiversity – in terms of both species richness and composition – of undisturbed primary forests (UPFs). However, the SFs we surveyed demonstrated limited convergence to an average UPF state, even after up to 40 years of regeneration. Moreover, the decreasing rate of biotic recovery we detected for most taxa (Figure 2) suggests that full recovery – if possible – is likely to take much longer still.

4.1 | Factors influencing biotic recovery

Three principal factors likely explain why our SFs fared better than some others. First, both Paragominas (PGM) and Santarém (STM) retain more than half of their primary forest cover (INPE, 2013), although much of this is in a fragmented state (Figure 1a & b). Regenerating secondary forests in these locations therefore benefit from relatively large pools of forest-adapted source populations. While the extent of deforestation in PGM and STM is near-average across the Brazilian Amazon, more consolidated zones along the region's eastern and south-eastern edge have lost the vast majority of their primary forests and those remaining are severely degraded by edge, area and isolation effects (Ewers & Didham, 2006; Figure 1a & b). Unsurprisingly, land-use contexts characterized by diffuse and discontinuous patches of remnant forest present much bleaker accounts of the conservation value of SFs than PGM and STM (Chazdon,

2003; Bihn et al., 2010).

Second, large-scale industrialized agriculture was absent from PGM and STM until the late 1990s (Steward, 2007; Gardner et al., 2013), after the majority of our SFs had begun regenerating. At the turn of the century, by contrast, mechanized agriculture already spanned approximately 40,000 km^2 across the agro-industrial frontier region of Mato Grosso, directly south of Pará (VanWey et al., 2013). Thus, unlike SFs regenerating at the same time in some other regions of the Brazilian Amazon, many of those that we assessed were not subjected to the most intensive agricultural practices that are known to reduce forest recovery rates (Nepstad et al., 1991).

Third, the duration of less-intensive, pre-abandonment agriculture was limited in PGM and STM. Consistent with other deforested regions of the Brazilian Amazon, extensive forest clearance began in our study municipalities only in the 1970s, driven by infrastructure investments and government policies promoting cattle ranching (DeFries et al., 2013). Consequently, the youngest SF sites we studied (in 2010) could have been under modern agricultural management for a maximum of 40 years, and most were likely to have been in use for much shorter durations. In other tropical regions, forest disturbance resulting from agricultural expansion has a substantially longer history; for instance, deforestation of Brazil's Atlantic Forest can be traced back five centuries, with large-scale sugar cane plantations dating to the 17th century (Joly et al., 2014). Landscape land-use composition and land-use history have often been found to be among the most important determinants of SF regrowth (e.g. Guariguata & Ostertag, 2001; Chazdon, 2008; Martínez-Ramos et al., 2016; but see Letcher & Chazdon, 2009). That our study regions offer relatively propitious recovery conditions on both these critical fronts probably explains, in large part, why our results are more positive than some previous findings.

The comparable recovery of species richness and composition in our SF sites (Figures 2, S3 & S4) also contrasts with some studies that report vastly different recovery timescales for these distinct dimensions of succession (e.g. Aide et al., 2000; Barlow et al., 2007; Dent et al., 2013). We suspect two reasons may account for this. First, as noted, many of our SF study sites are

located relatively close to primary forest (median distance from SF to nearest primary forest equals 313 m). Coupled with the considerable vagility of many tropical species (Kettle, 2012), this means the probability of colonization by forest species is likely to be high. This notion is supported by the fact that, for all taxa, species favouring high-biomass conditions were encountered in early- to mid-successional sites (Figure 5). Where regenerating forests exist beyond the dispersal capacity of forest biota, recovery may be limited to species not characteristic of UPF (e.g. Dalling et al., 1998; Reid et al., 2015; Martínez-Ramos et al., 2016). Second, we found that species richness recovered more quickly than composition – though not significantly so – only during early succession (Figure 2, S3 & S4). Had we been limited to young SF, as most previous studies have (Dent & Wright, 2009; Whitworth et al., 2016), and then extrapolated recovery times from such a limited sample, we may have erroneously concluded that compositional recovery was bound to lag far behind that of species richness. Only by sampling SFs along a substantial proportion of the successional gradient were we able to uncover the non-linear changes that led to analogous recovery rates.

