Title: Tropical nature reserves are losing their buffer zones, but leakage is not to blame

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Abstract

Tropical forests provide important ecosystem services to humanity, yet are threatened by habitat loss resulting from deforestation and land-use change. Although reserves are considered the cornerstones of conservation efforts in the tropics, their efficacy remains equivocal. One question that remains unresolved is whether leakage – the unanticipated displacement of deforestation from inside reserves into the unrestricted zones just beyond a reserve's administrative boundary – is common around tropical forest reserves, or whether the zones are acting as buffers between the protected area and the outside world. To resolve this question, we used the Landsat-derived Global Forest Change dataset to estimate deforestation rates between 2000 and 2012 inside and outside of 60 nature reserves spread across the tropics. Deforestation rates inside reserves (within 5 km of the administrative boundary) were generally lower than those immediately outside the reserves (i.e. in buffer zones 0-10 km from the boundary), suggesting that reserves are effective at protecting forests. We hypothesised that leakage would result in greater deforestation rates in reserve buffer zones than in the broader reserve landscapes, but such a pattern was observed in only five African sites, suggesting that leakage does not often occur on the edge of established reserves. However, roughly 80% of reserves experienced deforestation rates that increased gradually from their interiors to the outer periphery of their buffer zones. Thus, while leakage may not be a pervasive phenomenon around tropical reserves worldwide, tropical reserves are often losing their buffer zones, resulting in increased isolation that could have ramifications for ecosystem services provisioning and tropical conservation strategies.

Keywords (5 max): Conservation; Global Forest Change dataset; leakage; protected areas; remote sensing

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Introduction

Tropical forests provide important ecosystem services to humanity, and thus their protection is key. Serving as globally significant stores of carbon, tropical forests also harbour the majority of terrestrial diversity, affect the earth's energy balance via their influence on hydrology, and support individual and community livelihoods across multiple scales (Naughton-Treves *et al.*, 2005; Bonan, 2008). However, habitat loss resulting from deforestation and land-use change serves as a core destructive force in the tropics (Asner *et al.*, 2005; Pereira *et al.*, 2010) and threatens the provisioning of these services. Designed to curb habitat loss and associated declines in biodiversity, protected areas are widely considered the cornerstones of modern conservation efforts in the context of rapid anthropogenic change (Dudley, 2008). Over the past several decades, the global protected area system has seen rapid expansion, to the extent that roughly 14.6% of the planet's terrestrial surface is now covered by ostensibly protected areas (Naughton-Treves *et al.*, 2005; Butchart *et al.*, 2015).

However, measuring the success of conservation action in protected areas remains challenging (Parrish *et al.*, 2003). Diverse, and at times competing, agenda imposed on protected areas inhibit the creation of a unified or globally accepted metric of protected area efficacy (Chape *et al.*, 2005; Naughton-Treves *et al.*, 2005). Meanwhile, from a conservation biology perspective, available evidence suggests that the success of protected areas at preserving biodiversity depends greatly on the effectiveness of local enforcement agencies and thus varies on a global scale (Leverington *et al.*, 2010; Geldmann *et al.*, 2013). In the tropics, protected areas have been able to prevent, or at least curtail, land clearing and deforestation within their boundaries (Bruner *et al.*, 2001; Naughton-Treves *et al.*, 2005). However, deeming a protected area with lower deforestation rates within its boundaries than in its immediate surroundings as "successful" may be unjustified if deforestation is, in fact, simply shifted to the protected area's exterior (Gaveau *et al.*, 2009; Joppa and Pfaff, 2010). This phenomenon is known as "leakage" – the unanticipated displacement of the very deforestation that protected areas are intended to control against into nearby, unrestricted areas beyond their administrative boundaries (Ewers and Rodrigues, 2008; Murray, 2008).

Quantifying leakage within the vicinity of protected areas is crucial because of the potential ramifications of leakage. For example, carbon management initiatives, such as Reducing Emissions from Deforestation and Forest Degradation (REDD+) projects, can be subverted by leakage if the deforestation that they aim to restrict within a specified area is offset by magnified deforestation rates elsewhere (Venter and Koh, 2012). Land-use change around protected areas can also reduce their core area and introduce detrimental edge effects (Hansen and DeFries, 2007). Such processes can constrain the abilities of protected areas to maintain species richness and ecosystem functions, and reduce additional conservation options in areas adjacent to the protected areas themselves (Ewers and Rodrigues, 2008).

Leakage analyses generally involve identifying any disproportionate spatial distribution of human impacts, quantified by metrics such as deforestation or habitat loss, across a reserve and its surrounding area. While many previous studies have analysed spatial deforestation patterns across reserve boundaries (see Joppa and Pfaff, 2010), few have attempted to quantify leakage (Clark *et al.*, 2008). Oliveira *et al.* (2007), for example, identified leakage arising from newly created forest concessions in the Peruvian Amazon, and others have explicitly identified evidence of leakage events in East Africa's tropical evergreen forests (Pfeifer *et al.*, 2012). However, little is known about the pervasiveness of leakage across the global network of reserves within tropical forest ecosystems

In this study, we aimed to fill critical knowledge gaps with respect to leakage as a global occurrence. To assess the prevalence of leakage around tropical forest reserves, we quantified deforestation that occurred between 2000 and 2012 near reserve boundaries for a pan-tropical network of 60 protected areas, comparing deforestation rates inside reserves with those on land bordering the reserves and in the wider landscape. Defining leakage as deforestation rates in border areas that exceed those within both the reserve and the wider landscape, we analysed the prevalence of leakage across the protected area network. If leakage were occurring, deforestation trends would be illustrated by a piece-wise function in which deforestation trends inside and immediately outside reserves differ quantifiably and exhibit a sharp change or jump at the reserve boundary. Deforestation immediately outside reserves would also likely be highest closest to the reserve boundary and decrease with distance from the boundary. If leakage were not occurring, the reserve boundary would have no effect on deforestation and we would expect the same deforestation trend inside the reserve as immediately outside the reserve, illustrated by a linear trend in deforestation across the reserve boundary.

Methods

Selection of protected areas

The 60 tropical forest reserves included in this study (20 each in Africa, the Americas, and the Asia-Pacific region) were the same as those studied by Laurance *et al.* (2012) (Fig. 1). Shapefiles of the boundaries of each of the 60 reserves were downloaded from the World

Database on Protected Areas (WDPA) (IUCN and UNEP-WCMC, 2014) which offers a comprehensive global spatial dataset inventory of the world's marine and terrestrial reserves. Accurate shapefiles of eight of the reserves were not available on the WDPA website and thus were obtained from academic experts conducting research at those sites (Table A.1.)

