

Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation

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Concerted political attention has focused on reducing deforestation^{1–3}, and this remains the cornerstone of many biodiversity conservation strategies^{4–6}. Yet maintaining forest cover may not reduce anthropogenic forest disturbances, which are rarely considered in conservation programmes⁶. These disturbances occur both within-forests, including selective logging and wildfires^{7,8}, and at the landscape level, through edge, area and isolation effects⁹. To date, the total combined effect of anthropogenic disturbance on the conservation value of remnant primary forests is unknown, making it impossible to assess the relative importance of forest disturbance and forest loss. We address these knowledge gaps using an unparalleled data set of plants, birds, and dung beetles (1538, 460 and 156 species, respectively) sampled in 36 catchments in the Amazonian state of Pará. Catchments retaining > 69-80% forest cover lost more conservation value from disturbance than from forest loss. For example, a 20% loss of primary forest, the maximum level of deforestation allowed on Amazonian properties under Brazil's Forest Code⁵, resulted in a 39-54% loss of conservation value, 96-171% more than expected without considering disturbance effects. We extrapolated the disturbance-mediated loss of conservation value throughout Pará, an area larger than South Africa covering 25% of the Brazilian Amazon. Although disturbed forests retained considerable conservation value compared to deforested areas, the toll of disturbance outside Pará's strictly protected areas is equivalent to the loss of 92,000-139,000 km² of primary forest. Even this lowest estimate is greater than the area deforested across the entire Brazilian Amazon between 2006 and 2015¹⁰. Species distribution models showed that landscape and within-forest disturbance both made substantial contributions to biodiversity loss, with the greatest negative effects on species of high conservation and functional value. These results demonstrate an urgent need for policy interventions that go beyond the maintenance

of forest cover to safeguard the hyper-diversity of tropical forest ecosystems.

Protecting tropical forests is a fundamental pillar of many national and international strategies for conserving biodiversity^{4–6}. Although improved regulatory and incentive measures have reduced deforestation rates in some tropical nations^{1,11,12}, the conservation value of the world's remaining primary forests may be undermined by the additional impacts of disturbance, which falls into two broad categories (see Methods). First, landscape disturbance results from deforestation itself, with area, isolation and edge effects degrading the condition of the remaining forests⁹. Second, within-forest disturbance, such as wildfires and selective logging, induces marked changes in forest structure and species composition^{8,13}.

Although the biodiversity consequences of both forms of disturbance are well studied, previous research has overwhelmingly focused on identifying the isolated effects of specific types of disturbance^{14,15}. Such studies provide an incomplete understanding of the total disturbance-mediated loss of conservation value arising from multiple interacting drivers¹⁶ and are unable to quantify the extent to which reducing forest loss will succeed in protecting tropical forest biodiversity. Addressing these knowledge gaps is vital for informing forest management strategies in tropical nations, not least because within-forest disturbance can increase even as deforestation rates fall^{7,12,17} and thus requires different policy interventions (Extended Data Table 1).

We estimated the combined effect of landscape and within-forest disturbance on biodiversity in primary forests and compared these impacts to the biodiversity loss expected in deforested areas, offering the first such analysis for anywhere in the world. Our study focused on two large (>10,000 km²) frontier regions of the Brazilian Amazon: Paragominas and Santarém, located in the state of Pará (see Methods). Large- and small-stemmed plants, birds and dung beetles were sampled in 371 plots

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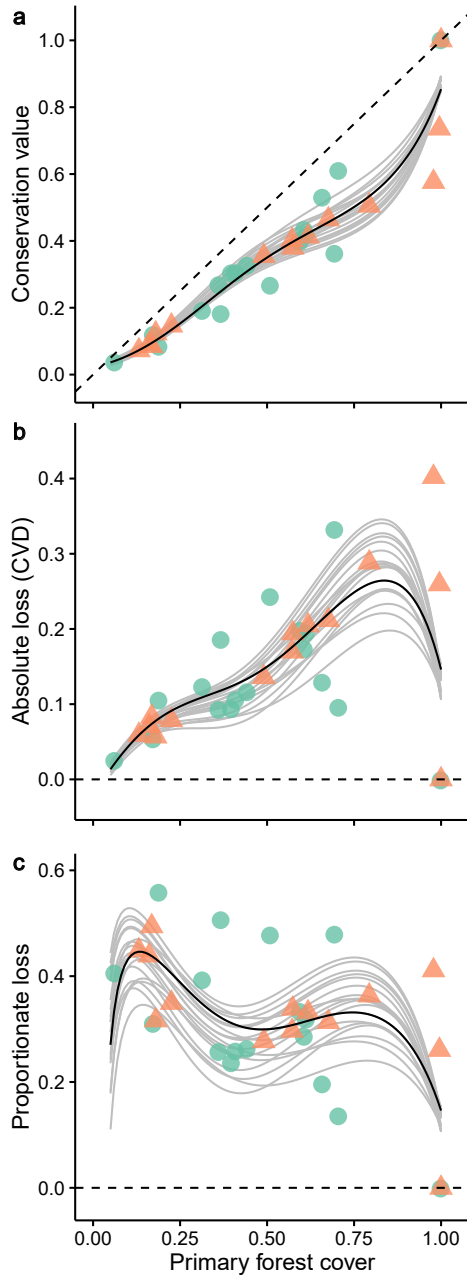


Figure 1: The conservation status of primary forests. **a**, Conservation value in Paragominas (circles) and Santarém (triangles). **b**, Total loss of conservation value due to disturbance. **c**, Total loss of conservation value due to disturbance expressed as a proportion of the expected conservation value without disturbance. Dashed lines show expectations without disturbance. Grey lines show all regressions, with the black solid line showing the median response (see Methods). Values were standardized across study regions. There was no significant difference in conservation values between regions in the median response ($F_{1;26} = 1.45$, $P = 0.24$, analysis of covariance (ANCOVA)).

in thirty-six study catchments distributed along a landscape deforestation gradient (0-94%) (Extended Data Fig. 1). Thirty-one catchments contained remnant primary forests. Within these catchments, we sampled 175 primary forest plots. Of these, 145 had visible evidence of within-forest disturbance (logging and/or fire). The remaining 30 had no evidence of within-forest disturbance and, being located in the largest remaining forest blocks, had minimal land-

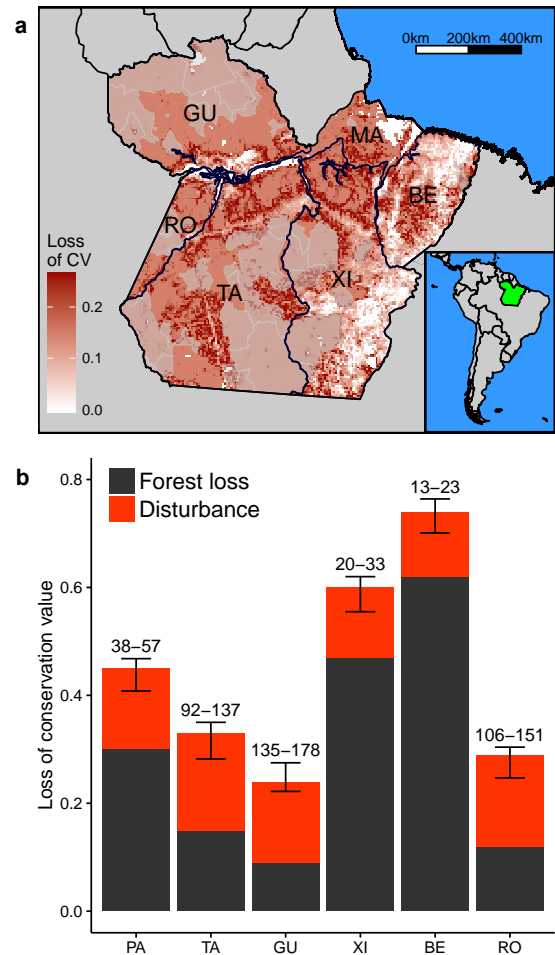


Figure 2: Conservation value deficit over large spatial scales. **a**, Proportionate loss of conservation value (CV) from disturbance in Pará (median estimate; see Methods). Areas of endemism (AoE) are: Belém (BE), Guiana (GU), Rondônia (RO), Tapajós (TA) and Xingu (XI). These do not include the island of Marajó (MA). Grey shading denotes strictly protected areas. **b**, Proportionate loss of CV in Pará (PA) and its AoEs from forest loss and disturbance (median estimate). Error bars show the range over all approaches to estimating conservation value (see Methods). Numbers show disturbance relative to forest loss (percentage range over approaches).

scape disturbance^{18,19} (see Methods). Irrespective of their disturbance history, these primary forest plots held considerably more forest species than all other major land-uses (Extended Data Fig. 2).