4.2 | The relationship between biodiversity and carbon

International initiatives, such as the Convention on Biological Diversity (CBD, 2014) and Reducing Emissions from Deforestation and Forest Degradation (REDD+; Gardner et al., 2011), seek to protect and enhance tropical biodiversity and carbon stocks, in part through forest regeneration (Martin et al., 2013; Gilroy et al., 2014). Given the reality of limited funding (Stern, 2007; Waldron et al., 2013), the success of such initiatives depends on identifying if and where carbon and biodiversity can be conserved simultaneously (Gilroy et al., 2014; Basham et al., 2016; Ferreira et al., 2018). In revealing: (i) that biomass is the most important predictor of SF biodiversity (Figure 4); and (ii) that the species richness and composition of the studied taxa recover at least as quickly as biomass (Figure 2), our findings point to PGM and STM as potential locations for this type of win-win scenario. These conclusions differ from those of a tropical SF carbon and biodiversity meta-analysis (Martin et al., 2013), which concluded that carbon pools recover more rapidly than floral biodiversity. However, the results from this

meta-analysis in fact show that tree species richness recovered quicker than carbon but epiphyte richness did not. By being dependent on the biodiversity components measured, as suggested by Martin et al. (2013) and the taxonomic variation in recovery trajectories outlined here (Figure 2), broad generalizations of carbon-biodiversity relationships in tropical SFs may remain elusive. Beyond biomass, our results highlight that forest structural complexity, represented by a diverse understory and closed canopy, can be as important in predicting SF species distributions as biomass for some taxonomic groups (Figure 4). To maximize biodiversity co-benefits of forest carbon restoration, these aspects of forest structure may need to be integrated into planning mechanisms alongside biomass.

The biomass-biodiversity successional transitions we identified can help inform SF management decisions. Those transitions indicate that 75 Mg ha^{-1} of biomass, which marks the influx of the most forest-dependent birds and trees (Figure 5), could serve as a useful benchmark beyond which forests in our study regions are protected from clearance. In 2014, the state of Pará, where our study regions are located, became the first Amazonian state to legally mandate the protection of SFs (Vieira et al., 2014). Under this law, SFs on private properties regenerating for greater than 20 years and those regenerating for between 5-20 years with a basal area of large trees ($\geq$ 10 cm DBH) greater than 10 m^2 ha^{-1} cannot be cleared. Remarkably, the 75 Mg ha^{-1} threshold that emerged from this study would result in near-identical – but slightly greater – levels of protection across PGM and STM as the current law in terms of the number of SFs protected and the amount of carbon and biodiversity conserved (Figure S5). Given rapid advances in high resolution biomass-mapping technologies, such as airborne LiDAR (Asner et al., 2011) and the European Space Agency's BIOMASS Earth Explorer mission (Le Toan et al., 2011), our threshold may provide a complementary approach for assessing the legal status of forests across the state.

4.3 | Secondary forest carbon sequestration

The interaction between persistently high rates of primary tropical forest loss (Keenan et al., 2015) and the proliferation of SFs has significant and complex implications for the global carbon

cycle. In PGM and STM, we found that carbon sequestration averaged 2.25 Mg ha^{-1} yr^{-1} during the first 20 years of succession (Figure 3), eight times the sequestration rate of Amazonian old-growth forests (Brienen et al., 2015) and 69% higher than in Amazonian forests selectively logged using reduced-impact techniques (Rutishauser et al., 2015). Cumulatively, however, 20 years of regeneration returned biomass stocks to only 24% of the UPF mean (Figure 3). As such, while SFs in the eastern Amazon may provide a valuable carbon sink, absent the cessation of primary forest loss, they are unlikely to compensate on meaningful timescales for deforestation-mediated carbon emissions that, globally, play a large role in driving anthropogenic climate change (Baccini et al., 2012).