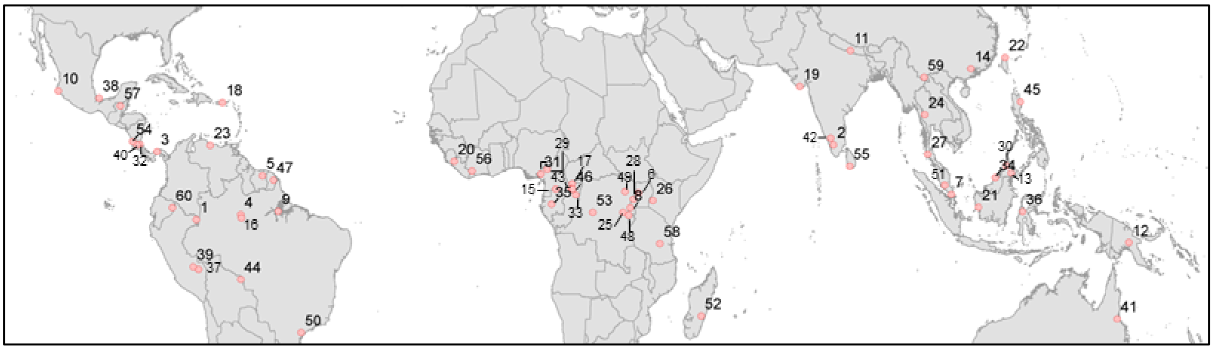

Figure 1. Map of all 60 reserves included in this study, with 20 reserves each in the Americas, Asia-Pacific, and Africa. Alphabetically: 1 = Amacayacú National Park (NP), Colombia; 2 = Anamalai Tiger Reserve, India; 3 = Barro Colorado Island Biological Station, Panama; 4 = Biological Dynamics of Forest Fragments Project, Brazil; 5 = Brownsberg Nature Park, Suriname; 6 = Budongo Forest Reserve, Uganda; 7 = Bukit Timah Nature Reserve (NR), Singapore; 8 = Bwindi Impenetrable NP, Uganda; 9 = Caxiuanã National Forest, Brazil; 10 = Chamela-Cuixmala Reserve, Mexico; 11 = Chitwan NP, Nepal; 12 = Crater Mountain Wildlife Management Area, Papua New Guinea; 13 = Danum Valley Conservation Area, Malaysia; 14 = Dinghushan Mountain NR, China ; 15 = Dja Faunal Reserve, Cameroon; 16 = Ducke, Brazil; 17 = Dzanga-Sangha Special Reserve, Central African Republic; 18 = El Yunque (Luquillo) National Forest, Puerto Rico; 19 = Gir NP and Wildlife Sanctuary, India; 20 = Gola Rainforest NP, Sierra Leone; 21 = Gunung Palung NP, Indonesian Borneo; 22 = Hahpen (Fushan) NR, Taiwan; 23 = Henri Pittier NP, Venezuela; 24 = Huai Kha Khaeng Wildlife Sanctuary, Thailand; 25 = Kahuzi Biéga NP, Democratic Republic of the Congo; 26 = Kakamega Forest National Reserve, Kenya; 27 = Khao Yai NP, Thailand; 28 = Kibale NP, Uganda; 29 = Kilum-Ijim/Mount Oku Forest Reserve, Cameroon; 30 = Kinabalu NP, Malaysia; 31 = Korup NP, Cameroon; 32 = La Selva Biological Station, Costa Rica; 33 = Lac Télé Community Reserve, Republic of the Congo; 34 = Lambir Hills NP, Malaysia; 35 = Lopé NP, Gabon; 36 = Lore Lindu NP, Indonesia; 37 = Los Amigos Conservation Concession, Peru; 38 = Los Tuxtlas Biosphere Reserve, Mexico; 39 = Manú NP, Peru; 40 = Monteverde Protective Zone, Costa Rica; 41 = Mount Spec/Paluma Range NP, Australia; 42 = Mudumalai Biosphere Reserve, India; 43 = Ndoki (Dzanga-Ndoki) NP, Central African Republic; 44 = Noel Kempff Mercado NP, Bolivia; 45 = Northern Sierra Madre Natural Park, Philippines; 46 = Nouabalé-Ndoki NP, Republic of the Congo; 47 = Nouragues National NR, French Guiana; 48 = Nyungwe Forest NR, Rwanda; 49 = Okapi Wildlife Reserve NP, Democratic Republic of the Congo; 50 = Paranapiacaba, Brazil; 51 = Pasoh Forest Reserve, Malaysia; 52 = Ranomafana NP, Madagascar ; 53 = Salonga NP, Democratic Republic of the Congo; 54 = Santa Rosa NP, Costa Rica; 55 = Sinharaja Forest Reserve NP, Sri Lanka; 56 = Taï NP, Cote d'ivoire; 57 = Tikal NP, Guatemala; 58 = Udzungwa Mountains NP, Tanzania; 59 = Xishuangbanna NR, China; 60 = Yasuni NP, Ecuador.

Estimating deforestation rates with the Global Forest Change dataset

Spatial deforestation patterns around each of the 60 shapefiles were analysed using ArcMAP 10.0. First, five "inner" rings, each of width 1 km, were created from the reserve boundary inwards towards its core (Fig. 2). If the reserve was too small for all five rings to fit within its interior (i.e. the distance from its core to its boundary was < 5 km), the maximum number of rings less than 5 that could fully fit within its interior was created. Next, 10 "outer" rings, each of width 1 km and representing a potential deforestation leakage zone surrounding the reserve, were created emanating from the reserve boundary 10 km outwards into its immediately surrounding region. While the extent of such leakage zones or "zones of influence" are undoubtedly highly variable depending on the realities of any given reserve (Defries *et al.*, 2010), we selected a leakage zone of 10 km here in light of a study by Dewi *et al.* (2013) on protected areas in the Asia-Pacific and Africa, which applied a zone of influence of at least 10 km around protected areas in order to quantify deforestation changes due to forest protection inside the protected area. Also, being cognizant that spatial heterogeneity is scale-dependent (Turner *et al.*, 1989; Wu *et al.*, 2002), we determined that it was reasonable to apply a standard fixed ring width of 1 km here given the range of reserve areas (from 1.6 to 35012 km^2) in our study. Using ring sizes greater than 1 km would render our attempts to quantify spatial patterns of deforestation within reserve interiors for many of the smaller reserves non-meaningful.

A third and final spatial zone comprising the region from the outermost edge of the outer rings (i.e. 10 km from the reserve edge) to 25 km from the reserve edge was created as the reserve "landscape." We used a 25 km landscape or reference area after drawing insights from a study by DeFries *et al.* (2005) on forest loss surrounding 198 highly protected areas throughout the world's tropical forests. DeFries *et al.* (2005) found similar forest cover and change values over the 20 years prior to their study around the protected areas at distances of 25, 50, 75, and 100 km from the reserve boundaries. DeFries *et al.* (2005) ultimately applied a 50 km perimeter around their reserves as an "arbitrary but reasonable" distance to capture ecological interactions between the reserves and their surroundings. However, as their reserves were all relatively large in size (greater than 256 km^2) and a quarter of the reserves in our study were less than 256 km^2 in area, we chose to define reserve "landscape" here as the area contained by the smaller 25 km perimeter around reserves. Further details on the spatial framework which we constructed to analyse leakage are provided in Fig. A.1.

Forest cover and change data were downloaded directly from the online Global Forest Change dataset (GFCD) of Hansen *et al.* (2013). The GFCD, made publicly available in February 2014, is the first moderate to high-resolution (30 m) globally consistent map of forest cover, loss, and gain from 2000-2012 (Hansen *et al.*, 2013). From the GFCD, raster files of "Tree canopy cover for year 2000," "Global forest cover loss 2000-2012," and "Data mask" were downloaded over each of the 60 reserves in our study. In "Tree canopy cover for year 2000," each grid cell is assigned a value from 0-100 representing the percentage of canopy closure for all vegetation taller than 5m in height within that grid cell. In "Global forest cover loss 2000-2012," grid cells are encoded as either 1 (representing loss, or change from a forest to non-forest state from year 2000 to year 2012) or 0 (representing no loss between that same time period) (see Fig. 2B). The “Data mask” files distinguish terrestrial surfaces from water bodies. If a reserve and its surrounding region spanned multiple GFCD raster files, we mosaicked together the raster files in ArcMAP using the relatively conservative minimum mosaic operator, in which the output cell value of any overlapping areas between the rasters is reported as the minimum value of the overlapping raster cells.

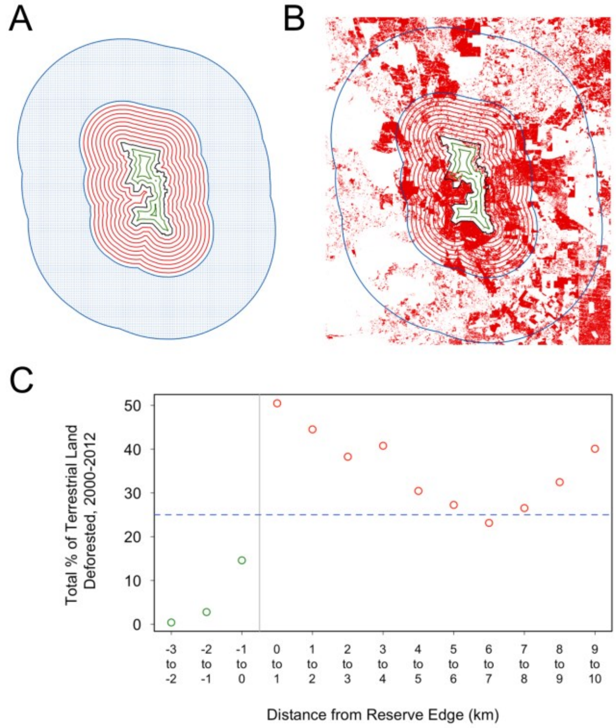

Figure 2. Spatial framework for quantifying spatial deforestation patterns across reserve boundaries. (A) Schematic of spatial framework using the example of Pasoh Forest Reserve (black outline), Malaysia. Green lines represent the “inner” rings up to 5 km within the reserve boundary, red lines represent the 10 “outer” buffer zone rings up to 10 km surrounding the reserve boundary, and the blue stippled region represents the “landscape” zone 10-25 km from the reserve edge. (B) As in (A), overlain with 2000-2012 forest loss pixels in red from the Global Forest Change dataset. (C) Deforestation that occurred between 2000-2012 in the inner (green) and outer (red) regions, separated by a vertical grey line, and compared with deforestation in the surrounding landscape (horizontal dashed blue line).

To determine total forested area in year 2000 across the reserves, all pixels with values > 10 in the “Tree canopy cover for year 2000” files were considered as forest cover, in accordance with the standard FAO definition of forest as land area with > 10% tree crown cover (FAO, 2010). These forest cover pixels were summed using ArcMAP’s Zonal Statistics tool within each of the (maximum) five inner rings, each of the 10 outer rings, and within the 10-25 km landscape zone. Forest pixels were then converted into land area (km^2), with each representing an area of approximately 30 m x 30 m. Deforestation within each of the inner rings, each of the outer rings, and the 10-25 km landscape zone was quantified in two ways: 1) by dividing the area of total forest loss between 2000 and 2012 (from the "Global forest cover loss 2000-2012" raster file) by total forested area in year 2000, and expressing as the percentage of year 2000 forested land area that was deforested between 2000 and 2012, hereafter "deforestation (% forest)" (Eq. 1); and 2) by dividing the area of total forest loss between 2000 and 2012 by total terrestrial area (from the "Data mask" GFCD files), and expressing as the percentage of terrestrial land area deforested between 2000 and 2012, hereafter "deforestation (% land)" (Eq. 2).

$$Deforestation\ (\%\ forest) = \frac{Total\ forest\ loss\ (2000-2012)}{Total\ forested\ area\ (2000)} \qquad \text{(Eq. 1)}$$

$$Deforestation\ (\%\ land) = \frac{Total\ forest\ loss\ (2000-2012)}{Total\ terrestrial\ area} \qquad \text{(Eq. 2)}$$

Both deforestation (% forest) and deforestation (% land) were calculated in this study since both metrics offer unique insights into the nature of observed deforestation. The latter provides an indication of absolute forest-clearing rates, while the former contextualises forest loss within the framework of existing forest cover, thus detailing changes in the local availability of forest resources over time.