We used the sum of forest species presences in primary forest plots to estimate a catchment's conservation value (see Methods). As plots were allocated in proportion to catchment forest cover, this measure is equivalent to the mean species richness (per unit area) in primary forests multiplied by the proportion of primary forest cover. In the absence of landscape or within-forest disturbance, the expectation of conservation value should respond linearly to forest cover, with slope equal to mean species density (see Methods). The difference between this linear expectation and the observed conservation value of the remaining primary forest provides an estimate of the total biodiversity impact of all landscape and within-forest disturbance. We refer to this difference as the conservation value

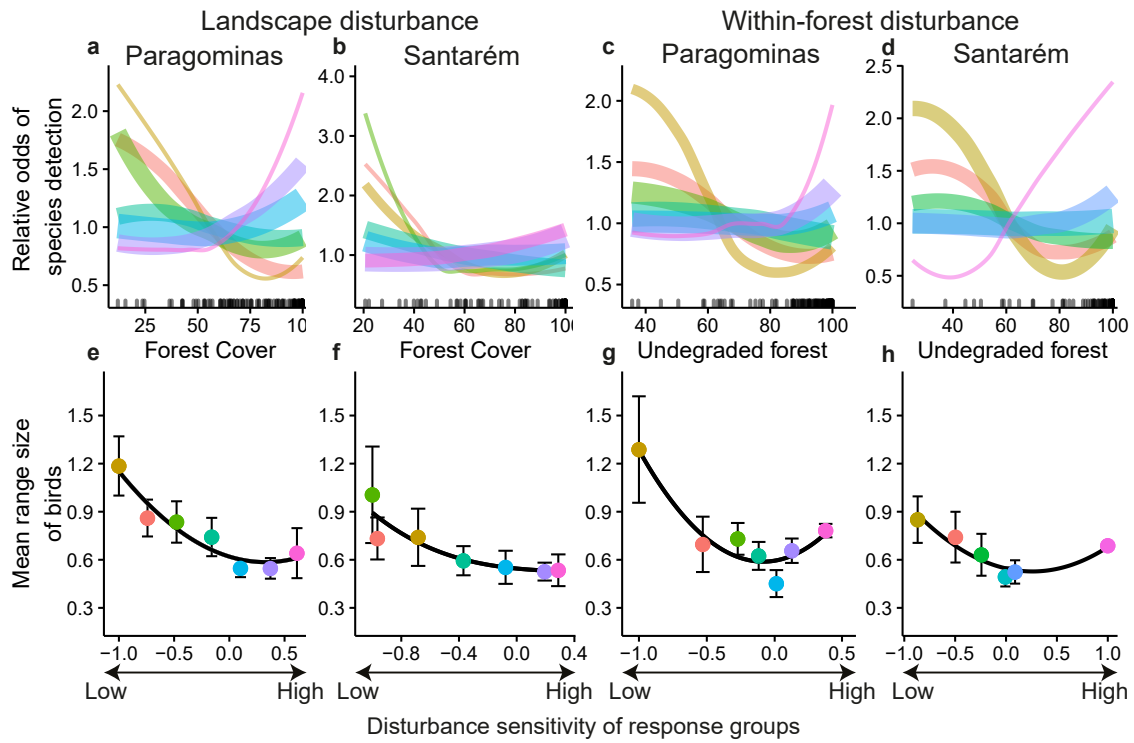


Figure 3: Response of forest birds to disturbance. a-d, The odds of detecting species groups along gradients of landscape (a, b) and within-forest (c, d) disturbance in Paragominas (a, c) and Santarém (b, d) (see Methods). Species groups, shown by different coloured lines, are composed of species with similar disturbance responses (see Methods). Line thickness represents the relative size of the groups. e-h, Disturbance sensitivity of the species groups related to their mean range size (10^7 km²). Error bars shows s.e.m. Group colours correspond to groupings in a-d. Black lines show significant relationships ($P < 0.05$, F -test) (see Methods).

deficit (CVD). We take a variety of approaches to calculating the CVD, reflecting different ways of classifying forest species, weighting their conservation value and calculating species density in undisturbed forest (see Methods). Here, we report median results from our sensitivity analysis along with the lower and upper bound range. Full results are shown in Figure 1 and Extended Data Figures 3 and 4.

The conservation value of the remaining primary forests was lower than expected along the entire deforestation gradient. The CVD was unimodal with forest cover, reaching its maximum in catchments with 83% of their primary forests. These catchments retained just 58% of their conservation value (range: 48-65%) (Fig. 1a). The CVD was relatively small at low levels of forest cover (Fig. 1b). Yet disturbance caused the greatest proportionate loss of conservation value in these catchments, accounting for a c. 20-50% shortfall in the level of biodiversity that would be predicted for undisturbed forests (Fig. 1c). The robustness of our estimates of the CVD was supported by the similarity of responses across study regions (Fig. 1) and sampled taxa (Extended Data Fig. 3).

The relationship we derived between forest cover and conservation value allowed us, for the first time, to estimate the additional total impact of forest disturbance over large spatial scales. We therefore mapped the disturbance-induced loss of conservation value (CVD) across Pará, which covers 1.26×10^6 km². We divided the state into grid cells approximately equal in area to our study catchments (c. 50 km²). Seventy-three percent of the c. 26,000 cells covering the state were

located in private lands or sustainable-use reserves. For these locations, which are most comparable to our study catchments, the total CVD was equivalent to c. 123,000 km² of forest loss (range: 92,000-139,000 km²). To put this figure in context, it is 51% (range: 38-57%) of the total area deforested across Pará to date (Extended Data Table 2).

Our state-wide analysis revealed considerable spatial variation in the CVD, reflecting differences in deforestation histories (Fig. 2a). We illustrate this variation by estimating the additional loss of conservation value due to disturbance across Pará's five major biogeographic zones (areas of endemism²⁰, AoE). Median disturbance impacts outweighed biodiversity losses in deforested areas alone in three of the five AoEs (Fig. 2b). The high relative impact of disturbance is shown in the Guiana AoE, where the predicted loss of conservation value from disturbance was 135-178% of the losses estimated in deforested areas. The relative impact of disturbance was lowest in the Belém AoE, which has lost 62% of its native forest cover and is the most deforested AoE in Amazonia. Nonetheless, overall disturbance effects reduced Belém's estimated conservation value from 38% when based on forest cover alone to just 26% (range: 24-30%).

The widespread and substantial depletion of conservation value in remaining primary forests highlights the pressing need for policies that target the most prominent drivers of disturbance-induced biodiversity loss. Although measures to combat deforestation may help limit landscape disturbance, they rarely consider the spatial configuration of remaining forests or work to actively reduce

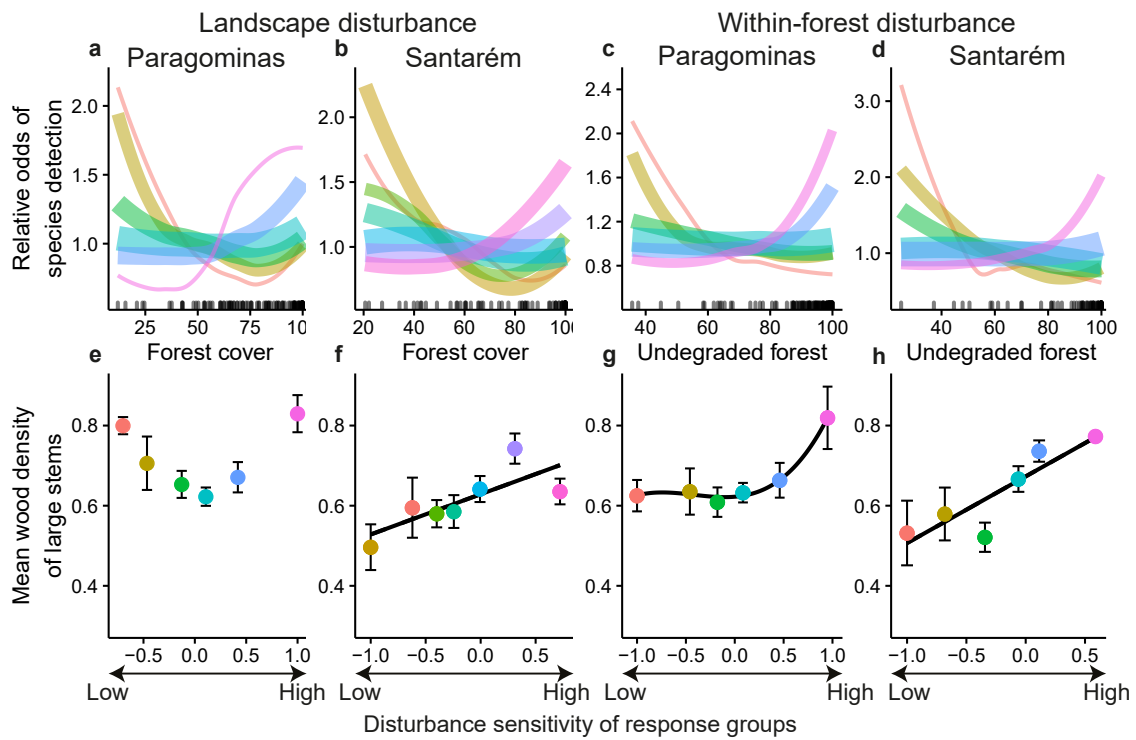


Figure 4: Response of large-stemmed plants to disturbance. **a-d**, The odds of detecting species groups along gradients of landscape (**a, b**) and within-forest (**c, d**) disturbance in Paragominas (**a, c**) and Santarém (**b, d**) (see Methods). Species groups, shown by different coloured lines, are composed of species with similar disturbance responses (see Methods). Line thickness represents the relative size of the groups. **e-h**, Disturbance sensitivity of the species groups related to their mean wood density (g cm^{-3}). Error bars shows s.e.m. Group colours correspond to groupings in **a-d**. Black lines show significant relationships ($P < 0.05$, F -test) (see Methods).

within-forest disturbance (Extended Data Table 1)^{6,21}.