While the magnitude of carbon sequestration in old-growth forests is relatively well quantified (Pan et al., 2011; Saatchi et al., 2011; Brienen et al., 2015), carbon uptake in regenerating forests is highly uncertain (Pan et al., 2011; Saatchi et al., 2011; Grace et al., 2014). Exemplifying this, the 20-year carbon sequestration rate we estimate for PGM and STM is 25% lower than the SF Neotropical average of 3.02 Mg ha^{-1} yr^{-1} (Poorter et al., 2016) and the recovery of biomass in our SFs averaged just 41%, and as low as 8%, of biomass recovery potential estimates for the eastern Amazon based on large-scale climatic variables (Figure S6; Poorter et al., 2016). Consequently, biome-wide estimates may be of limited value in understanding regional SF biomass resilience and, at these finer spatial scales, local environmental factors may play a greater role in shaping successional outcomes.

4.4 | Overestimating secondary forest recovery

The SFs we studied demonstrated a high degree of resilience. However, there is reason to suppose that we – and SF analyses more generally – may be overestimating the scale of recovery success. When considering the effect of all anthropogenic disturbance in Pará, primary forests have lost substantial amounts of their conservation value – where conservation value is represented by the occurrence of forest species (Barlow et al., 2016). This is so even in landscapes comprised of mostly intact forests with little evidence of within-forest degradation. Given that many impacts of human disturbance in forests – such as over-hunting and climate

change-caused shifts in species distributions – are difficult or impossible to detect on the ground or remotely (Peres et al., 2006), forests considered to be 'undisturbed' are unlikely to have been completely sheltered from the widespread anthropogenic alteration of the biosphere. While this ongoing cryptic disturbance affects SFs, species of higher conservation concern, which disproportionately inhabit the least-disturbed forests, are far more sensitive to disturbance than many of those that inhabit already-disturbed forests (Barlow et al., 2016). Consequently, we are likely comparing the biomass and biodiversity of SFs to an artificially low UPF benchmark (Moura et al., 2014).

4.5 | The management of secondary forests

Overall, we show that SFs can accumulate large amounts of carbon and support many forest-dependent species. However, given that the sites we surveyed failed to regain the biomass and biodiversity typical of UPF after several decades of succession, our results show that SFs are not substitutes for primary forests. Indeed, if not for the large areas of native vegetation in our study regions, we would almost certainly have found considerably weaker succession. As such, the conservation of primary forests remains imperative.

While the SFs we surveyed have not attained the characteristics of UPF, our results highlight that these naturally regenerating forests can deliver a range of high-value ecosystem services, including habitat provision, carbon sequestration, and the suite of services linked to biomass resilience, such as soil conservation and the maintenance of hydrological systems (Feldpausch et al., 2004; Suding, 2011; Lohbeck et al., 2015). Thus, forest restoration strategies that rely on the spontaneous recovery of native species, which are more economically viable than expensive active restoration alternatives, can deliver significant benefits (Crouzeilles et al., 2017). Despite their potential ecological and socio-economic significance, SFs in deforestation frontier regions exist in dynamic agro-forest mosaics, making them often transient features of the environment: the mean half-life of SFs in the Brazilian Amazon is a mere 5.2 years (Aguiar et al., 2016). For SFs to return the types of biomass and biodiversity benefits found here, where sites have been regenerating for up to 40 years, they should be incorporated as key elements of

landscape management and conservation planning (Freeman et al., 2015), especially in regions where regeneration potential is high. Yet, in Brazil and beyond, SF regulatory frameworks are beset by legal uncertainties, inconsistent decision-making, and the chronic undervaluation of these important ecosystems (Vieira et al., 2014). Moreover, millions of marginalized smallholder farmers around the world use SFs as part of fallow-based agricultural systems. Socially equitable SF governance regimes that balance rural livelihoods, the provision of ecosystem services, and effective agricultural development are challenging to design and implement but urgently needed.