We defined leakage as disproportionately higher rates of deforestation in a reserve's unprotected 10 km surrounding area when compared to the reserve interior as well as a "baseline" deforestation rate from the 10-25 km broader landscape surrounding a reserve. These "baseline" rates were assumed to serve as baselines for the regions within which each reserve exists. In general, evaluations of the impact of a protected area must involve a comparison of what happened in the protected area versus a counterfactual area to see what would have happened in that same area had it not been protected. The underlying assumption is that any differences arising from the comparison are a result of the protection status of the reserve. The counterfactual can be determined by metrics such as country-wide or regional deforestation rates, deforestation rates in the immediate vicinity or buffer zone of the reserve, or historical deforestation rates prior to reserve establishment (Joppa and Pfaff, 2010). In this study, we combined the former two (spatial) approaches, as recommended by Ewers and Rodrigues (2008), using deforestation rates in a reserve's 10 km outer buffer zone to assess the presence of leakage against the "baseline" counterfactual of deforestation rates in the 10-

25 km regional landscape zone surrounding the reserve. To test for leakage, differences in the response variable of 2000-2012 deforestation (both % forest and % land) across the three categorical explanatory variables of inner reserve region, outer reserve buffer region, and the 10-25 km landscape zone were analysed for significance with a Kruskal-Wallis test and post-hoc Wilcoxon-Mann-Whitney (Wilcoxon matched pairs) tests.

Statistical analyses of deforestation trends

We log10 transformed the observed deforestation rates (replacing zero values with the lowest non-zero values calculated across sites) and analysed the data by (a) fitting smoothed curves and interpreting them visually; and (b) fitting linear models and using formal inference tests. For the curve-fitting approach, we fitted splines through each dataset using the *smooth.spline* function in the *car* package of R, with 4 degrees of freedom (see Results, Fig. 3). Estimates of deforestation from concentric zones are likely to show a degree of serial autocorrelation, with implications when making inferences. Applying the Durbin-Watson test to residuals of the spline models, we obtained an average value of 1.5 with a standard error of 0.065. Since $d = 2$ indicates no autocorrelation, and $d < 1$ indicates strong positive autocorrelation, the observed d values indicate residuals were only weakly autocorrelated (Gujarati and Porter, 2009), so no further consideration was given to this.

The formal analysis focussed on fitting linear models to log-transformed deforestation rates at each site (using the *lm* function in R), and then testing for marked changes in deforestation rates at reserve boundaries by also fitting linear models to the inner and outer zones separately. Regressions for inner deforestation were only conducted for reserves with greater than two deforestation bands in their interiors, i.e. reserves that were large enough to fit at least 3 1-km wide rings in their interiors. Then, we tested whether the piecewise regression model segmented at the reserve boundary led to an improvement of fit over the original linear regression model by computing the Akaike Information Criterion (AIC) value for each model. AIC values were based on the log-likelihood of the model given the data and penalized by the number of parameters included in the model. The two models were considered similar if $\Delta AIC < 2$, while a model with the lower AIC was considered the better supported if $\Delta AIC \geq 2$.

All statistical analyses were conducted in R version 3.0.2 (R Core Team, 2013) using the R Studio version 0.98.932 (RStudio, 2012) environment.

Results

Deforestation rates across the pantropical network

The average deforestation rate (% land / year) within reserves was 0.073 ± 0.009% (mean ± standard error), which was significantly lower ($p < 0.0001$) than that observed immediately outside the reserve boundaries (0.29 ± 0.02%) and the wider landscape (0.32 ± 0.07%) (Table 1, Table A.2). All but 9 of the 60 reserves had lower deforestation rates inside their boundaries than observed in the wider landscape (i.e. deforestation rates in inner rings were consistently below the landscape average), the exceptions being Kakamega Forest National Reserve (site 26), Lac Télé Community Reserve (33), and Lopé National Park (35) in Africa; Brownsberg Nature Park (5), El Yunque National Forest (18), and Nouragues National Nature Reserve (47) in the Americas; and Gir National Park and Wildlife Sanctuary (19), Lore Lindu National Park (36), and Mount Spec National Park (41) in Asia-Pacific (Fig. A.2). Additionally, the majority of reserves (37 of 60) had consistently lower rates of deforestation inside their boundaries than in their outer zones, suggesting the outer zones were acting as a buffer. However, there was considerable variation among reserves (Fig. A.2).

Globally, there was no significant difference between average deforestation rates (% land / year) in the outer and landscape regions ($p > 0.1$) (Table 1, Table A.2). Thus, there was no evidence that leakage (defined as deforestation rates in the outer zone that exceed those in both the inner zone and wider landscape) is rife. However, our study pinpoints sites, all in Africa, where deforestation patterns are consistent with leakage, namely Dzanga-Sangha, Kahuzi Biéga, Kakamega, Lac Télé, and Lopé (Fig. A.2). At these five sites, deforestation rates significantly increased from the reserve core to the reserve edge, only to significantly decrease from the reserve edge out towards the broader landscape. For 12 other reserves (in Africa: Budongo, Bwindi, Nyungwe; in the Americas: Chamela-Cuixmala, Ducke, Los Tuxtlas, Nouragues; in Asia-Pacific: Huai Kha Khaeng, Khao Yai, Lore Lindu, Northern Sierra Madre, Pasoh), most of the 10 buffer zone rings featured deforestation rates that exceeded those both in reserve interiors and in the surrounding landscape, but deforestation patterns were not conclusively indicative of leakage (e.g. deforestation did not significantly increase from reserve core to reserve edge, or deforestation in the buffer zone did not significantly decrease from reserve edge out towards landscape) (Fig. A.2).

Globally, deforestation rates calculated as a percentage of forested area were significantly greater than rates calculated as a percentage of land area. The average annual inner deforestation (% forest) rate between 2000 and 2012 (0.080 ± 0.010%) was significantly less then the outer buffer deforestation (% forest) rate (0.35 ± 0.03%) ($p <$ 0.0001), which in turn was significantly less than the landscape deforestation (% forest) rate

(0.41 ± 0.09%) ($p < 0.05$).(Table 1, Table A.2). So, rather than leakage, these data provide evidence for buffer areas less rapidly declining in forest cover than the wider landscape globally.

Regionally, inner, outer, and landscape deforestation (% land) rates generally saw significantly lower inner deforestation rates than deforestation in both the outer and landscape zones, with outer deforestation being statistically similar to that in the broader landscape (Table 1, Table A.2). Deforestation (% forest) in Africa and the Asia-Pacific region showed similar qualitative patterns, although deforestation in the Americas was significantly different across all three reserve regions, continually increasing from the reserve interior out to its broader landscape (Table 1).

While the reserves in Africa featured the greatest percentage of forest cover in 2000 when compared to reserves in the Americas and Asia-Pacific, they also featured some of the lowest deforestation rates (both % land and % forest) across the inner, outer, and landscape regions (Table 1). On the other hand, Asia-Pacific reserves featured both the lowest percentage of forest cover yet the highest deforestation rates (both % land and % forest) across the inner, outer, and landscape regions (Table 1). Across the African reserves, both % land and % forest deforestation rates were similar to each other given the relatively high percentage of forested land in 2000 (Table 1). However, reserves in the Americas and, to an even greater extent, in the Asia-Pacific region experienced higher deforestation (% forest) rates than deforestation (% land) rates (Table 1), an indication of the magnitude of existing forest-cover loss and the high demand for forest resources from these geographies.

When compared to deforestation values reported above, all of which were based on the spatial framework of quantifying deforestation 5 km into reserves and 10 km just outside of reserves, we found similar qualitative results when comparing deforestation rates up to 10 km into reserves with those up to 10 km outside of reserves, as well as those up to 5 km into reserves with those up to 5 km outside of reserves (results not shown).

Table 1. Summary of deforestation rates from 2000 to 2012 in the inner 5 km, outer 10 km, and 10-25 km landscape regions of tropical forest reserves, aggregated globally and across each of the three major world regions. Deforestation rates are presented as both average annual percentage of land deforested from 2000-2012 ± SE (% land), and average annual percentage of year 2000 forested land that was deforested from 2000-2012 ± SE (% forest). Percentages of terrestrial forest cover in year 2000 are also presented. Significant differences at the 95% confidence level within columns are identified with superscript letters; Table A.2 details the test statistics associated with these statistical analyses. Global inner, outer, and landscape deforestation rates are means from 60 samples each. Inner, outer, and landscape deforestation rates by world region are means from 20 samples each.

	GLOBAL			AFRICA			THE AMERICAS			ASIA-PACIFIC		
Region	Annual deforestation rate		% forested (2000)	Annual deforestation rate		% forested (2000)	Annual deforestation rate		% forested (2000)	Annual deforestation rate		% forested (2000)
	% land	% forest		% land	% forest		% land	% forest		% land	% forest	
Inner	0.073 ± 0.009^{a}	0.080 ± 0.010^{a}	88.1 ± 1.1^{a}	0.050 ± 0.005^{a}	0.053 ± 0.006^{a}	93.8 ± 0.4^{a}	0.046 ± 0.008^{a}	0.053 ± 0.009^{a}	87.3 ± 1.9^{a}	0.13 ± 0.03^{a}	0.14 ± 0.03^{a}	82.2 ± 2.7^{a}
Outer	0.29 ± 0.02^{b}	0.35 ± 0.03^{b}	77.1 ± 1.0^{b}	0.17 ± 0.01^{b}	0.18 ± 0.01^{b}	93.0 ± 0.3^{a}	0.20 ± 0.01^{b}	0.26 ± 0.02^{b}	72.1 ± 1.7^{b}	0.50 ± 0.06^{b}	0.62 ± 0.08^{b}	66.1 ± 1.9^{b}
Landscape	0.32 ± 0.07^{b}	0.41 ± 0.09^{c}	72.4 ± 3.3^{c}	0.16 ± 0.04^{b}	0.17 ± 0.04^{b}	89.8 ± 1.7^{b}	0.24 ± 0.05^{b}	0.32 ± 0.05^{c}	68.3 ± 5.8^{b}	0.57 ± 0.20^{b}	0.75 ± 0.24^{b}	59.1 ± 6.3^{c}