Here we provide insights into the need for additional policies to reduce forest disturbance by examining the relative importance of landscape and within-forest disturbance on species distributions using Random Forests (see Methods). In ranking the importance of remotely-sensed disturbance measures, we found that both forms of disturbance had significant additional effects on species' distributions, albeit with some region- and taxon-specific variation (Extended Data Figs. 5-7, see Methods). We then used the measures of landscape and within-forest disturbance that were most frequently ranked highest to examine changes in taxon community structure, using Latent Trajectory Analysis to group species by their responses to disturbance (see Methods). Results showed a consistent and high level of community turnover from both forms of disturbance, with some species groups responding negatively and others positively (Figs. 3 and 4, Extended Data Fig. 8). These responses may explain the unimodal shape of the disturbance impact (Fig. 1b) because they are consistent with the loss of highly sensitive species at relatively low levels of forest disturbance and the dominance of more resistant taxa in the most disturbed forests. Finally, we linked species' response groups with life-history data available for birds and large-stemmed plants (see Methods). Both types of disturbance contributed to marked declines in species of high conservation and functional importance (birds with smaller range sizes^{22,23} and plants with higher wood density²⁴⁻²⁶, respectively) (Figs. 3 and 4). These analyses almost certainly underestimate the adverse effects of disturbance because rare species, which are often most sensitive to human impacts in forest ecosystems²⁷, cannot be adequately modelled.

We provide compelling evidence that Amazonian conservation initiatives must address forest disturbance as well as deforestation. At its most stringent, Brazil's centrepiece forest legislation the Forest Code mandates Amazonian landowners to maintain 80% of their primary forest cover. Our results show that even in landscape that achieve this level of compliance, the remaining primary forests may only retain 46-61% of their potential conservation value and are likely to have lost many species of high conservation and functional importance. These findings reinforce the need to reduce the effects of landscape fragmentation by zoning development activities, thereby ensuring the protection of large blocks of remaining forest in all biogeographic zones. Where deforestation has already occurred, further conservation losses can be minimised by preventing within-forest disturbance, aiding the recovery of already degraded forests, and investing in forest restoration to improve connectivity and buffer remnant forests from edge effects. Engendering change will require a mixture of incentive and regulatory-based measures to improve the sustainability of both forestry and farming practices. Crucially, because reducing forest disturbance requires coordinated efforts by many actors, interventions need to move beyond individual properties and address entire landscapes and regions. Such actions are urgently needed in the Amazon where logging operations are rapidly expanding across federal and state forests²⁸, wildfires are increasingly prevalent during more frequent and severe dry seasons²⁹, and the expansion of industrial agriculture, energy and mining threaten even strictly protected areas and indigenous lands³⁰.

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Methods

Study regions. Pará is the second largest state in Brazil and a focal point for deforestation, accounting for 34% of all forest loss in the Brazilian Amazon between 1988 and 2015¹⁰. It holds exceptionally high biodiversity, with c. 10% of the world's bird species and five of the eight major AoEs in Amazonia²⁰. Within Pará, we focused on two geographically and biologically distinct regions: the municipalities of Paragominas and Santarém-Belterra-Mojuí dos Campos (abbreviated to Santarém) (Extended Data Fig. 1). These regions lie in different AoEs (Belém and Tapajós, respectively) and shared just 49% of our sampled taxa. Although they differ in their human colonization history¹⁸, both retain > 50% of their native forest cover.

Study design and biodiversity sampling. We divided each region into third- or fourth-order drainage catchments. In each region, 18 study catchments (32-61 km²) were then distributed along forest cover gradients. We distributed study plots on *terra firme* in proportion to forest and non-forest cover at a density of approximately 1 plot/4 km², resulting in 8-12 plots separated by ≥ 1.5 km in each catchment (Extended Data Fig. 1). Forest plots ($n = 234$) were distributed without prior knowledge of anthropogenic disturbance¹⁸ and included primary forests (i.e. under permanent forest cover; $n = 175$) and secondary forests recovering after agricultural abandonment ($n = 59$). Non-forest plots ($n = 133$) were predominantly located in pastures ($n = 76$) and mechanised agricultural lands ($n = 31$).

Thirty-one of the 36 catchments contained primary forest plots. In Paragominas and Santarém respectively, these included undisturbed (13 and 17), logged (44 and 26), burned (0 and 7) and logged and burned primary forests (44 and 24)¹⁹. Disturbance categories were based on field assessments of fire scars, charcoal and logging debris, and an analysis of canopy disturbance, deforestation and regrowth in time series satellite images (1988 to 2010)^{18,19}. Plots in the undisturbed forest had no evidence of within-forest disturbance and, because they were located > 2 km from edges in the largest forest blocks, had minimal landscape disturbance. Observations of hunting-sensitive large game birds, such as razor-billed curassow *Pauxi tuberosa* and trumpeters *Psophia spp.*^{31,32}, indicated low hunting pressure³³ in undisturbed plots.

Biodiversity surveys occurred during 2010 and 2011. The following descriptions apply to sampling at the plot level. Large and small stems: Live trees and palms with ≥ 10 cm diameter at breast height were identified in 10 \times 250 m plots. Smaller individuals (2-10 cm diameter) were sampled in five 5 \times 20 m subplots (Extended Data Fig. 1). Liana diameters were measured at 1.3 m from the main root. Large- and small-stemmed plants were analysed separately because they may differ in their disturbance responses. Individuals were identified to species level by local parobotanists¹⁹. In total across all catchments, 175 plots and 825 subplots were sampled in primary forests. Birds: There were two repeat surveys of 15-min point counts at three sampling points (0, 150 and 300 m) (Extended Data Fig. 1). Sampling was undertaken between 15 minutes before dawn and 09:30. Lists of voucher sound-recordings and images are available for both regions^{31,32}. In total across all catchments, 1050 point counts were undertaken in primary forests. Dung beetles: Sampled using pitfall traps (14 cm radius, 9 cm height) baited with 50 g of dung (80% pig and 20% human) and half filled with a killing solution (5%

detergent and 2% salt). Traps were left for 48 hours prior to inspection. Three traps were placed at the corners of a 3 m equilateral triangle, repeated at three sampling points (0, 150 and 300 m). In total across all catchments, 1575 pitfall traps were set in primary forests (Extended Data Fig. 1).

Defining the biodiversity consequences of forest loss, landscape and within-forest disturbance. We limit the biodiversity consequences of forest loss to those that occur in deforested areas themselves, excluding any additional effects on remaining forests. Landscape disturbance then captures the combined edge, area and isolation effects that accompany the deforestation process. Within-forest disturbance refers to anthropogenic disturbance events that are not inevitable consequences of forest loss or land cover change, including wild-fires, hunting and selective logging. Although often associated with landscape factors, such as distance from forest edge, within-forest disturbance can occur independently of changes in forest cover or landscape configuration.

Estimating the conservation value deficit. We used the sum of forest species presences in primary forest plots to measure a catchment's conservation value. In practice, this means that if a forest species occurs on x plots within a catchment, the species contributes x to the catchment's conservation value. Total catchment conservation value is found by summing presences over all forest species. This measure is equivalent to mean species richness (per unit area) in primary forests multiplied by primary forest cover. In the absence of disturbance, conservation value should therefore respond linearly to forest cover, with slope equal to mean species density, d_e . We term the difference between this linear expectation and a catchment's observed conservation value as its conservation value deficit (CVD). We took a variety of approaches to calculating the CVD, reflecting different methods of defining forest species, weighting their importance, and calculating d_e .

Defining forest species. We restricted our analysis to "forest species" to avoid attributing value to invasive and open-area species. We used three species classification filters: (i) an automatic filter defined forest species as those that occurred at least once in a primary forest plot, irrespective of the plot's disturbance history ($n = 1621$ species); (ii) a high basal area (HBA) filter defined forest species to be those that occurred at least once in plots with a high average basal area (i.e. \geq the lowest basal area recorded in undisturbed forests in each region) ($n = 1290$); and (iii) a convex hull filter where we first applied a two-dimensional non-metric multidimensional scaling (MDS) to primary and secondary forest plots based on a stem-size classification (stress = 0.14), and then defined forest species to be those that occurred at least once in plots within the minimum convex hull of undisturbed primary forest plots on the MDS ($n = 1140$).

Species conservation or functional importance. We used three approaches to weight species' importance. First, we assumed that all forest species had a value equal to 1. Second, we applied a linear weighting to birds according to their range size and plants according to their wood density. The bird species with the smallest range size was given a value of 1, and that with the largest range size was given a value of 0 (vice versa for plants and wood density), with all other species' values mapped linearly between these two points. Third, we squared the linear weighting to give an even higher relative value to species of highest conservation or functional importance.

There are many important life-history traits that correlate with species' conservation or functional importance. Our choices were based on a priori knowledge and the availability of data for diverse tropical taxa. For birds we chose range size because it is the single most important predictor of threat status²³, especially among lowland passerines where it is inversely correlated with other important factors such as population density²². For plants we chose wood density because it is the most important size-independent determinant of carbon storage within individual stems, a strong predictor of carbon stocks across the biome^{24,26}, and is also linked with other functional properties²⁴ including drought resistance²⁵. Bird range sizes were extracted from the Birdlife Datazone <http://www.birdlife.org/datazone/index.html>. Wood densities were adapted from the global wood density database³⁴, using the genus or family average where species or genus data were unavailable. Lianas were given a nominal value of 0.01.

As part of the broader sensitivity analysis we also undertook the same analysis described above for birds replacing species range size for species mean body size (body size data was also extracted from Birdlife Datazone). This analysis was undertaken to determine if the population density of birds, which is strongly and inversely correlated with body size, significantly affected results. It did not: the median estimate of the disturbance impact decreased by just 0.5%, and we do not report the full results here.