Where SFs are managed sustainably, priority should be given to the conservation of older stands with the most developed forest structure; as we show, it is these forests that provide the greatest repositories of biodiversity and carbon (Figures 2, 3 & S4). Nonetheless, given the rapidity of succession towards a UPF state we found for most taxa (Figures 2 & S4), protecting young SFs may yield large future dividends. Moreover, succession is a multi-scale, multi-factorial process, dependent on a complex array of local and regional socio-environmental forces. This complexity notwithstanding, our results suggest a measure of consistency in regeneration rates: on average, all taxonomic groups recovered at least as quickly as biomass and reached similar proportions of UPF species richness and composition (Figures 2 & S4). This provides some support for the expectation of high predictability of secondary succession in areas dominated by forest matrices where dispersal limitation, ecological filtering and antagonistic biotic interactions do not act as strong recolonization constraints (Arroyo-Rodríguez et al., 2017). Nonetheless, even in regions with relatively high forest cover, our results show that second-growth stands with similar levels of biomass (Figure 2) and which have been recovering for the same time (Figures 3 & S4) can display a wide spectrum of biotic attributes. As a result, monitoring and adaptive management should form central planks of SF conservation. This will allow idiosyncratic and arrested successional trajectories to be identified and, where cost effective, set on a path to maximize SF socio-ecological benefits (Chazdon et al., 2009). With conditions favorable to succession, such as those present in Paragominas and Santarém, combining clear and equitable SF governance, an understanding of the processes that determine successional outcomes, and smart management techniques may see SFs form valued components of tropical forest landscapes.