Trends within reserves: preliminary analyses

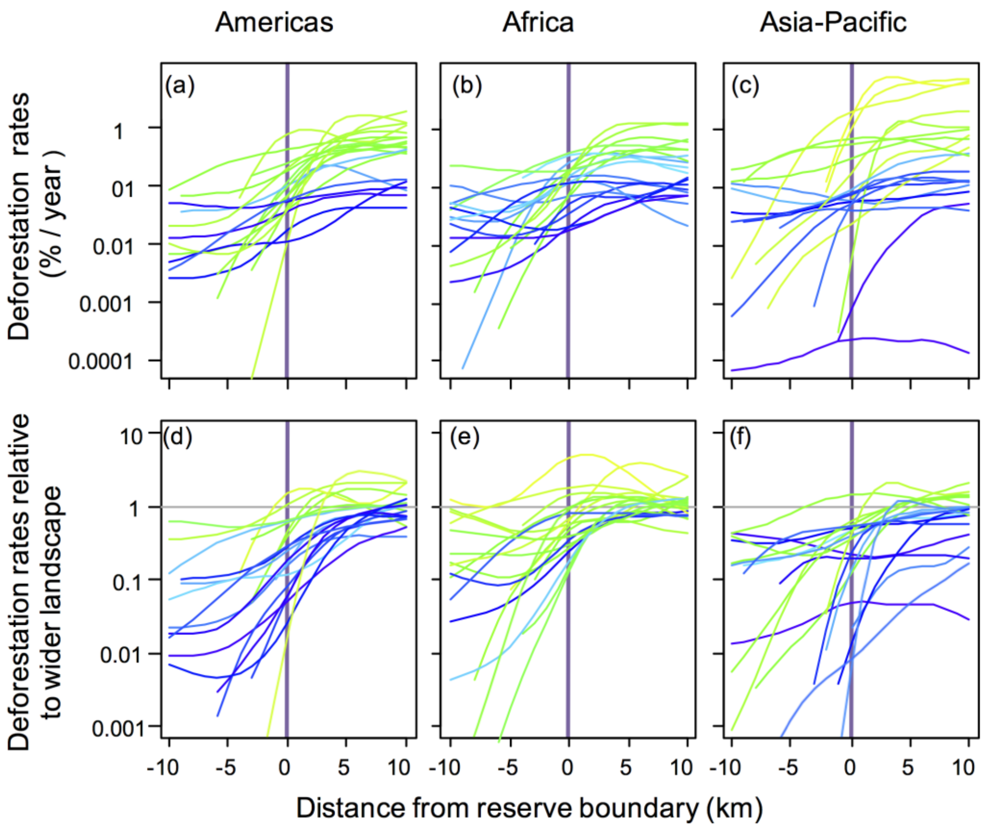

Figure 3. Deforestation rate (top row) and deforestation rate relative to wider landscape (bottom row), as a function of distance from the edge of 60 reserves spanning three geographic regions (negative distance = inside reserve, positive distance = outside reserve). The curves were obtained by fitting smoothing splines through deforestation rates estimated in rings of land around reserves (see Figure 1). Colours vary with maximum deforestation rates (top row) and relativized rate (bottom row).

Visual inspection of curves allows us to draw several tentative conclusions. Firstly, they confirm that reserves are successful at curbing deforestation within their borders, as most curves trend downwards when entering the reserve. Secondly, they illustrate that deforestation rates in the outer zones are sometime higher and sometimes lower than those measured in the wider landscapes (e.g. in the bottom row of Fig. 3, curves in the +0-10 km zone are clustered around a value of one). Thirdly, Asia differs from the other continents in the range of responses; some sites show exceptionally high deforestation rates in their outer zones, while others show barely detectable deforestation rates. Fourthly, there is little evidence of leakage (i.e. relativized deforestation > 1 in the outer zone) except in a few sites. Fifthly, the effectiveness of the outer zone as a buffer zone appears to differ among continents. In Africa, deforestation rate is similar to the wider landscape until 1-2 km from the reserve boundary. In the Americas, there is a gradual transition within the outer zone, with buffering effects extending out to 10 km from the edge in several cases. In Asia, the trends defy any generalisation.

Trends within reserves: formal analyses

Log-transformed deforestation (% land) rates from 2000-2012 exhibited significant relationships with distance from reserve boundary, at 1 km intervals, for 81% of the reserves, with 78% of reserves seeing significant increases in deforestation from 5 km inside the reserve across the reserve boundary to 10 km outside of the reserve (Table 2, Table A.3, "IO" columns; Fig. A.2). However, for 87% of the reserves, these continuous linear regressions of log-transformed deforestation rates across reserve boundaries performed more poorly in describing spatial deforestation patterns across reserve boundaries when compared to piecewise linear regressions of log-transformed deforestation rates as a function of distance from reserve boundary, with a break at the boundary (Table 2, Table A.3, Fig. A.2). Specifically, at the 95% confidence level, 27% of reserves experienced deforestation that increased significantly from the reserve interior to the reserve boundary, while 5% experienced deforestation that decreased significantly from the reserve interior to the reserve boundary (Table 2, Table A.3, "I" columns; Fig. A.2). When considering deforestation in the outer 10 km buffer zone surrounding reserves, a third of the reserves experienced deforestation that significantly increased with greater distance away from the reserve boundary at the 95% confidence level (Table 2, Table A.3, "O" columns; Fig. A.2). Another 17% experienced deforestation in the outer buffer zone that significantly decreased with increased distance away from the reserve boundary at the 95% confidence level (Table 2, Table A.3, "O" columns; Fig. A.2).

Table 2. Comparison of support for two alternative models describing log-transformed deforestation (% land) rates across the administrative boundaries of 60 tropical forest reserves. Model "IO" fits one continuous regression line through all inner and outer region deforestation rates. Model "I+O" is a piecewise model comprising two regression lines: one through deforestation rates up to 5 km inside reserves from their boundaries (sub-model "I") and a second through deforestation rates up to 10 km outside reserves (sub-model "O"). Values represent the percentage reserves for which deforestation showed a significant positive ("+" columns) or negative ("-" columns) relationship with distance from reserve boundary under each model or sub-model. The percentage of reserves for which fitting the piecewise I+O model was better support (by AIC) than having a single IO model is shown.

	IO		I		O		I + O better
	+	-	+	-	+	-	(%)
Global (60)	78%	3%	27%	5%	33%	17%	87%
Africa (20)	75%	0%	50%	0%	20%	35%	95%
The Americas (20)	85%	0%	20%	5%	40%	5%	90%
Asia-Pacific (20)	75%	10%	10%	10%	40%	10%	75%

Discussion

Given the high levels of threat facing tropical forests and uncertainty surrounding the efficacy of efforts in preserving such areas, the aim of this study was to evaluate the degree of protection success across a global network of tropical forest reserves. We used leakage as a metric of protection success by analysing spatial patterns of deforestation across reserve boundaries between 2000 and 2012. Overall, we found that leakage was generally not occurring at a global scale, nor was it occurring at the level of major world regions on the whole (Table 1). In other words, our findings indicate that, on both regional and global scales, deforestation rates tend to be lower inside tropical forest reserves than outside, but not at the expense of disproportionate levels of deforestation being displaced from within protected areas to their broader surroundings. Serving as the first analysis of leakage around a tropical forest protected area network that spans the globe, our work also supports the existing literature base that recognises the effectiveness of tropical forest reserves in reducing forest-cover loss within their boundaries (Bruner *et al.*, 2001; Gaveau *et al.*, 2009; Scharlemann *et al.*, 2010).

Our results even indicate to a slight extent a promising, positive effect of tropical forest reserves, in which reserve presence may reduce or at least temper rates of forest-cover change in at least the areas immediately surrounding them. We found that, on a global scale, although the 10 km buffer zones immediately outside of reserves featured significantly greater proportions of forest cover than the broader 10-25 km landscapes did, deforestation (% forest) in these outer 10 km regions were still significantly lower than those in the broader 10-25 km landscapes (Table 1). This slightly positive leakage of conservation benefits from reserves into their surrounding areas has previously been observed (Andam *et al.*, 2008; Gaveau *et al.*, 2009). It is also possible that this finding reflects the prevalence of geographically targeted conservation efforts on a global scale. In some cases, conservation activities are deliberately implemented in the buffer zone surrounding a core protected area, such as the buffer zone being legally declared as part of the protected area itself (Dudley, 2008).

Our study's conclusion that leakage is not a pervasive phenomenon around the pan-tropical network of forest reserves corroborates the previously proposed notion that leakage extent – and, perhaps by extension, reserve effectiveness – may be primarily determined by factors that hold more relevance on regional and local scales (Douglas *et al.*, 2013; Joppa *et al.*, 2008). Rates, patterns, extents, and drivers of deforestation have indeed been found to differ for reserves in Asia, Africa, and Latin America (Nagendra, 2008). Factors on the ground that have been found to contribute to conservation effectiveness include geographic variables such as site elevation and distance to roads, towns, and major water bodies (Brown *et al.*, 2007); the presence of on-site guards monitoring the area (Bruner *et al.*, 2001; Pelkey *et al.*, 2000); the degree to which natural resources found within the park are integral to the livelihoods of local communities (Straede and Treue, 2006); country-level poverty and corruption (Sodhi *et al.*, 2009; Wright *et al.*, 2007); and the long-term presence of researchers (Campbell *et al.*, 2011) – a so-called "science safe-guarding effect" in which scientists function as *de facto* park guards (Laurance, 2013). Also of import in determining the efficacy of protected areas are the political economies within which they are steeped. The extent of land-clearing pressures and threats to which protected areas are exposed can be influenced by the type and effectiveness of protection governance practised on the reserve (Leverington *et al.*, 2010; Pfaff *et al.*, 2014) and its assigned protection category (i.e. strict protection, multiple-use protection, or indigenously protected areas) (Nelson and Chomitz, 2009). Broader, national land tenure action and policies also serve as some of the most influential underlying determinants of deforestation and successful carbon management in tropical forests (Larson *et al.*, 2013; Robinson *et al.*, 2014; Sunderlin *et al.*, 2014). Extensions of our study could include efforts to identify the extent to which these ground-level variables can explain not only the presence but also the intensity of leakage identified for the 60 reserves studied here.