Alternative undisturbed baselines. Estimating d_e (mean species density in undisturbed landscapes) requires species distribution data from catchments with no within-forest or landscape disturbance. As we do not have a set of such catchments in either region, we took three approaches to calculating d_e . The first two approaches rely on the least disturbed catchment in each region. In both Paragominas and Santarém, this reference catchment had minimal landscape disturbance (> 99% primary forest). However, ground-based observations indicated that either selective logging or wildfire had affected at least 25% of the sampling plots within the reference catchments in both regions. We therefore calculated d_e as the mean species density over all plots in the reference catchment and, to correct for within-forest disturbance, as the mean density over only undisturbed reference catchment plots. Finally, to account for potential biases in underlying (natural) species distributions, we also calculated d_e using all undisturbed plots throughout each region ($n = 30$). This represents a more conservative estimate because it includes plots in catchments with less than 100% forest cover.

Selecting representative estimates of CVD. Combining the three forest species selection methods, the three species' weighting approaches, and the three estimates of d_e returns 27 estimates of the CVD. For all approaches, we determined the average CVD with respect to primary forest cover by modelling the catchments' summed presences with Poisson polynomial generalized linear models. We selected the best fitting model over all polynomials of degree up to cubics.

To express uncertainty over our estimates of the CVD, in the main text we present the median relationship between conservation value and forest cover along with the lower and upper bound range. We excluded from this range the estimate of d_e that included disturbed reference catchment plots, because it is not reflective of species density in the absence of disturbance. For the purposes of comparison, we have included these results in Extended Data Figure 4. The median, lower and upper

bound estimates of the CVD were given by, respectively: the convex hull filter, linear species weighting, and undisturbed reference catchment plots; the convex hull filter, no species weighting, and all undisturbed plots; and the high basal area filter, exponential species weighting, and undisturbed reference catchment plots.

Adjusting for proportionality. Although the number of plots in catchments was proportional to forest cover, proportionality was not exact because the original distribution was based on the extent of both primary and secondary forests¹⁸. We therefore corrected sampling effort by calculating the factor required to make sampling proportional to primary forest cover in each catchment and scaled our estimates of conservation value accordingly. For each catchment i , this factor is given by p_i/t_i , where p_i is the proportion of catchment i that is primary forest and t_i is the number of primary forest transects in catchment i .

Extrapolating the CVD. To estimate disturbance impacts throughout Pará, we divided the state into grid cells approximately equal in size to our study catchments. We then used Brazil's 2010 TerraClass product³⁵ to determine the area of each cell that was deforested, first removing non-forested areas that were covered by water or tropical savannah. We then calculated each cell's conservation value by applying the median, lower and upper bound estimates of the CVD. The disturbance impact in forest loss equivalent terms for cell i is given by $p_i - (a_i - n_i)v_i$, where p_i , a_i , n_i and v_i are, respectively, the cell's primary forest extent, area, non-forest area and conservation value.

Linking landscape and within-forest disturbance with species distributions and traits. We investigated the importance of landscape and within-forest disturbance at the plot level rather than the catchment level because many disturbance drivers act at local scales^{8,13}. Variables representing landscape and within-forest disturbance were based on the analysis of georeferenced 30 m resolution Landsat TM (Thematic Mapper) and eTM images from 1988 to 2010 in Paragominas and 1990 to 2010 in Santarém. These were complemented by covariates that represent natural variation in soil conditions, elevation and slope. A full description of the data is available elsewhere¹⁸. Variable abbreviations match those in Extended Data Figs. 5-7.

Within-forest disturbance. We measured the cumulative extent of canopy disturbance³⁶ by calculating the percentage of the remaining primary forest in a 1 km buffer around each plot that had never been classified as disturbed (undisturbed primary forest, UPF). We also included two measures of the frequency of disturbance within plots: the number of times the plot was logged (NL) and the number of times the plot was burnt (NB) in visual inspections of satellite images or field observations.

Landscape disturbance. We used two landscape configuration measures: the density of forest-agriculture edges (ED) and the percentage of primary and secondary (>10 years old) forest cover (FC) in 1 km buffers around plots. We used two measures of landscape history³⁷: the deforestation curvature profile (DC) and the land-use intensity profile (LI) in 500 m buffers around plots.

Natural environmental covariates. We used soil samples and digital elevation models to derive covariates reflecting natural conditions. Soil variables were based on average values from five 30 cm deep soil profiles in each plot, and include acidity

(pH), clay content (Cl), and carbon stock (Ca). We applied a 100 m buffer around each plot in a digital elevation model to calculate mean plot elevation (El) and slope (Sl).

Linking landscape and within-forest disturbance with species distributions and traits. We used Random Forests (RF), a decision-tree classification methodology, to identify species that are well-modelled by our data and to rank the importance of individual variables in accounting for species distributions. RF was adapted for spatial autocorrelation within catchments using a modified “residual autocorrelation” approach³⁸. The fit of the RF models and their predictive performance was measured using area under receiver-operator curves (AUC)³⁹. AUC evaluates the ability of models to correctly predict higher probability of occurrence where species are present than where they are absent. An AUC value of 1 indicates perfect discrimination; a value of 0.5 suggests predictions no better than random. We performed multiple cross-validations to evaluate model predictive performance. For each species, data from each study catchment were used in turn as test data for models built with data from the other catchments. The cross-validated AUC value, AUC_{cv}, was calculated as the average AUC value over all cross-validation tests for each species. Species present on a minimum of three transects and with a summed AUC_{cv} ≥ 0.6 over all variables were classified as well-modelled and included in the analyses (31% of species). The importance of a variable was measured as its mean AUC_{cv} over all well-modelled species.

Models included the within-forest disturbance, landscape disturbance and natural environment covariates described above. Given multicollinearity, we selected two variables from each group using three variable-selection methods: (i) we selected variables that we hypothesized to have the greatest influence on species’ presences (hypothesis driven selection); (ii) we used principal component analysis (PCA) on the full set of variables in each group and selected the highest loaded variable on the first two principal axes (PCA selection); and (iii) we ran RF on the full set of variables and selected the two highest ranked in each group (step-wise selection). Results for each method are shown in Extended Data Figs. 5-7.

Next, we used RF to determine species’ partial responses along disturbance gradients (Figs. 3 and 4 and Extended Data Fig. 8). These partial responses give the relative odds ($\exp(\text{logit}(p) - \text{mean}(\text{logit}(p)))$, where p is the probability of species’ presence and logit is $\ln(p/(1-p))$) of detecting each species along a single variable gradient, holding all other variables constant. For this analysis we selected the landscape and within-forest disturbance variables that were most frequently ranked highest in their group across the three variable selection methods.

We then used latent trajectory analysis (LTA), which groups species’ partial responses into homogenous classes, to characterise the main types of response to the selected variables. We built models with up to eight classes and selected that with the lowest Bayesian Information Criterion (BIC) score. LTAs were carried out in R package “lcmm” <http://cran.r-project.org/web/packages/lcmm/lcmm.pdf>. In Figures 3 and 4, we show the LOWESS smoothed response of

each species class along the associated disturbance gradient, with bandwidth set to 0.75.

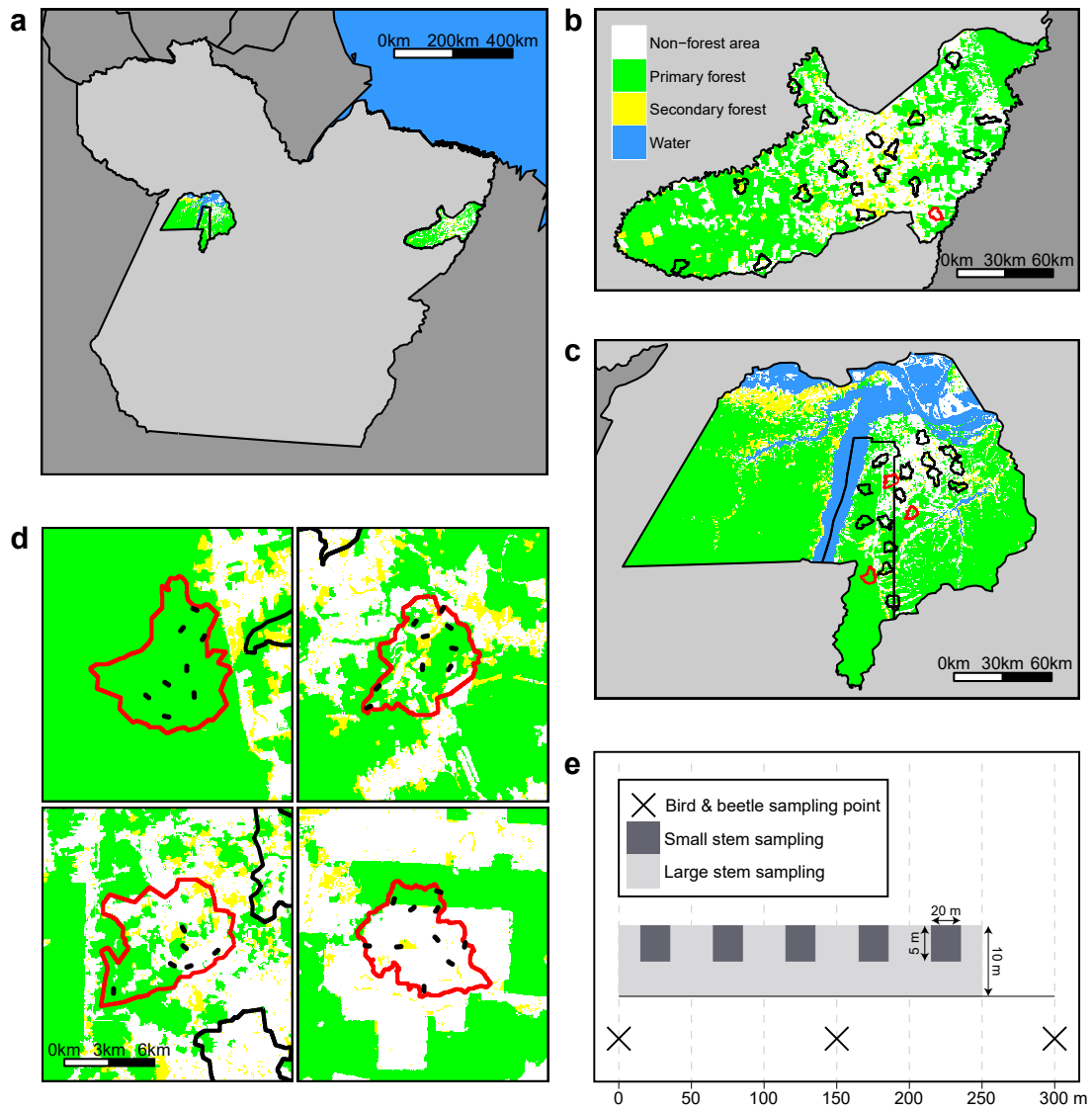
Finally, we investigated the relationship between the disturbance sensitivity of species classes, as determined by LTA, and species traits. To undertake this analysis, we defined a metric that represents the propensity of species classes to be detected along the variable gradients, which thus provides a measure of the sensitivity of the class to disturbance. The measure is:

$$h_c(x) = \int_m^u (x-m)d_c(x) dx - \int_l^m (m-x)d_c(x) dx$$

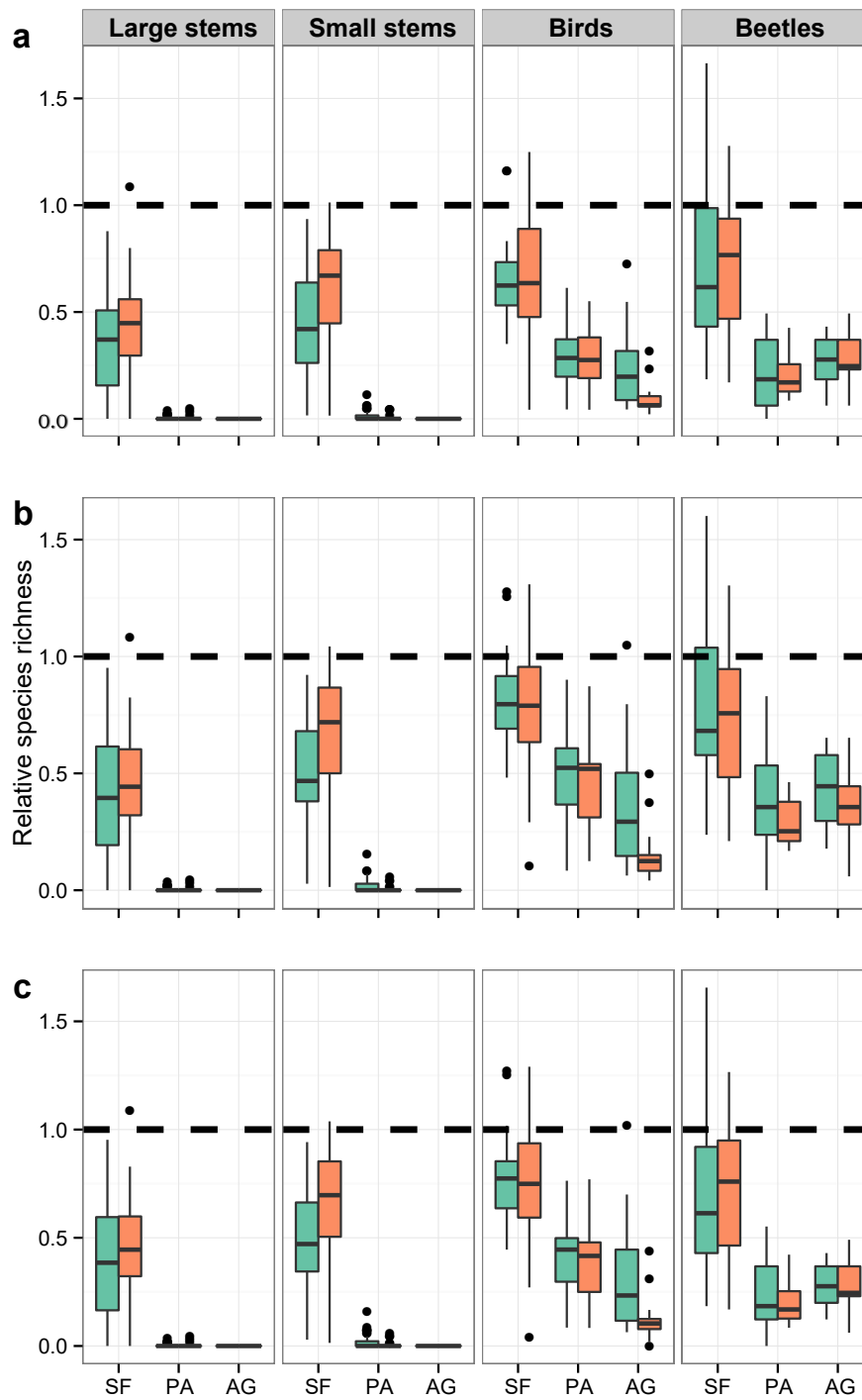
where m , l and u are, respectively, the gradient’s mid-point and lower and upper bounds, and $d_c(x)$ is the relative odds of detecting species class c at point x on the gradient, as determined by RF. We scaled h_c to lie between ± 1 . Values of h_c close to 1 indicate that species class c is much more likely to be detected at the maximum than minimum extreme of the gradient, values close to -1 indicate that species class c is much more likely to be found at the minimum than maximum extreme. Values near 0 indicate that species class c is equally likely to be detected at either extreme. We tested the relationship between h_c and species’ traits by fitting polynomial models weighted by group size. In all cases, the response variable was the average value of the species trait over all species in each class. We investigated polynomial fits up to cubics and selected that with the lowest BIC score.