Acknowledgments

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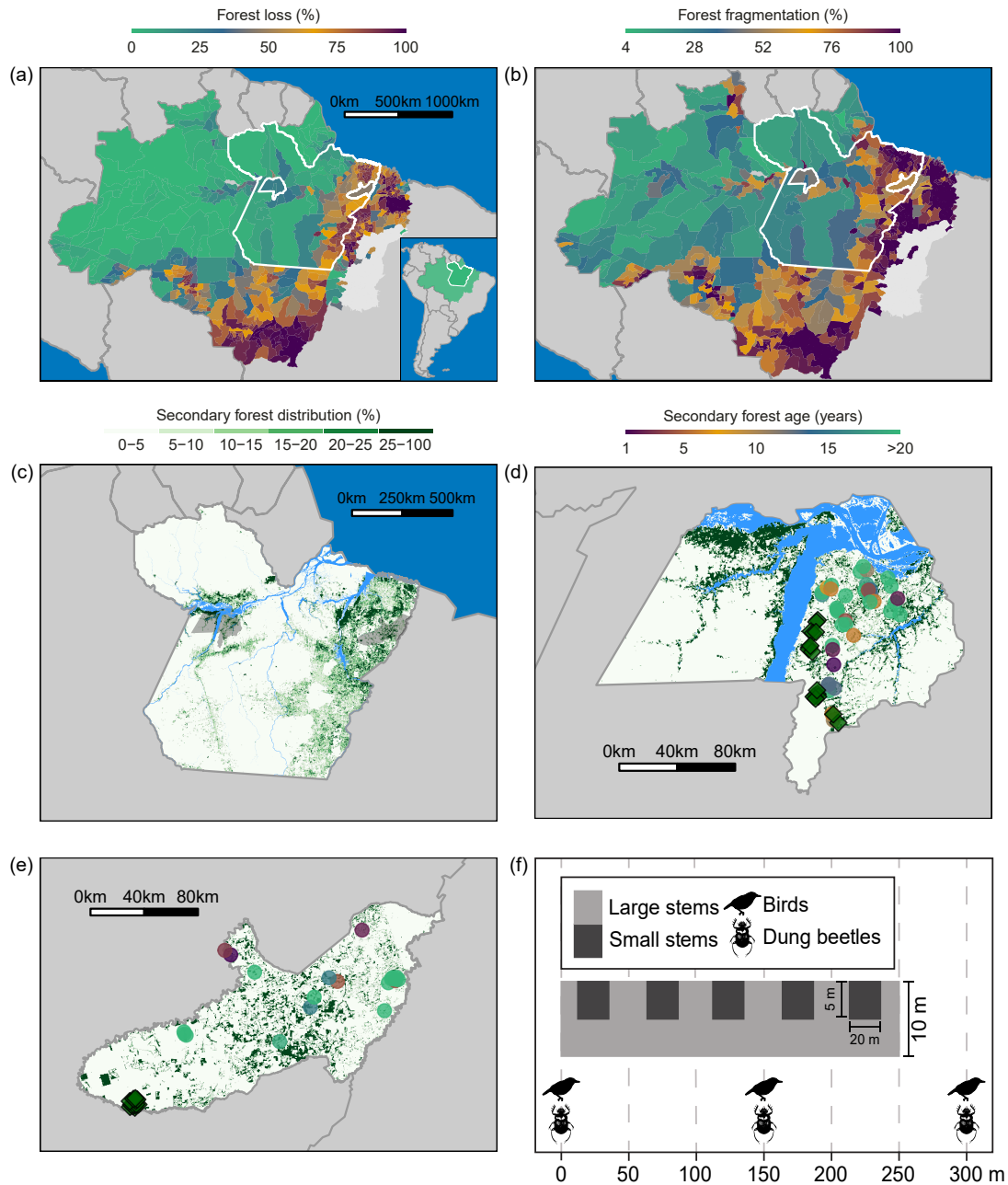
FIGURE 1 Study area and design. Municipality-level forest loss (a) and fragmentation (b) across the Brazilian Amazon. The locations of the state of Pará and the municipalities of Paragominas and Santarém-Belterra (in the east and west of Pará, respectively) are shown in white. Municipalities in light gray had no native forest cover. The proportion of land covered by secondary forest in 50 km² cells across Pará (c) and 1 km² cells across Santarém (d) and Paragominas (e). Also shown in these latter two panels is the distribution and age of the secondary forest study plots and the distribution of the undisturbed primary forest plots (dark green diamonds). (d) Floral and faunal sampling within the study plots.
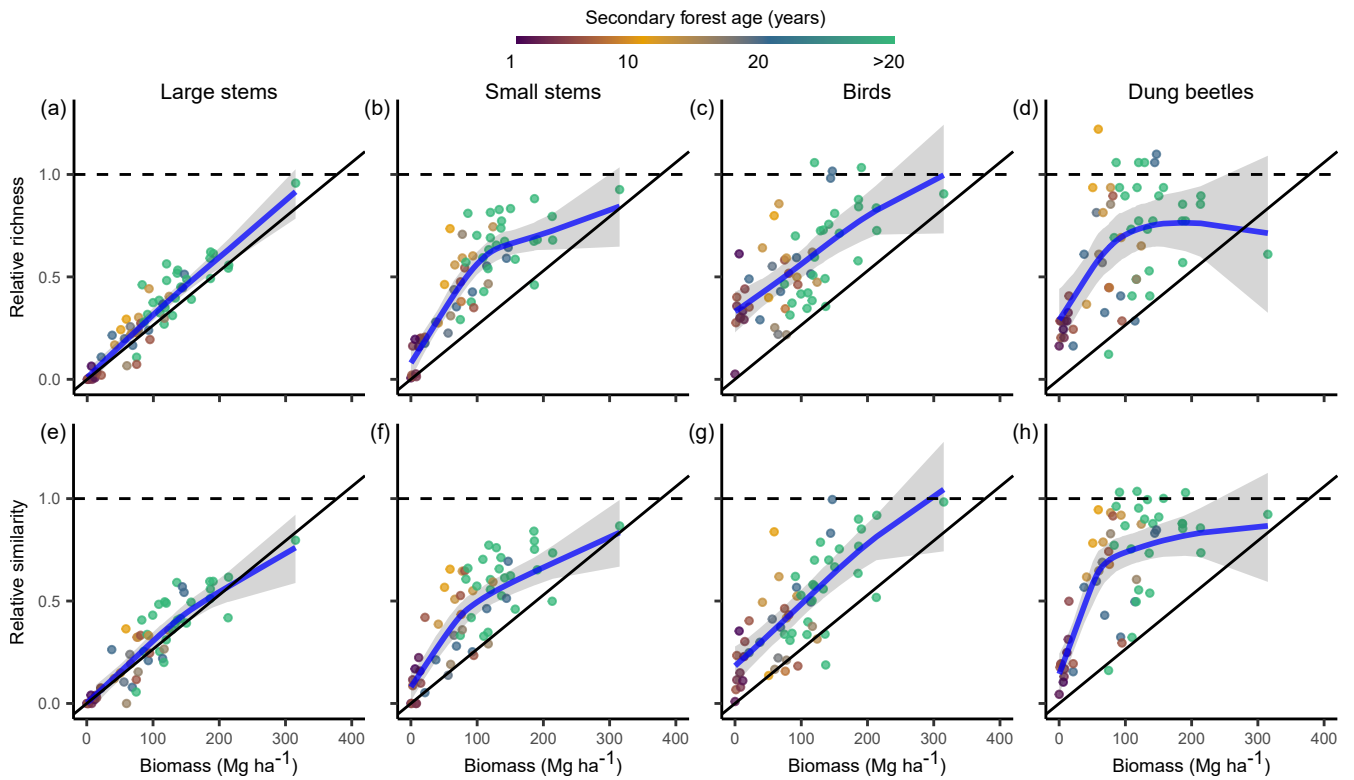