The notion that reserve efficacy is highly dependent upon local variables is illustrated by our study's ability to pinpoint site-specific occurrences of possible leakage across the world despite its finding that deforestation leakage is not globally pervasive. Of the 60 reserves in this study, the five reserves that we found to have experienced deforestation patterns consistent with leakage events between 2000 and 2012 are located exclusively on the African continent, and primarily in Central Africa (Fig. 1, Fig. A.2). In Central Africa, selective industrial logging of high-value tree species has become an extensive form of land use over recent decades, with new logging expansion frontiers rapidly forming in the Democratic Republic of Congo in particular (Laporte *et al.*, 2007). Meanwhile, inadequate protected area management due to shortcomings in law enforcement and poaching threats has been found to dominate protected areas in the Central African Republic (Blom *et al.*, 2004). Evidence of leakage events driven by human population growth and forest accessibility in East Africa's tropical evergreen forests has also been previously identified (Pfeifer *et al.*, 2012). Alternatively, rather than deforestation being actively displaced from within the reserve interiors, reserve buffers may be disproportionately targeted for deforestation activities at these five sites and the additional 12 sites featuring greater deforestation rates in their buffer zone rings than their broader landscapes. Given the projected expansion and intensification of tropical agriculture, particularly in Sub-Saharan Africa, the regulation of opportunistic agricultural expansion that particularly disrupts unprotected habitats adjoining nature reserves is viewed as an urgent priority in the tropics (Laurance *et al.*, 2014). Our results may directly capture this process of opportunistic land conversion in unprotected areas bordering reserves.

Our results underscore the need for further scrutiny and investigation of perceived protection efficacy on the ground. Results from our study corroborate forest cover-change patterns in and around tropical forest reserves previously derived from site-specific satellite imagery studies – see land cover-change studies at, for example, Kibale by Naughton-Treves *et al.* (2011), Kinabalu by Phua *et al.* (2008), and Gunung Palung by Zamzani *et al.* (2009). Thus, our global study demonstrates at least some degree of local relevance, and can be used to inform, prompt, and manage ground-level conservation efforts that balance leakage prevention with efforts that work to ensure the livelihoods of the local communities that may still heavily depend on natural resources from such protected areas and their surroundings (Straede and Treue, 2006).

Despite our finding that leakage may be a phenomenon that occurs on a site-by-site basis, we cannot ignore the lack of significant difference we found globally between deforestation rates in the 10 km buffer zones immediately surrounding reserves and their broader 10-25 km landscapes. These deforestation rates, both in the surrounding buffer and landscape of a reserve, tend to be significantly higher than those within reserves (Table 1). Furthermore, deforestation rates tend to intensify from a reserve's interior to its outermost 10 km buffer (Table 2, Fig. A.2) – even, on a global scale and in the Americas, continuing on to increase through its 10-25 km landscape region (Table 1). Taken together, these findings underscore the conclusions of previous studies (DeFries *et al.*, 2005; Seiferling *et al.*, 2012): that protected areas are becoming increasingly isolated habitat remnants due to deforestation and land-use changes in their immediately surrounding regions.

The implications of such land cover-change dynamics are of critical importance to the integrity of reserves. DeFries *et al.* (2005) reported that healthy forest surrounding tropical forest reserve boundaries can increase the effective size of protected areas and thus support vital ecological processes between protected areas and their surroundings. Changes in land cover surrounding reserves have also been shown to affect material flows and disturbances into and out of reserves, influence population source and sink dynamics, and introduce a number of edge effects, each of which harbours a unique set of implications for reserve health (Hansen and DeFries, 2007). Reserves that are smaller in area have also been found to be especially susceptible to transformation – in fact, degradation – to the dominant land use-change pattern in their embedded landscapes (Maiorano *et al.*, 2008). Alternatively, the surrounding landscape matrix can also play a key role in promoting the rapid recovery of tropical forests (Chazdon, 2003). Thus, structurally and compositionally intact forest landscapes are fundamental and necessary for sustaining the world's increasingly degraded and disturbed tropical forests.

Confounding factors involving the location bias of protected areas must be considered when interpreting the results of our leakage analysis. We used deforestation rates in the surrounding landscape of reserves as a metric of "baseline" land cover-change dynamics, or deforestation rates that we might see in the absence of the reserve. However, reserves are often non-randomly distributed through space, such that landscape characteristics of protected areas and their immediately surrounding unprotected areas may not in fact be comparable (Mas, 2005). For example, reserve networks have been known to experience *de facto* protection simply because they occupy "rock and ice"; their placement, especially for reserves afforded higher protection status, is biased towards locations that are unlikely to face high land-conversion pressures even in the absence of protection (e.g. regions of high elevations, steep slopes, and greater distance to roads and cities) (Joppa and Pfaff, 2009). In such scenarios, higher deforestation rates detected immediately surrounding reserves, even if greater than "baseline" rates in the broader landscape, may simply be a consequence of the heterogeneity of spatial variables that might allow for, say, greater accessibility to the immediately surrounding region, rather than a direct outcome of *displaced* deforestation due to the reserve's protection status. To address this problem, matching studies have been proposed (Andam *et al.*, 2008; Beresford *et al.*, 2013; Nelson and Chomitz, 2009). In matching studies, protected areas are paired with unprotected areas that have similar likelihoods of receiving protection based on their landscape characteristics (e.g. slope, elevation, rainfall, proximity to major roads and cities). Then, land-cover change in the two matched areas is compared. Matching studies have already been demonstrated to decrease estimates of reserve success in the tropics (Alix-Garcia *et al.*, 2012; Joppa and Pfaff, 2010; Mas, 2005). Determining baseline deforestation rates and assessing leakage through the use of matching methodologies would serve as a highly informative means of refining and extending the analysis conducted here.

Conclusion

Tropical forests provide important ecosystem services to humanity as a whole, sustaining the livelihoods of local peoples by improving social welfare, guarding local security, and providing economic benefits. Thus, reducing the impact of global change on these forests and the services they provide is a defining issue of our time. Our study has demonstrated the utility in using contemporary satellite imagery-based global forest-cover data products such as the GFCD to enhance our understanding and evaluation of conservation success in tropical forest protected areas. As the first leakage analysis conducted across a pan-tropical protected area network, our study indicates that deforestation is not disproportionately displaced outside of reserve boundaries on a global scale and addresses knowledge gaps surrounding the phenomenon of leakage as a detrimental consequence of land protection. Our study also indicates that deforestation occurring in the regions immediately surrounding tropical forest reserves is converting such areas into increasingly isolated habitat remnants, a finding that holds critical ramifications for modern conservation strategies. Our study comes at a time when the conservation community is increasingly recognising the need to account for deforestation leakage when estimating reserve efficacy and capitalising upon the use of modern remote sensing products to achieve this very aim. We demonstrate the utility of new remote sensing products such as the GFCD in directing the modification and priority-setting of conservation efforts so that they more appropriately address the most urgent and relevant conservation challenges of today – particularly with respect to understanding the linkages between priority areas of high conservation value and the surrounding landscapes within which they exist.

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Appendices

Table A.1. **Alternative sources of reserve boundary shapefiles that were unavailable on the World Database Of Protected Areas website.**

Protected Area	Source and Affiliation
Biological Dynamics of Forest Fragments Project (BDFFP)	*Dr. Marion Pfeifer* Faculty of Natural Sciences, Imperial College
Dinghushan Biosphere Reserve	*Dr. Xiuzhi Chen* Dinghushan Forest Ecosystem Research Station, Chinese Academy of Sciences
Hahpen (Fushan) Nature Reserve	*Dr. Jung-Tai Chao* Division of Forest Protection, Taiwan Forestry Research Institute
Kilum-Ijim/Mount Oku Forest Reserve	*Mark Balman* GIS Support Analyst, BirdLife International
La Selva Biological Station	*Antonio Trabucco* GIS Laboratory Manager, Organization for Tropical Studies (file downloaded from *http://www.arcgis.com/home/item.html?id=231b3aa3503347978dac65622c9a6aef*)
Los Amigos Conservation Concession	*Megan MacDowell* Amazon Conservation Association
Paranapiacaba Remnant	*Dr. Beatriz Beisiegel* Centro Nacional de Pesquisas para a Conservação dos Predadores Naturais
Pasoh Forest Reserve	*Dr. Joseph Wright* and *Dr. Patrick Jansen*, Smithsonian Tropical Research Institute