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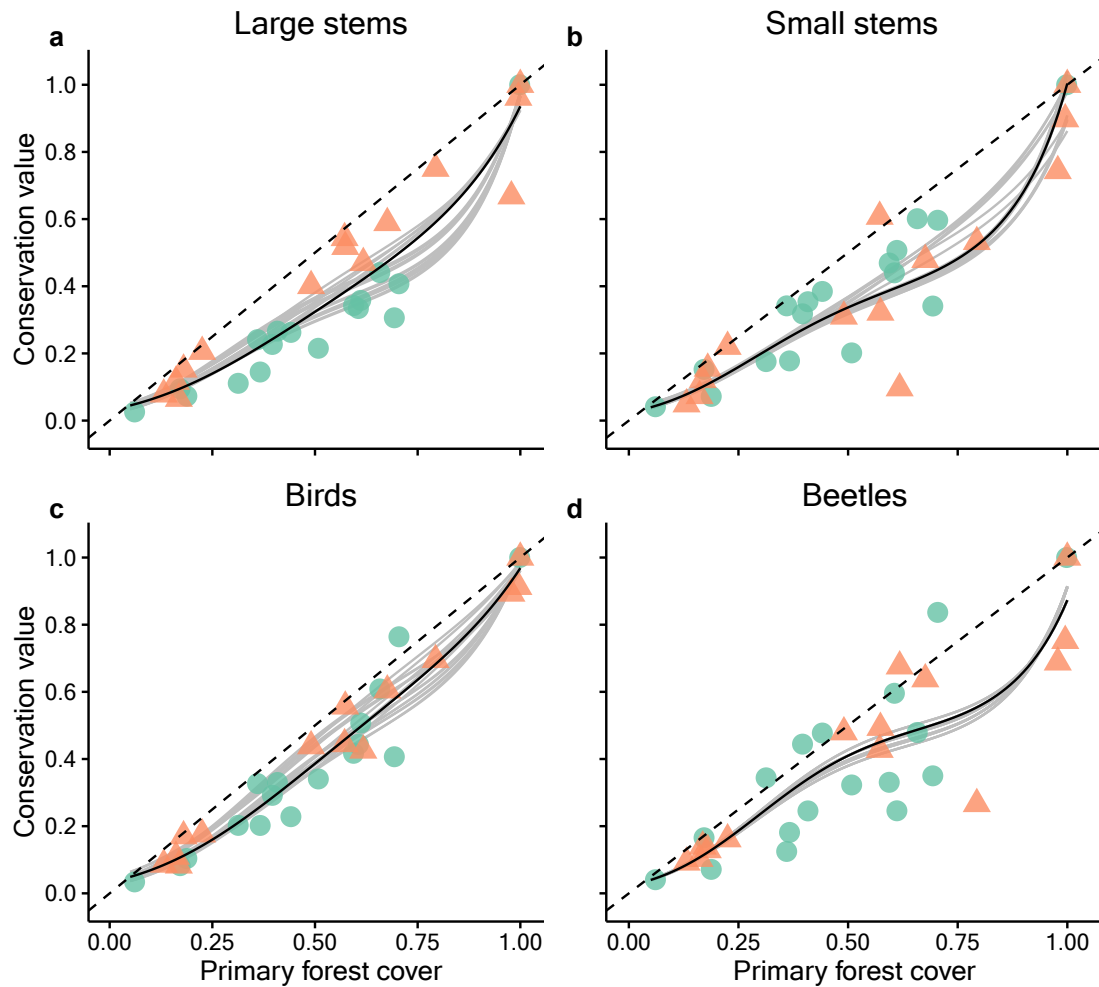
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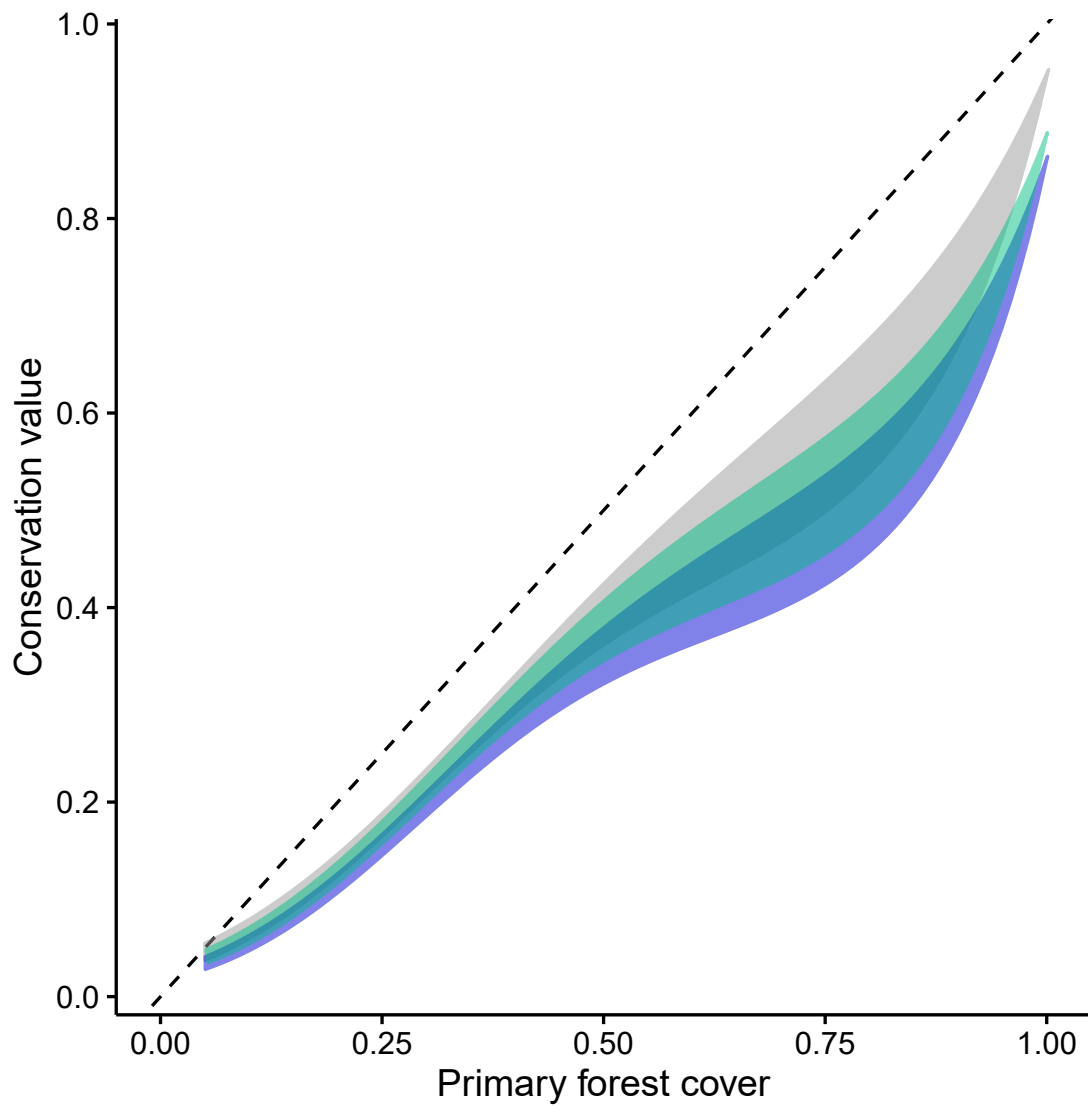
Extended Data Figure 1: Study design. **a**, The location of Paragominas and Santarém within Pará. **b**, **c**, The distribution of study catchments ($n = 36$) within Paragominas and Santarém, respectively. **d**, The distribution of study plots ($n = 175$) in example catchments spanning the gradient of primary forest. Selected catchments are shown in red in **a** and **b**. **e**, Sampling design within each plot.



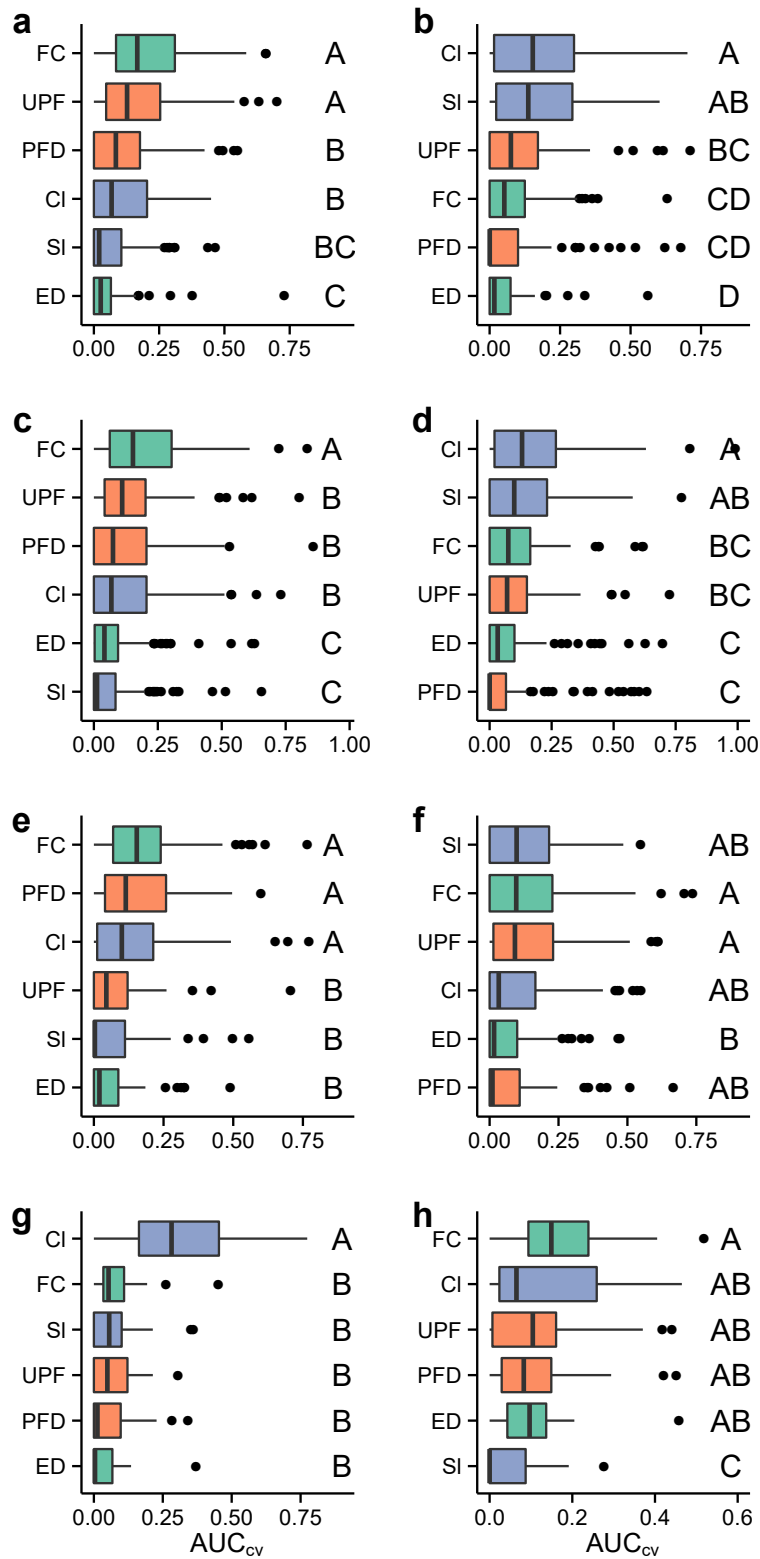
Extended Data Figure 2: Richness of forest species. a-c, The richness of forest species in secondary forests (SF), pastures (PA), and mechanised agricultural lands (AG) relative to the average richness of forest species in all undisturbed and disturbed primary forests (dashed line) in Paragominas (green) and Santarém (orange). Panels show the convex hull (a), automatic (b) and high basal area filters (c) used to classify forest species (see Methods).



