

# Averting biodiversity collapse in tropical forest protected areas

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The rapid disruption of tropical forests probably imperils global biodiversity more than any other contemporary phenomenon<sup>1–3</sup>. With deforestation advancing quickly, protected areas are increasingly becoming final refuges for threatened species and natural ecosystem processes. However, many protected areas in the tropics are themselves vulnerable to human encroachment and other environmental stresses<sup>4–9</sup>. As pressures mount, it is vital to know whether existing reserves can sustain their biodiversity. A critical constraint in addressing this question has been that data describing a broad array of biodiversity groups have been unavailable for a sufficiently large and representative sample of reserves. Here we present a uniquely comprehensive data set on changes over the past 20 to 30 years in 31 functional groups of species and 21 potential drivers of environmental change, for 60 protected areas stratified across the world's major tropical regions. Our analysis reveals great variation in reserve 'health': about half of all reserves have been effective or performed passably, but the rest are experiencing an erosion of biodiversity that is often alarmingly widespread taxonomically and functionally. Habitat disruption, hunting and forest-product exploitation were the strongest predictors of declining reserve health. Crucially, environmental changes immediately outside reserves seemed nearly as important as those inside in determining their ecological fate, with changes inside reserves strongly mirroring those occurring around them. These findings suggest that tropical protected areas are often intimately linked ecologically to their surrounding habitats, and that a failure to stem broad-scale loss and degradation of such habitats could sharply increase the likelihood of serious biodiversity declines.

Tropical forests are the biologically richest ecosystems on Earth<sup>1–3</sup>. Growing concerns about the impacts of anthropogenic pressures on tropical biodiversity and natural ecosystem services have led to increases in the number and extent of protected areas across the tropics<sup>10</sup>. However, much remains unknown about the likelihood of biodiversity persisting in such protected areas. Remote-sensing technologies offer a bird's-eye view of tropical forests and provide many important insights<sup>6,11–13</sup>, but are largely unable to discern crucial on-the-ground changes in forest biodiversity and ecological functioning<sup>14</sup>.

To appraise both the ecological integrity and threats for tropical protected areas on a global scale, we conducted a systematic and uniquely comprehensive assessment of long-term changes within 60 protected areas stratified across the world's major tropical forest regions (Supplementary Fig. 1). To our knowledge, no other existing data set includes such a wide range of biodiversity and threat indicators for such a large and representative network of tropical reserves. Our study was motivated by three broad issues: whether tropical reserves will function as 'arks' for biodiversity and natural ecosystem processes; whether observed changes are mainly concordant or idiosyncratic among different protected areas; and what the principal predictors of reserve success or failure are, in terms of their intrinsic characteristics and drivers of change.

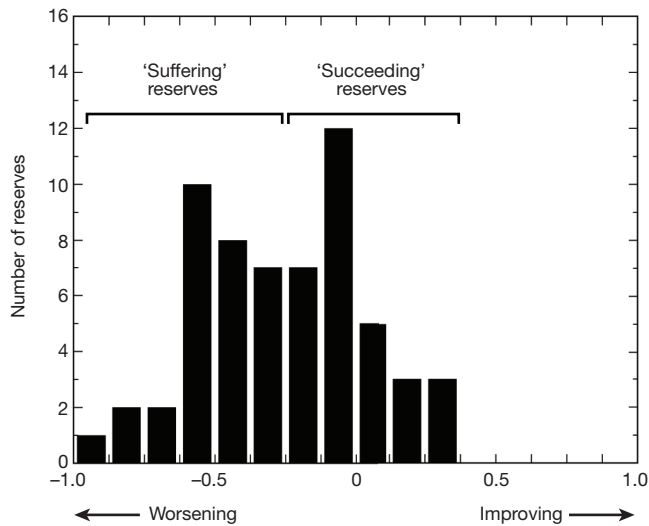
To conduct our study we amassed expert knowledge from 262 detailed interviews, focusing on veteran field biologists and environmental scientists who averaged nearly 2 decades of experience

(mean  $\pm$  s.d., 19.1  $\pm$  9.6 years) at each protected area. Each interviewed researcher completed a detailed 10-page questionnaire, augmented by a telephone or face-to-face interview (see Supplementary Information). The questionnaires focused on longer-term (approximately 20–30-year) changes in the abundance of 31 animal and plant guilds (trophically or functionally similar groups of organisms), which collectively have diverse and fundamental roles in forest ecosystems (Table 1). We also recorded data on 21 potential drivers of environmental change both inside each reserve and within a 3-km-wide buffer zone immediately surrounding it (Table 1).

Our sample of protected areas spans 36 nations and represents a geographically stratified and broadly representative selection of sites across the African, American and Asia-Pacific tropics (Supplementary Fig. 1). The reserves ranged from 160 ha to 3.6 million ha in size, but most (85%) exceeded 10,000 ha in area (median = 99,350 ha; lower decile = 7,000 ha; upper decile = 750,000 ha). The protected areas fall under various International Union for Conservation of Nature (IUCN) reserve classifications. Using data from the World Database on Protected Areas (<http://www.wdpa.org>), we found no significant difference ( $P = 0.13$ ) in the relative frequency of high-protection (IUCN Categories I–IV), multiple-use (Categories V–VI) and

**Table 1 | The 31 animal and plant guilds, and the 21 environmental drivers assessed both inside and immediately outside each protected area.**