FIGURE 2 Secondary forest species richness (a-d) and compositional similarity to undisturbed primary forests (e-h) for large-stemmed plants (a & e), small-stemmed plants (b & f), birds (c & g), and dung beetles (d & h) relative to the recovery of biomass (black solid lines) and the undisturbed primary forest expectation (black dashed lines). Points show the site values. Point color denotes site age. Solid blue lines show the Bayesian piecewise-linear splines. Grey shaded areas show the 95% credible intervals.
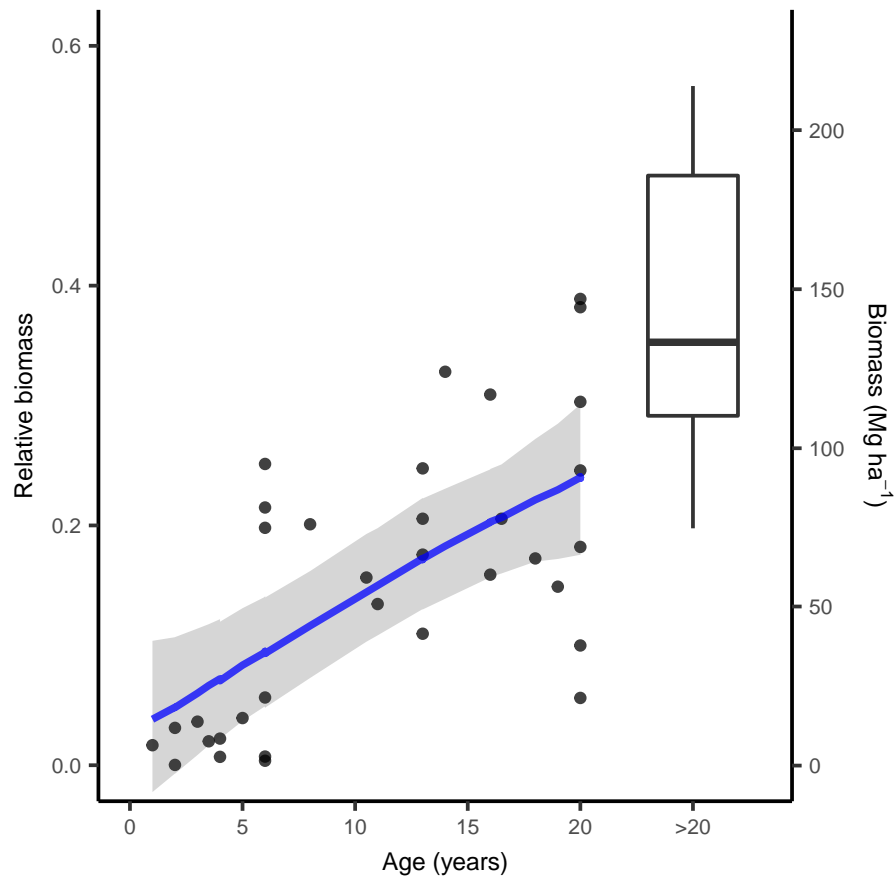
FIGURE 3 Biomass recovery over the first 20 years of secondary succession shown relative to the mean biomass in undisturbed primary forests (left axis) and in Mg ha^{-1} (right axis). Points show the site values. The blue line shows the Bayesian piecewise-linear splines. Grey shaded areas show the 95% credible intervals. The boxplot shows the distribution of biomass for all sites the age of which we can only specify as greater than 20 years. Note that we do not show the outlier for the one secondary forest with biomass greater than 300 Mg ha^{-1} (Figure 2).