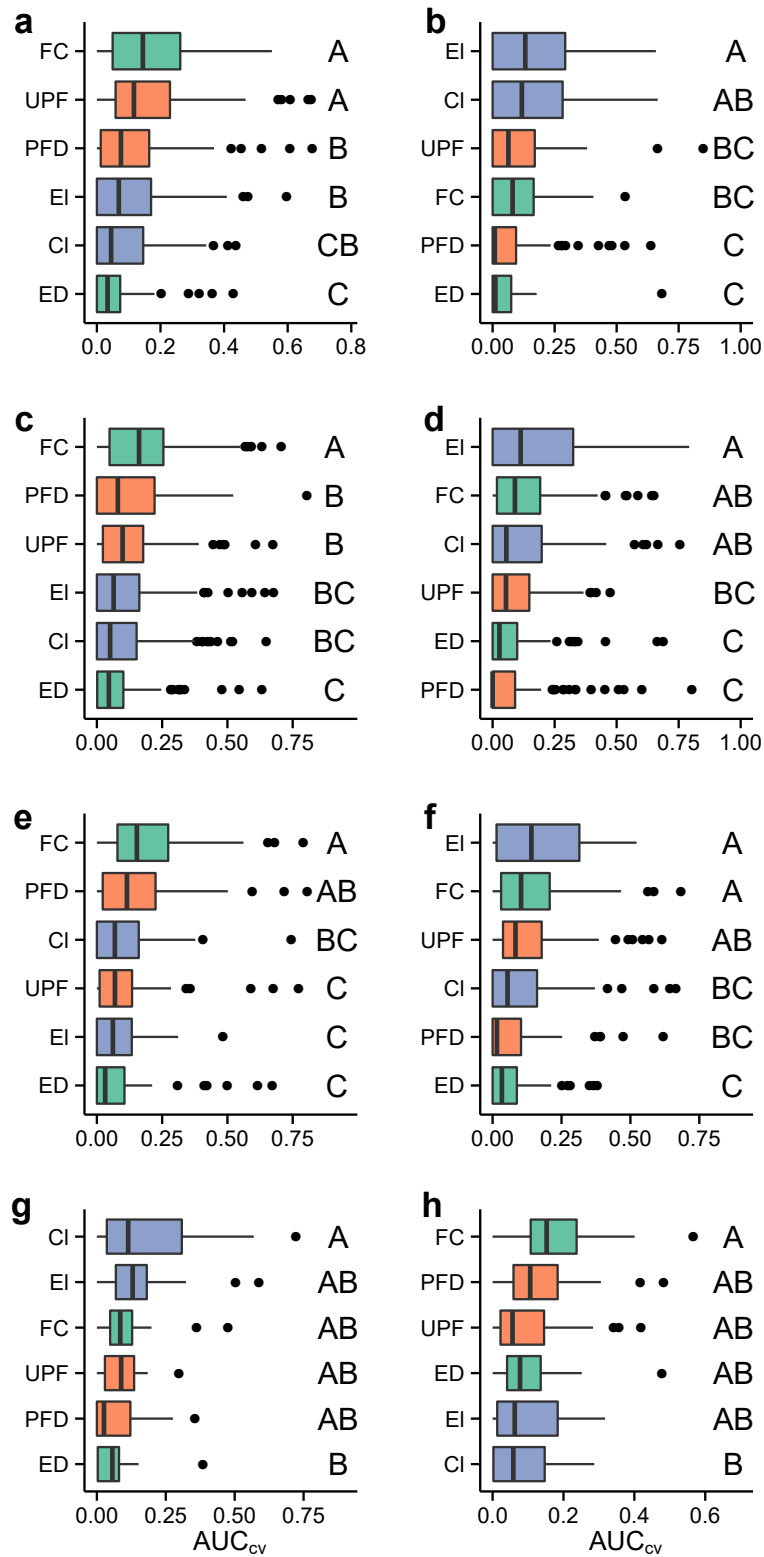
Extended Data Figure 3: Conservation value of primary forests measured by individual taxa. a-d, Estimates of conservation value in the Paragominas (circles) and Santarém (triangles) study regions from large-stemmed plants (a) small-stemmed plants (b) birds (c) and dung beetles (d). Dashed lines show expectations without disturbance. Grey lines show all regressions, with the black solid line showing the median response (see Methods). Values were standardized across study regions and taxa. There was no significant difference between taxa in the median estimate ($F_{3,117} = 1.36$, $P = 0.26$, ANCOVA).



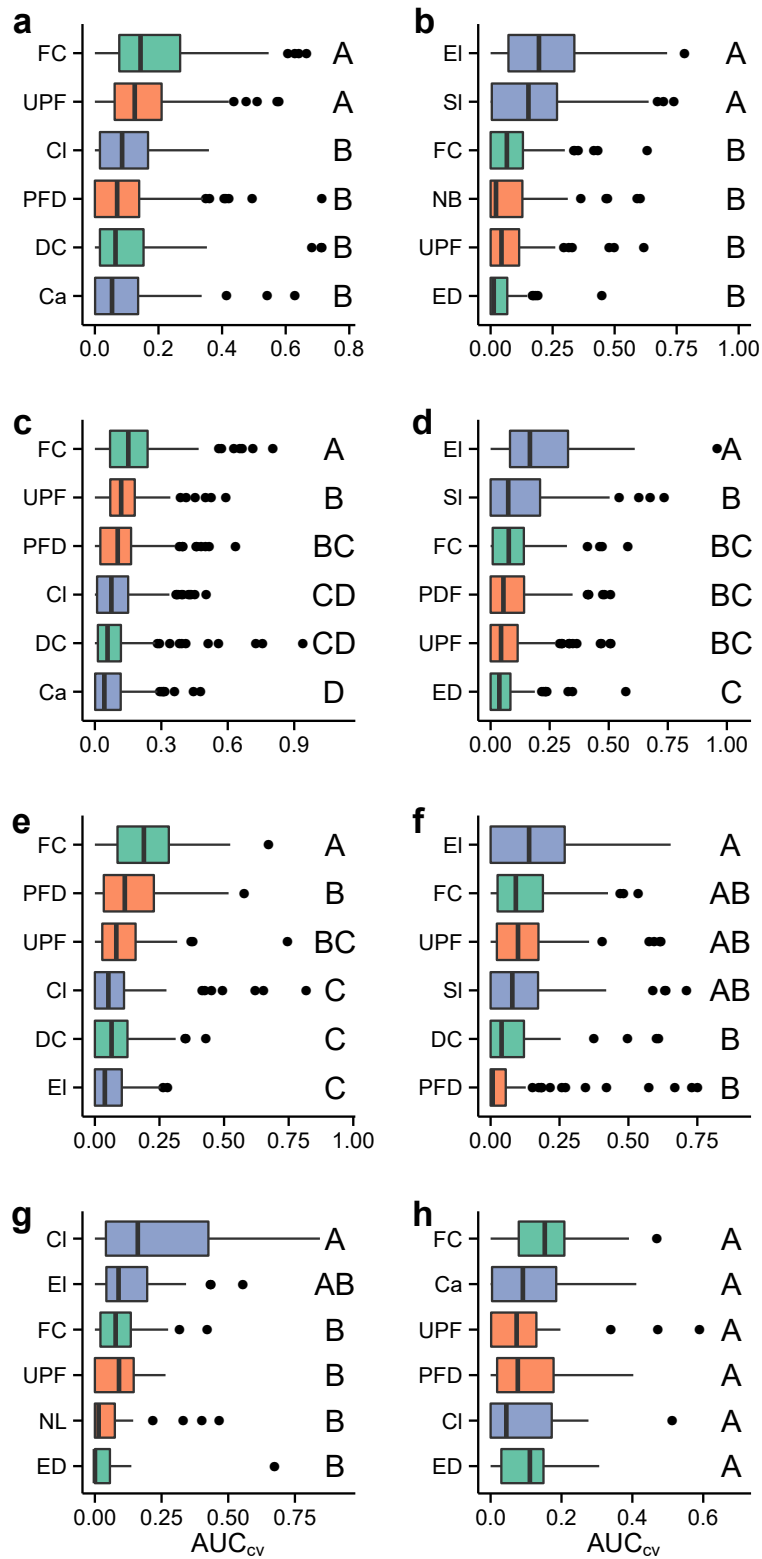
Extended Data Figure 4: Range of conservation value estimates using three alternative sets of reference plots. Mean species density (d_e) is measured by: all disturbed and undisturbed plots in the least disturbed reference catchments (grey shaded region), all undisturbed plots throughout a region (green shaded region), and undisturbed plots in the reference catchments (purple shaded region). See Methods for details.