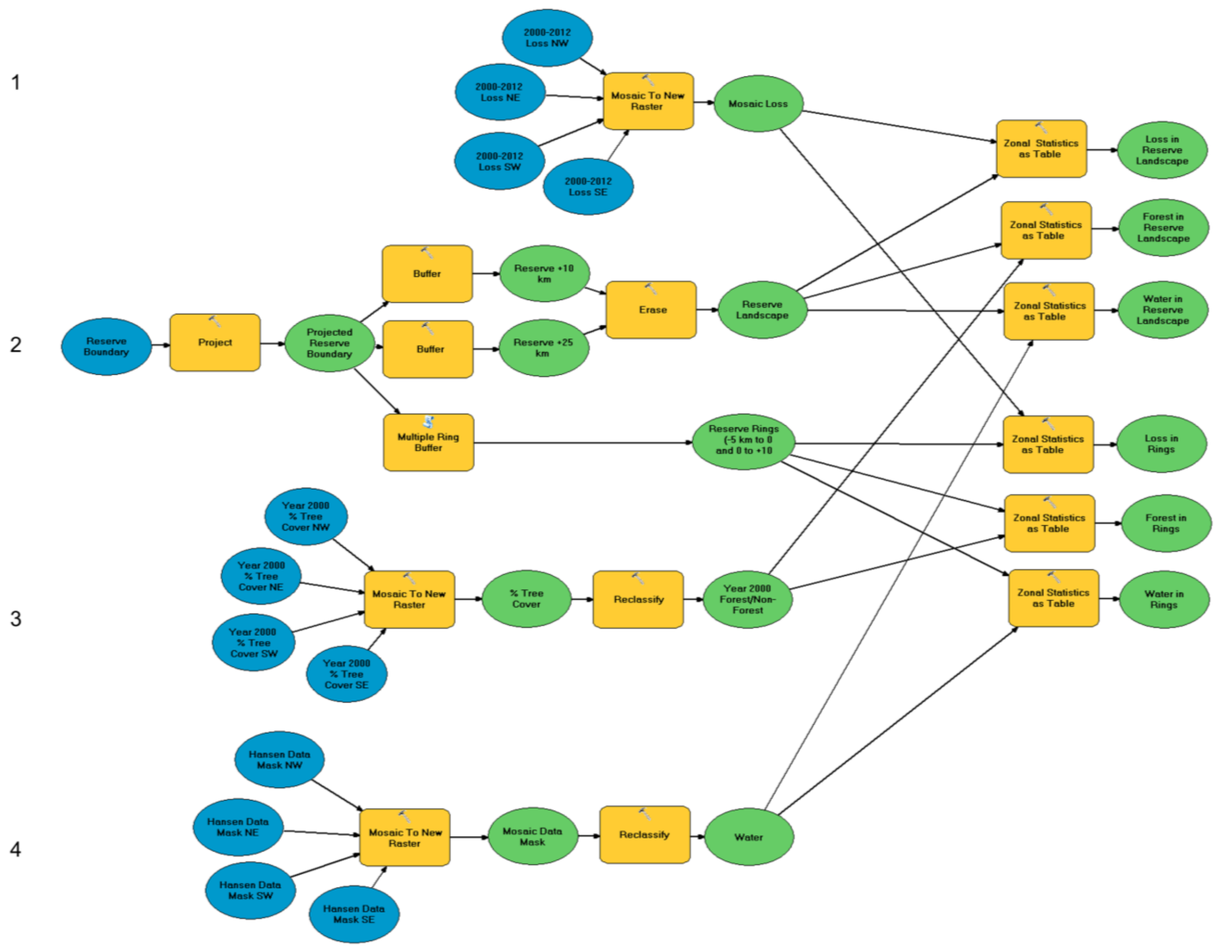
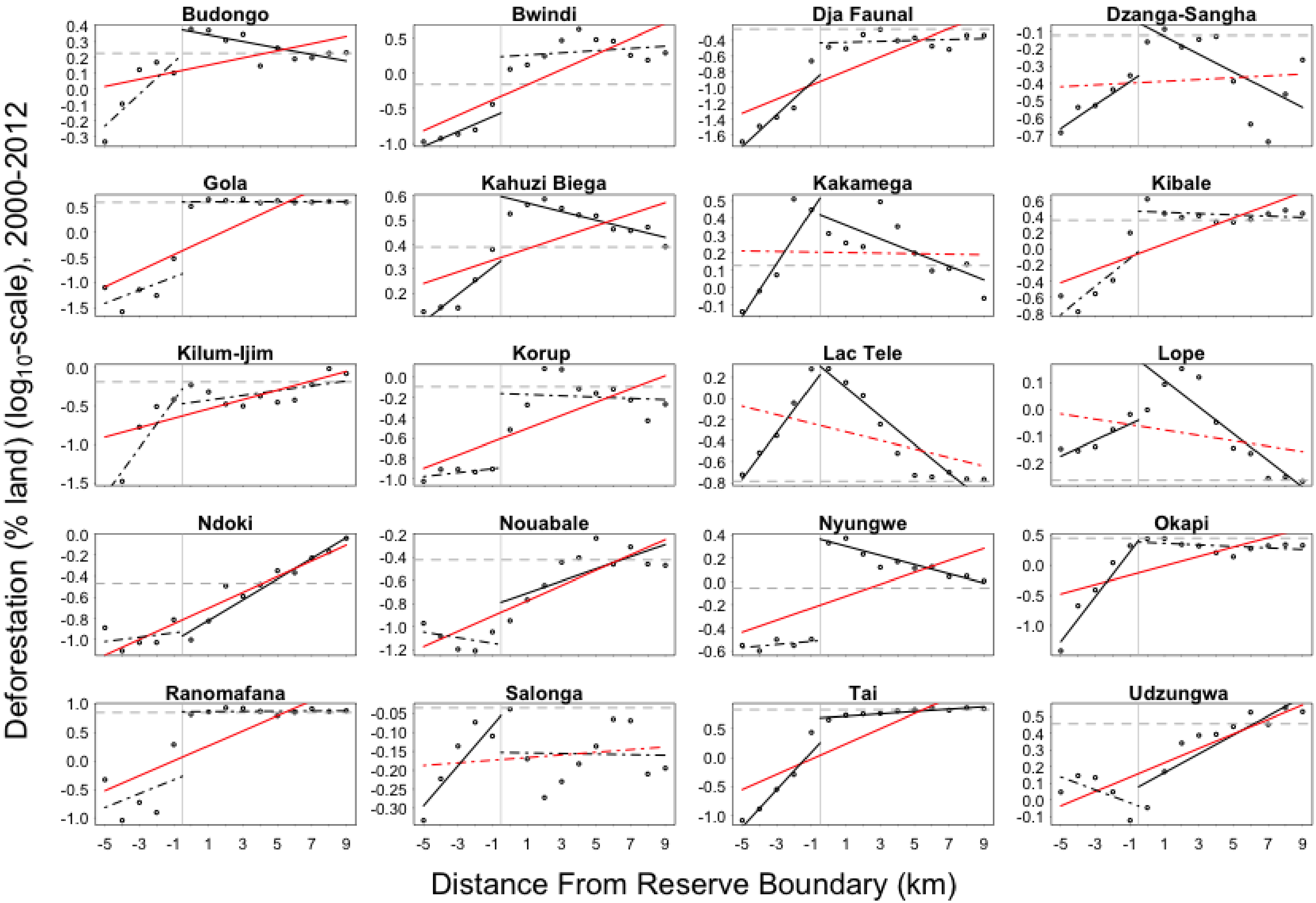


Figure A.1. Illustrative representation of ArcGIS workflow used to quantify spatial deforestation patterns around reserves. Blue circles represent data inputs, yellow rectangles represent ArcGIS analysis tools, and green circles represent derived data outputs. Broadly, Rows 1, 3, and 4 represent the steps necessary to prepare forest loss (row 1), forest cover (row 2), and water (row 3) raster files from the Global Forest Change dataset for analysis. Row 2 represents the steps necessary to create the 5 interior rings from the reserve edge, the 10 rings emanating up to 10 km outside of the reserve, and the broader 25 km landscape zone surrounding the reserve.

Table A.2. Results of Wilcoxon matched pairs tests comparing deforestation rates across three spatial zones of interest globally and by region. Comparisons are listed by order in which they appear in the in-text Results section. *** = $p < 0.0001$; ** = $p < 0.001$; * = $p < 0.05$.

Geography	Unit	Spatial Zone Comparison			V	n	*p*-value	
Global	% land	Inner deforestation	<	Outer deforestation	55	120	< 0.0001	***
Global	% land	Inner deforestation	<	Landscape deforestation	93	120	< 0.0001	***
Global	% land	Outer deforestation	=	Landscape deforestation	785	120	> 0.1	
Global	both	Deforestation (% forest)	>	Deforestation (% land)	0	120	< 0.0001	***
Global	% forest	Inner deforestation	<	Outer deforestation	41	120	< 0.0001	***
Global	% forest	Inner deforestation	<	Landscape deforestation	61	120	< 0.0001	***
Global	% forest	Outer deforestation	<	Landscape deforestation	621	120	< 0.05	*
Africa	% land	Inner deforestation	<	Outer deforestation	6	40	< 0.001	**
Africa	% land	Inner deforestation	<	Landscape deforestation	35.5	40	< 0.0001	***
Africa	% land	Outer deforestation	=	Landscape deforestation	135	40	> 0.1	
Americas	% land	Inner deforestation	<	Outer deforestation	0	40	< 0.0001	***
Americas	% land	Inner deforestation	<	Landscape deforestation	2	40	< 0.0001	***
Americas	% land	Outer deforestation	=	Landscape deforestation	62	40	> 0.1	
Asia-Pacific	% land	Inner deforestation	<	Outer deforestation	20	40	< 0.0001	***
Asia-Pacific	% land	Inner deforestation	<	Landscape deforestation	13	40	< 0.0001	***
Asia-Pacific	% land	Outer deforestation	=	Landscape deforestation	89	40	> 0.1	