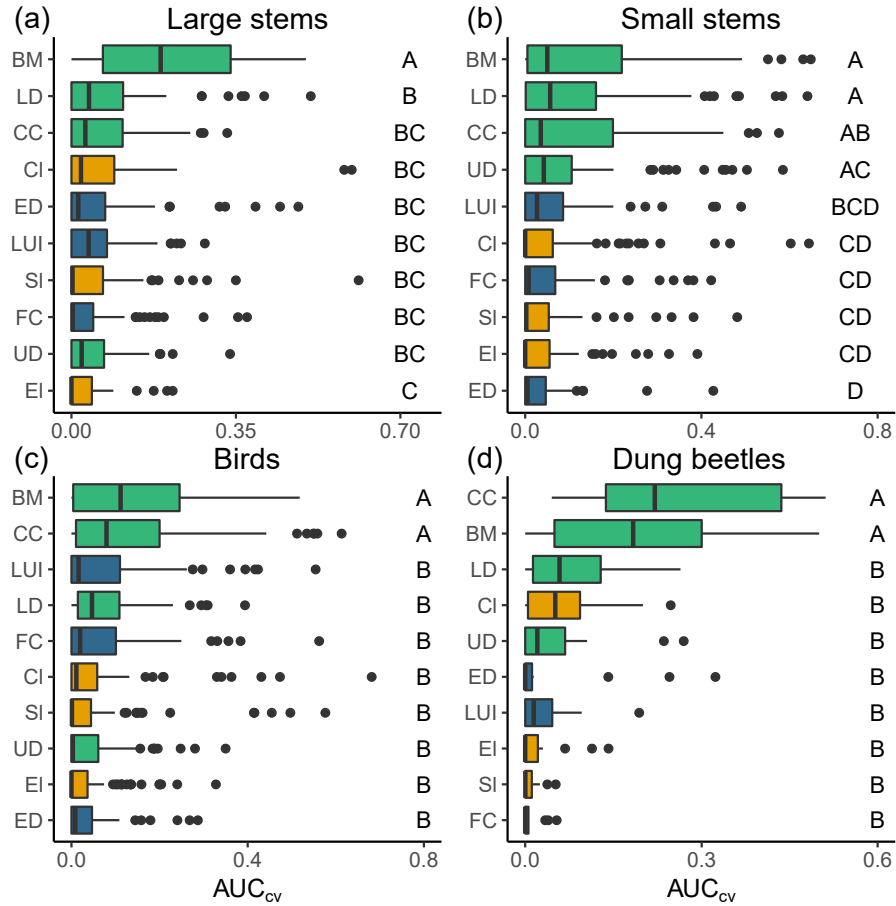
FIGURE 4 The importance of forest structure (green), landscape context (blue), and topoedaphic variables (orange) in accounting for the secondary forest occurrences of large-stemmed plants (a), small-stemmed plants (b), birds (c), and dung-beetles (d). Forest structure variables: biomass (BM), canopy cover (CC), understory density (UD), liana density (LD). Landscape context variables: forest cover (FC), edge distance (ED), land-use intensity (LI). Topoedaphic variables: soil clay content (Cl), elevation (El), slope (Sl). Variable importance was measured by the mean AUC_{cv} over all well-modeled species. Letters show the results of multiple pair-wise comparisons of variable means. Variables that do not share a letter have statistically different mean importance (*p-value* < 0.05).