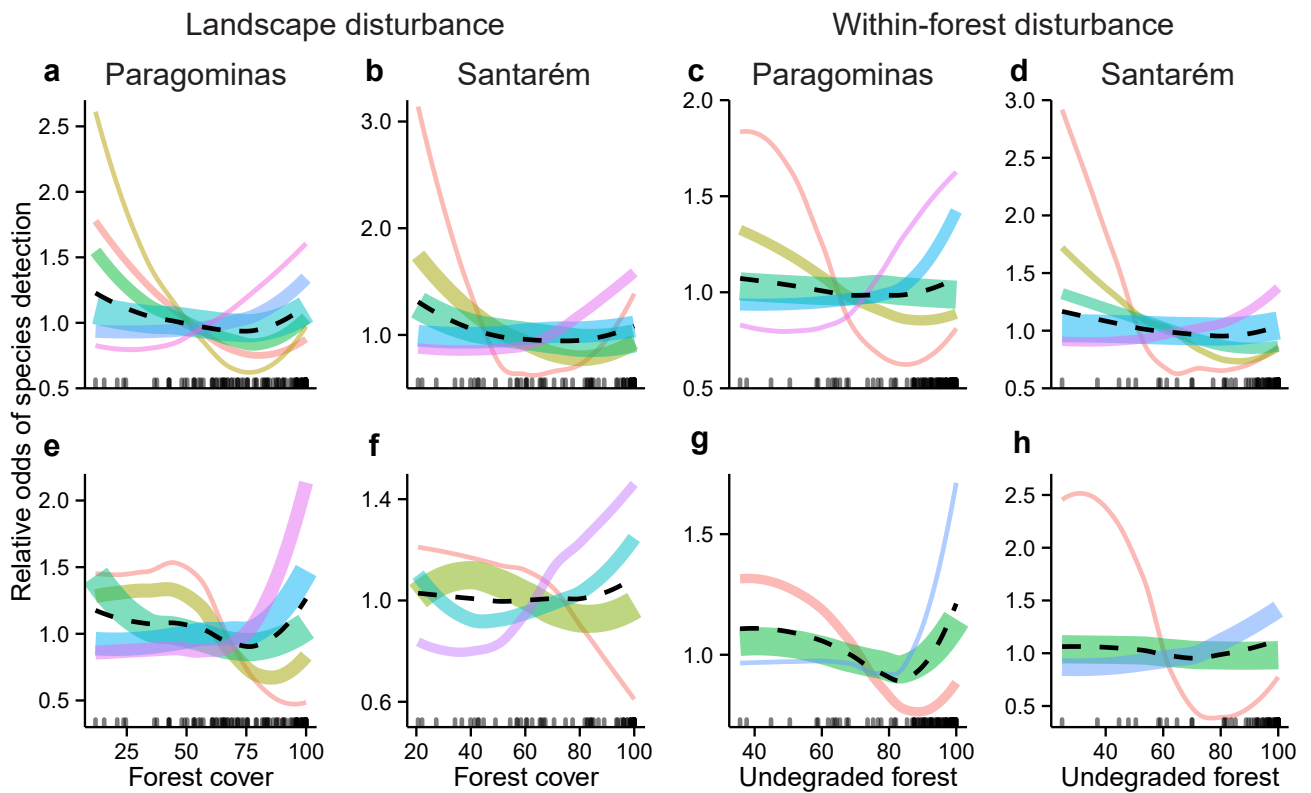
Extended Data Figure 5: The importance of hypothesis selected variable. a-h, Species AUC_{CV} values for each variable in Paragominas (a, c, e, g) and Santarém (b, d, f, h) for large-stemmed plants (a, b), small-stemmed plants (c, d), birds (e, f) and beetles (g, h). Variable importance was measured by the mean AUC_{CV} over all well-modelled species (see Methods). Variable colours denote group membership: green, orange and blue represent landscape disturbance, within-forest disturbance and natural variables, respectively (see Methods for variable descriptions). Letters show the results for multiple pair-wise comparisons of group means using Tukey's range test. Variables which do not share a letter have significantly different mean importance ($P < 0.05$).



Extended Data Figure 6: The importance of PCA selected variable. a-h, Species AUC_{CV} values for each variable in Paragominas (a, c, e, g) and Santarém (b, d, f, h) for large-stemmed plants (a, b), small-stemmed plants (c, d), birds (e, f) and beetles (g, h). Variable importance was measured by the mean AUC_{CV} over all well-modelled species (see Methods). Variable colours denote group membership: green, orange and blue represent landscape disturbance, within-forest disturbance and natural variables, respectively (see Methods for variable descriptions). Letters show the results for multiple pair-wise comparisons of group means using Tukey's range test. Variables which do not share a letter have significantly different mean importance ($P < 0.05$).



Extended Data Figure 7: The importance of step-wise selected variable. a-h, Species AUC_{CV} values for each variable in Paragominas (a, c, e, g) and Santarém (b, d, f, h) for large-stemmed plants (a, b), small-stemmed plants (c, d), birds (e, f) and beetles (g, h). Variable importance was measured by the mean AUC_{CV} over all well-modelled species (see Methods). Variable colours denote group membership: green, orange and blue represent landscape disturbance, within-forest disturbance and natural variables, respectively (see Methods for variable descriptions). Letters show the results for multiple pair-wise comparisons of group means using Tukey's range test. Variables which do not share a letter have significantly different mean importance ($P < 0.05$).



Extended Data Figure 8: Responses of small-stemmed plants and dung beetles to disturbance. a-h, The odds of detecting small-stemmed plants (a-d) and dung beetles (e-h) species groups along gradients of landscape disturbance (a, b, e, f) and within-forest disturbance (c, d, g, h) in Paragominas (a, c, e, g) and Santarém (b, d, f, h) (see Methods). Species groups, shown by different coloured lines, are composed of species with similar disturbance responses (see Methods). Line thickness represents the relative size of the groups.

Extended Data Table 1: Policy interventions used to reduce deforestation and their effect on disturbance.

| <i>Policy intervention</i> | <i>Direct effects on reducing landscape disturbance</i> | <i>Direct effects on reducing within-forest disturbance</i> |
|--|---|--|
| Protected areas (IUCN classes I-IV) | Positive if there is no leakage of deforestation | Positive if park management is effective and leakage of logging is avoided |
| Sustainable-use reserves (IUCN class VI) | Positive if there is no leakage of deforestation | Positive where more sustainable approaches replace conventional approaches, and if leakage of logging is avoided Negative if forest-use is incentivised in areas that would not otherwise be disturbed |
| Legal stipulation to maintain forest cover on private lands | Positive, but there is no stipulation to consider landscape configuration | No likely impact without additional measures |
| Agricultural intensification on deforested lands | Positive if this prevents further forest loss Negative if increased profits encourage further land-use change Negative if the matrix becomes more hostile to forest species, increasing isolation | Positive if reduced fire use in agriculture prevents wildfires No likely impact on selective logging or hunting Negative if there are new spillover effects from agriculture, such as deposition of nutrients and pesticides |
| Industrial and community based reduced impact logging | Positive if economic returns protect forests from clearance Negative when new roads and logging patios increase edge-effects and isolation | Positive if more sustainable approaches replace conventional logging Negative when logging is incentivised in undisturbed forests |
| Protecting forests through moratoria & certification | Positive if this prevents further forest loss and there is no leakage of deforestation | No likely impact without additional measures |

Extended Data Table 2: Forest loss and disturbance in Pará and its areas of endemism. a-c, The loss of primary forest conservation value from forest loss and forest disturbance in forest loss-equivalent terms across c. 50 km² cells covering all land in Pará (**a**), private lands and sustainable use reserves only (**b**), and private lands only (**c**). Disturbance losses are calculated using the median estimate of conservation value with the lower and upper bound range in parentheses (see Methods). *Area* is the total area of the region in km². *Forest area* gives the area of the region that was or is primary forest cover in km². *Forest loss* gives the total loss of primary forest in km². *Disturbance* gives the loss of conservation value due to disturbance in km². *Relative* gives the disturbance-mediated loss of conservation value relative to that from forest loss.

| All land (a) | | | | | |
|---|-----------|-------------|-------------|---------------------------|---------------|
| Region | Area | Forest area | Forest loss | Disturbance | Relative (%) |
| Pará state | 1,259,916 | 1,141,659 | 245,288 | 171,695 (130,827-187,328) | 70 (53-76) |
| Belém AoE | 138,351 | 131,637 | 80,861 | 15,431 (10,904-18,743) | 19 (13-23) |
| Guiana AoE | 273,692 | 246,802 | 12,290 | 37,044 (29,134-37,124) | 301 (237-302) |
| Rondônia AoE | 66,222 | 56,876 | 5,728 | 9,366 (7,227-10,103) | 163 (126-177) |
| Tapajós AoE | 418,201 | 388,738 | 37,783 | 65,221 (50,117-70,951) | 173 (133-188) |
| Xingu AoE | 321,304 | 294,543 | 109,687 | 40,502 (30,173-45,918) | 37 (28-42) |
| Private lands + sustainable use reserves (b) | | | | | |
| Pará state | 918,694 | 820,636 | 242,578 | 122,881 (92,144-139,033) | 51 (38-57) |
| Belém AoE | 136,405 | 129,691 | 80,432 | 15,099 (10,652-18,358) | 19 (13-23) |
| Guiana AoE | 157,288 | 137,468 | 12,084 | 20,879 (16,278-21,497) | 173 (135-178) |
| Rondônia AoE | 55,109 | 45,832 | 5,559 | 7,631 (5,859-8,379) | 137 (105-151) |
| Tapajós AoE | 271,761 | 250,309 | 36,466 | 43,980 (33,303-49,795) | 121 (91-137) |
| Xingu AoE | 253,884 | 232,681 | 109,029 | 30,891 (22,572-36,260) | 28 (21-33) |
| Private lands (c) | | | | | |
| Pará state | 530,931 | 490,200 | 230,293 | 68,694 (49,731-82,024) | 30 (22-36) |
| Belém AoE | 129,570 | 125,209 | 79,072 | 14,324 (10,077-17,435) | 18 (13-22) |
| Guiana AoE | 55,068 | 42,069 | 11,615 | 6,567 (4,912-7,491) | 57 (42-64) |
| Rondônia AoE | 33,676 | 28,033 | 4,551 | 4,692 (3,574-5,248) | 103 (79-115) |
| Tapajós AoE | 125,089 | 118,409 | 31,401 | 21,982 (16,126-26,436) | 70 (51-84) |
| Xingu AoE | 196,824 | 182,752 | 106,276 | 22,159 (15,783-26,675) | 21 (15-25) |