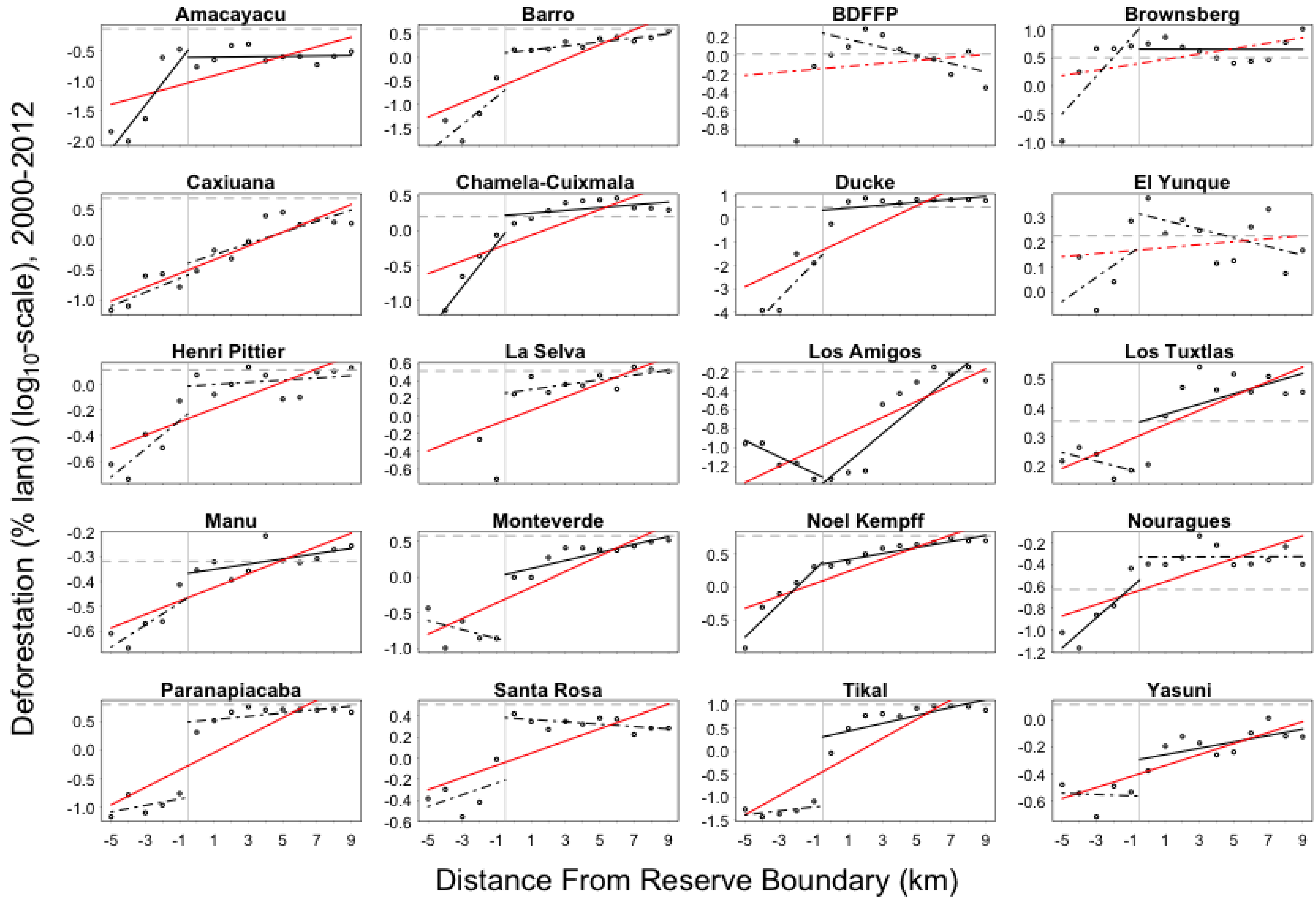
A



Budongo
Bwindi
Dja Faunal
Dzanga-Sangha
Gola
Kahuzi Biega
Kakamega
Kibale
Kilum-Ijim
Korup
Lac Tele
Lope
Ndoki
Nouabale
Nyungwe
Okapi
Ranomafana
Salonga
Tai
Udzungwa
Deforestation (% land) ($\log_{10}$-scale), 2000-2012
Distance From Reserve Boundary (km)

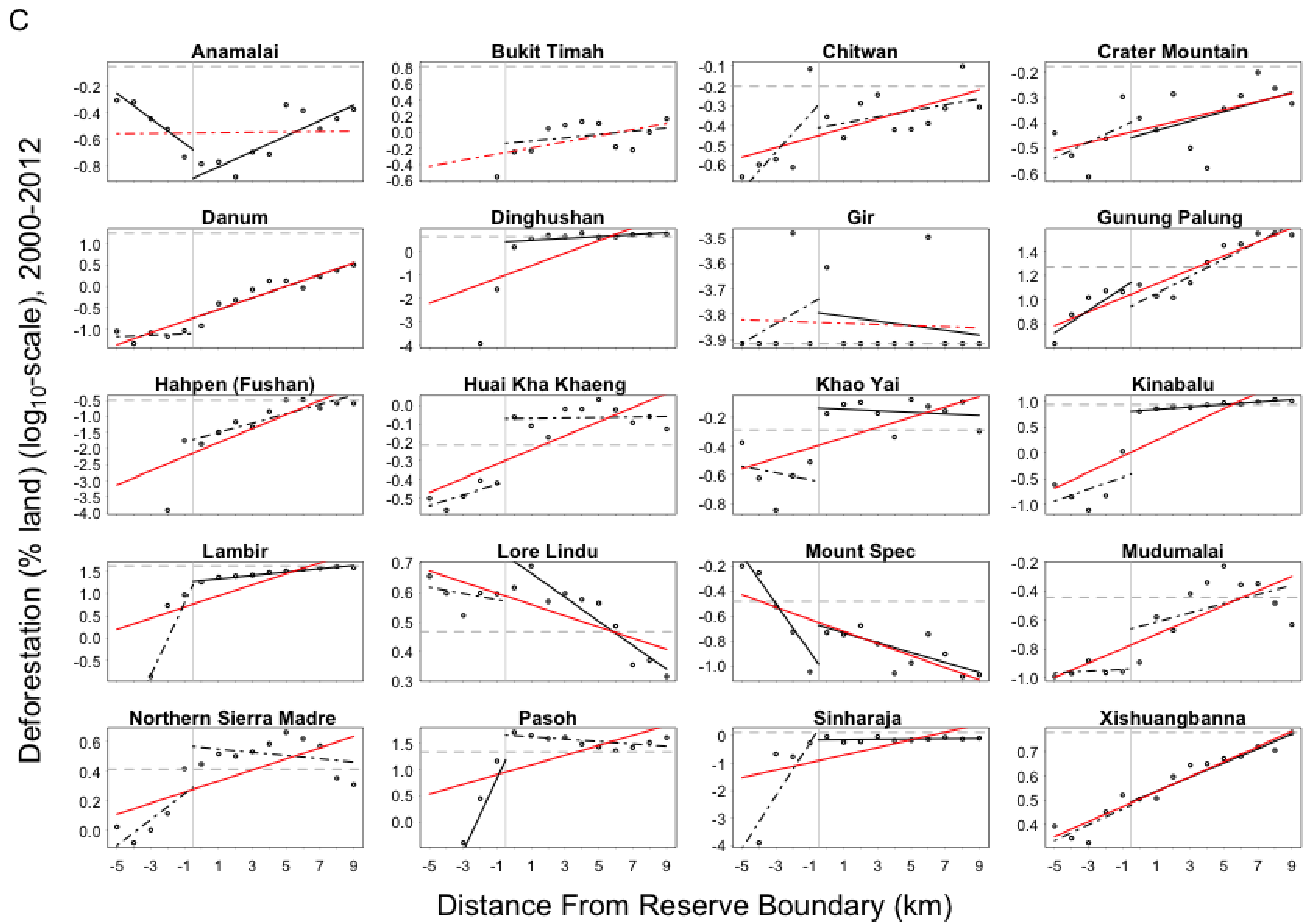
725

B



Amacayacu
Barro
BDFFP
Brownsberg
Caxiuana
Chamela-Cuixmala
Ducke
El Yunque
Henri Pittier
La Selva
Los Amigos
Los Tuxtlas
Manu
Monteverde
Noel Kempff
Nouragues
Paranapiacaba
Santa Rosa
Tikal
Yasuni
Deforestation (% land) (log10-scale), 2000-2012
Distance From Reserve Boundary (km)

726


C
Anamalai
Bukit Timah
Chitwan
Crater Mountain
Danum
Dinghushan
Gir
Gunung Palung
Hahpen (Fushan)
Huai Kha Khaeng
Khao Yai
Kinabalu
Lambir
Lore Lindu
Mount Spec
Mudumalai
Northern Sierra Madre
Pasoh
Sinharaja
Xishuangbanna
Deforestation (% land) (log10-scale), 2000-2012
Distance From Reserve Boundary (km)

727

Figure A.2. Deforestation (% land) rates across reserve boundaries for 60 tropical forest reserves in (A) Africa, (B) the Americas, and (C) Asia-Pacific. Data points represent rates within single 1 km-wide rings in the inner and outer zones, while the horizontal grey dashes represent average deforestation within the 10-25 km landscape surrounding each reserve (see Fig. 2 for further explanation). Red lines represent ordinary least-squares regression fits of log-transformed deforestation rates across the inner and outer regions combined. Black lines represent ordinary least-squares regression fits of log-transformed deforestation rates in the inner region and outer region separately. Solid red or black lines represent regressions with significant slopes at the 95% confidence level. Dot-dash red or black lines represent regressions with non-significant slopes at the 95% confidence level. X-axis label “-5” refers to the region from -5 to -4 km from reserve boundary, “-4” to the region from -4 to -3 km from reserve boundary, and so on. In all but eight reserves, there was strong statistical support for fitting two regression lines rather than a single line (Table A.3).