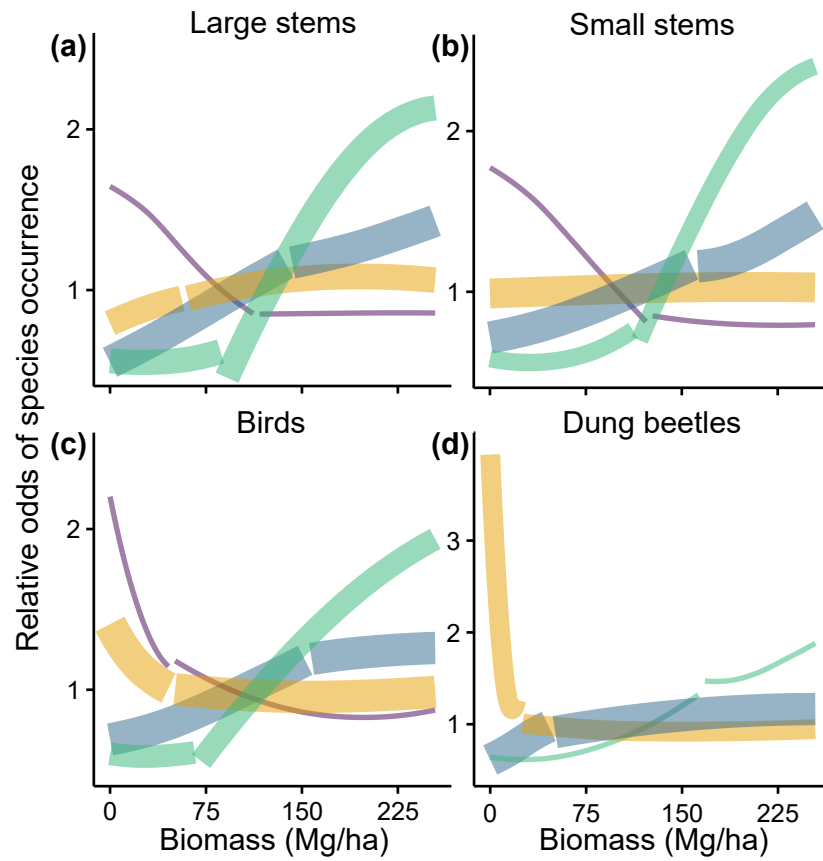
FIGURE 5 The relative odds of detecting large-stemmed plants (a), small-stemmed plants (b), birds (c), and dung beetles (d) along the secondary forest biomass gradient. Coloured lines show the LOWESS-smoothed response of species in the LTA-defined response classes about the response thresholds. Line thickness represents relative class size.
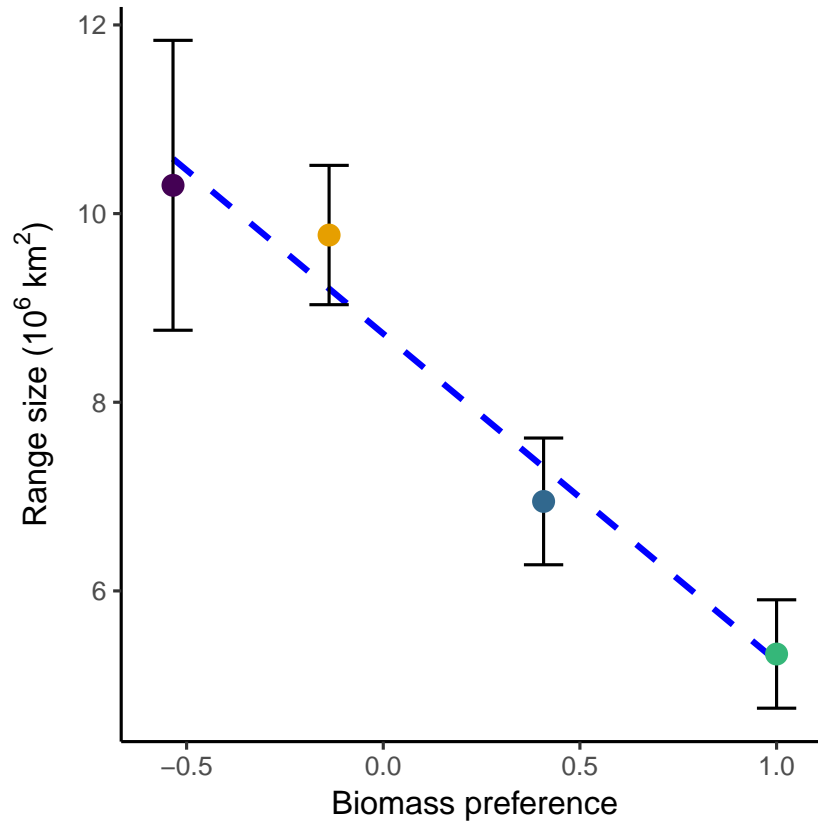
FIGURE 6 The mean biomass preference of bird species in the LTA-defined species classes related to species mean geographic range size. Class colors correspond to the LTA classes shown in Figure 5. The blue dashed line shows the linear trend ($R^2 = 0.94$, *p-value* = 0.02). Error bars show 1 standard error of the mean. We did not show error bars on the biomass preference values because for three of the four classes the bars were too narrow to be visible.