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Table A.3. Comparison of two linear models describing log-transformed deforestation (% land) rates at 1 km intervals between 2000 and 2012 across the administrative boundaries of 60 tropical forest reserves arranged alphabetically within geographic region. Model "I+O" is a piecewise model comprising two regression lines: one through deforestation rates inside reserves 5 km from reserve boundaries (sub-model "I") measured at 1 km intervals, and a second through deforestation rates outside reserves 10 km from reserve boundaries (sub-model "O") measured at 1 km intervals. Model "IO" fits one continuous regression line through all inner and outer region deforestation rates. ΔAIC values represent the AIC of the IO model less the AIC of the I+O model; values greater than or equal to two indicate the I+O model as a better fit for the data, and values less than two indicate the IO model as a better fit for the data. The " < " symbol indicates that the I+O model has a lower AIC value than the IO model, and thus is a better fit for the data; " > " indicates that the I+O model has a higher AIC value than the IO model, and thus is a worse fit for the data. Boldface values represent regression lines with slopes significantly different from zero at the 95% confidence level. Sites with "—" symbols were too small to fit more than two rings in their interiors, and thus regressions for their inner deforestation rates and AIC_{I+O} values were not determined.

			I + O					IO		
			I		O					
Site Name	Site No. (see Fig. 1)	Region	Slope	Y-intercept	Slope	Y-intercept		Slope	Y-intercept	ΔAIC ($AIC_{IO} - AIC_{I+O}$)
Budongo Forest Reserve	6	Africa	0.113	0.222	**-0.02**	**0.374**	<	**0.023**	**0.109**	20
Bwindi Impenetrable National Park	8	Africa	**0.119**	**-0.564**	0.015	0.239	<	**0.109**	**-0.38**	18
Dja Faunal Reserve	15	Africa	**0.227**	**-0.836**	0.005	-0.433	<	**0.089**	**-0.965**	26
Dzanga-Sangha Special Reserve	17	Africa	**0.077**	**-0.357**	**-0.049**	**-0.051**	<	0.005	-0.399	20
Gola Rainforest National Park	20	Africa	0.147	-0.829	0.001	0.601	<	**0.16**	**-0.45**	50
Kahuzi Biéga National Park	25	Africa	**0.062**	**0.333**	**-0.017**	**0.597**	<	**0.024**	**0.335**	33
Kakamega Forest National Reserve	26	Africa	**0.17**	**0.515**	**-0.037**	**0.42**	<	-0.002	0.206	14
Kibale National Park	28	Africa	0.195	-0.032	-0.008	0.465	<	**0.08**	**-0.099**	24
Kilum-Ijim/Mount Oku Forest Reserve	29	Africa	0.346	-0.277	0.03	-0.472	<	**0.061**	**-0.662**	8

Korup National Park	31	Africa	0.022	-0.892	-0.006	-0.161	<	**0.065**	**-0.637**	21
Lac Télé Community Reserve	33	Africa	**0.248**	**0.224**	**-0.129**	**0.306**	<	-0.041	-0.236	31
Lopé National Park	35	Africa	**0.034**	**-0.04**	**-0.047**	**0.183**	<	-0.01	-0.057	22
Ndoki (Mondika) National Park	43	Africa	0.023	-0.927	**0.093**	**-0.967**	<	**0.075**	**-0.851**	1
Nouabalé-Ndoki National Park	46	Africa	-0.027	-1.155	**0.05**	**-0.788**	<	**0.066**	**-0.908**	3
Nyungwe Forest Nature Reserve	48	Africa	0.015	-0.51	**-0.038**	**0.366**	<	**0.052**	**-0.23**	52
Okapi Wildlife Reserve National Park	49	Africa	**0.42**	**0.41**	-0.012	0.381	<	**0.078**	**-0.167**	36
Ranomafana National Park	52	Africa	0.137	-0.269	0.002	0.86	<	**0.131**	**0.003**	42
Salonga National Park	53	Africa	**0.059**	**-0.056**	-0.001	-0.153	<	0.003	-0.174	3
Taï National Park	56	Africa	**0.364**	**0.253**	**0.019**	**0.685**	<	**0.13**	**-0.027**	56
Udzungwa Mountains National Park	58	Africa	-0.044	-0.037	**0.054**	**0.079**	<	**0.04**	**0.137**	3
Amacayacú National Park	1	Americas	**0.414**	**-0.485**	0.003	-0.609	<	**0.08**	**-1.073**	21
Barro Colorado Island Biological Station	3	Americas	0.329	-0.687	**0.04**	**0.098**	<	**0.153**	**-0.648**	35
BDFFP	4	Americas	—	—	**-0.042**	**0.247**	<	0.016	-0.149	—
Brownsberg Nature Park	5	Americas	0.381	1.023	-0.001	0.658	<	0.048	0.378	9
Caxiuanã National Forest	9	Americas	0.128	-0.586	**0.087**	**-0.39**	>	**0.113**	**-0.562**	-4
Chamela-Cuixmala Reserve	10	Americas	**0.351**	**-0.03**	0.019	0.22	<	**0.092**	**-0.249**	28
Ducke Forest Reserve	16	Americas	0.849	-1.531	0.059	0.382	<	**0.349**	**-1.517**	25
El Yunque (Luquillo) National Forest	18	Americas	0.054	0.18	-0.017	0.312	<	0.006	0.165	1
Henri Pittier National Park	23	Americas	0.124	-0.228	0.008	-0.012	<	**0.052**	**-0.293**	10
La Selva Biological Station/Protected Zone	32	Americas	—	—	**0.026**	**0.259**	<	**0.076**	**-0.088**	—

Los Amigos Conservation Concession	37	Americas	**-0.096**	**-1.313**	**0.143**	**-1.381**	<	**0.086**	**-1.027**	16
Los Tuxtlas Biosphere Reserve	38	Americas	-0.017	0.178	0.017	0.351	<	**0.025**	**0.292**	4
Manú National Park	39	Americas	0.05	-0.464	0.01	-0.367	<	**0.027**	**-0.478**	7
Monteverde Protective Zone	40	Americas	-0.071	-0.895	**0.054**	**0.031**	<	**0.11**	**-0.363**	20
Noel Kempff Mercado National Park	44	Americas	**0.282**	**0.37**	**0.043**	**0.341**	<	**0.092**	**0.046**	27
Nouragues National Nature Reserve	47	Americas	**0.156**	**-0.541**	0	-0.332	<	**0.052**	**-0.662**	14
Paranapiacaba	50	Americas	0.064	-0.83	0.027	0.49	<	**0.153**	**-0.352**	32
Santa Rosa National Park	54	Americas	0.062	-0.209	-0.011	0.383	<	**0.058**	**-0.069**	28
Tikal National Park	57	Americas	0.048	-1.197	**0.081**	**0.306**	<	**0.21**	**-0.554**	26
Yasuni National Park	60	Americas	-0.005	-0.565	**0.022**	**-0.294**	<	**0.04**	**-0.42**	2
Anamalai Tiger Reserve	2	Asia-Pacific	**-0.106**	**-0.677**	**0.055**	**-0.893**	<	0.001	-0.553	20
Bukit Timah Nature Reserve	7	Asia-Pacific	—	—	0.019	-0.137	<	0.038	-0.269	—
Chitwan National Park	11	Asia-Pacific	0.107	-0.296	0.015	-0.41	<	**0.024**	**-0.463**	1
Crater Mountain Wildlife Management Area	12	Asia-Pacific	0.036	-0.398	0.018	-0.459	>	**0.016**	**-0.445**	-5
Danum Valley Conservation Area	13	Asia-Pacific	0.018	-1.104	**0.129**	**-0.748**	<	**0.137**	**-0.817**	2
Dinghushan Mountain Nature Reserve	14	Asia-Pacific	—	—	**0.038**	**0.437**	<	**0.268**	**-1.127**	—
Gir National Park and Wildlife Sanctuary	19	Asia-Pacific	0.043	-3.741	-0.009	-3.795	>	-0.002	-3.831	-5
Gunung Palung National Park	21	Asia-Pacific	**0.105**	**1.143**	**0.067**	**0.945**	>	**0.058**	**1.015**	0
Hahpen (Fushan) Nature Reserve	22	Asia-Pacific	—	—	**0.139**	**-1.721**	<	**0.219**	**-2.255**	—
Huai Kha Khaeng Wildlife Sanctuary	24	Asia-Pacific	0.032	-0.411	0.001	-0.073	<	**0.038**	**-0.317**	20
Khao Yai National Park	27	Asia-Pacific	-0.025	-0.642	-0.005	-0.134	<	**0.036**	**-0.413**	10

Kinabalu National Park	30	Asia-Pacific	0.13	-0.414	**0.023**	**0.809**	<	**0.155**	**-0.067**	57
Lambir Hills National Park	34	Asia-Pacific	0.922	1.201	**0.036**	**1.28**	<	**0.125**	**0.7**	52
Lore Lindu National Park	36	Asia-Pacific	-0.012	0.57	**-0.039**	**0.726**	<	**-0.019**	**0.597**	8
Mount Spec/Paluma Range National Park	41	Asia-Pacific	**-0.217**	**-0.981**	**-0.038**	**-0.672**	<	**-0.048**	**-0.624**	14
Mudumalai Biosphere Reserve	42	Asia-Pacific	0.007	-0.94	0.03	-0.661	<	**0.05**	**-0.799**	7
Northern Sierra Madre Natural Park	45	Asia-Pacific	0.099	0.292	-0.01	0.567	<	**0.037**	**0.259**	10
Pasoh Forest Reserve	51	Asia-Pacific	**0.782**	**1.185**	-0.021	1.651	<	**0.093**	**0.905**	44
Sinharaja Forest Reserve National Park	55	Asia-Pacific	1.084	0.224	0.005	-0.157	<	**0.14**	**-0.974**	43
Xishuangbanna Nature Reserve	59	Asia-Pacific	0.036	0.48	**0.028**	**0.493**	>	**0.03**	**0.474**	-1