Guilds	Potential environmental drivers
<b>Broadly forest-dependent guilds</b>	
Apex predators	Changes in natural-forest cover
Large non-predatory species	Selective logging
Primates	Fires
Opportunistic omnivorous mammals	Hunting
Rodents	Harvests of non-timber forest products
Bats	Illegal mining
Understory insectivorous birds	Roads
Raptorial birds	Automobile traffic
Larger frugivorous birds	Exotic plantations
Larger game birds	Human population density
Lizards and larger reptiles	Livestock grazing
Venomous snakes	Air pollution
Non-venomous snakes	Water pollution
Terrestrial amphibians	Stream sedimentation
Stream-dwelling amphibians	Soil erosion
Freshwater fish	River & stream flows
Dung beetles	Ambient temperature
Army or driver ants	Annual rainfall
Aquatic invertebrates	Drought severity or intensity
Large-seeded old-growth trees	Flooding
Epiphytes	Windstorms
<b>Other functional groups</b>	
Ecological specialists	
Species requiring tree cavities	
Migratory species	
<b>Disturbance-favouring guilds</b>	
Lianas and vines	
Pioneer and generalist trees	
Exotic animal species	
Exotic plant species	
Disease-vectoring invertebrates	
Light-loving butterflies	
Human diseases	



**Figure 1** | Distribution of the 'reserve-health index' for 60 protected areas spanning the world's major tropical forest regions. This relative index averages changes in 10 well-studied guilds of animals and plants, including disturbance-avoiding and disturbance-favouring groups, over the past 20 to 30 years.

unclassified reserves between our sample of 60 reserves and all 16,038 reserves found in the same tropical nations (Supplementary Fig. 2). We also found no significant difference ( $P = 0.08$ ) in the geographical isolation of our reserves (travel time to the nearest city with greater than 50,000 residents) relative to a random sample of 60 protected areas stratified across the same 36 nations (Supplementary Fig. 3).

We critically assessed the validity of our interview data by comparing them to 59 independent time-series data sets in which change in a single guild or environmental driver was assessed for one of our protected areas. Collectively, our meta-analysis included some data on 15 of the guilds, 13 of the drivers and 27 of the protected areas in our study (Supplementary Table 1). Most (86.4%) of the independent data sets supported our interview results, and in no case did an independent test report a trend opposite in sign to our interview-based findings.

Our analyses suggest that the most sensitive guilds in tropical protected areas include apex predators, large non-predatory vertebrates, bats, stream-dwelling amphibians, terrestrial amphibians, lizards and larger reptiles, non-venomous snakes, freshwater fish, large-seeded old-growth trees, epiphytes and ecological specialists (all  $P < 0.0056$ , with effect sizes ranging from  $-0.36$  to  $-1.05$ ; Supplementary Table 2). Several other groups were somewhat less vulnerable, including primates, understory insectivorous birds, large frugivorous birds,

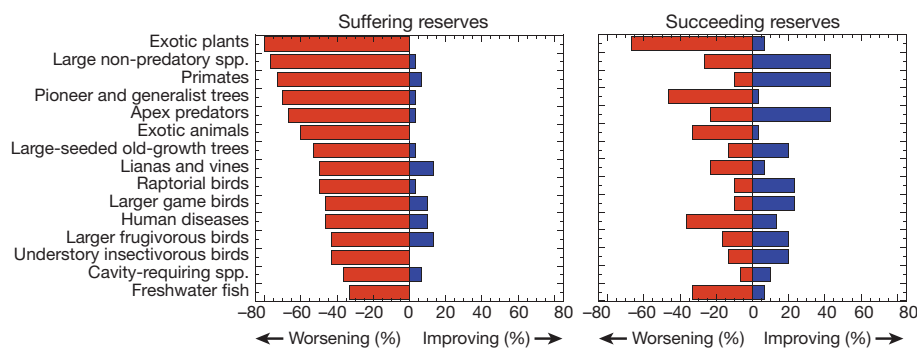
raptorial birds, venomous snakes, species that require tree cavities, and migratory species (all  $P < 0.05$ , with effect sizes from  $-0.27$  to  $-0.53$ ). In addition, five groups increased markedly in abundance in the reserves, including pioneer and generalist trees, lianas and vines, invasive animals, invasive plants and human diseases (all  $P < 0.0056$ , with effect sizes from 0.44 to 1.17).

To integrate these disparate data, we generated a 'reserve-health index' that focused on 10 of the best-studied guilds (data for each available at  $\geq 80\%$  of reserves), all of which seem to be sensitive to environmental changes in protected areas. Six of these are generally 'disturbance avoiders' (apex predators, large non-predatory vertebrates, primates, understory insectivorous birds, large frugivorous birds and large-seeded old-growth trees) and the remainder seem to be 'disturbance-favouring' groups (pioneer and generalist trees, lianas and vines, exotic animals and exotic plants). For each protected area, we averaged the mean values for each group, using negative values to indicate increases in abundance of the disturbance-favouring guilds.

The reserve-health index varied greatly among the different protected areas (Fig. 1). About four-fifths of the reserves had negative values, indicating some decline in reserve health. For 50% of all reserves this decline was relatively serious (mean score  $< -0.25$ ), with the affected organisms being remarkable for their high functional and taxonomic diversity (Fig. 2). These included plants with varying growth forms and life-history strategies, and fauna that differed widely in body size, trophic level, foraging strategies, area needs, habitat use and other attributes. The remaining reserves generally exhibited much more positive outcomes for biodiversity (Fig. 2), although a few disturbance-favouring guilds, such as exotic plants and pioneer and generalist trees, often increased even within these areas.

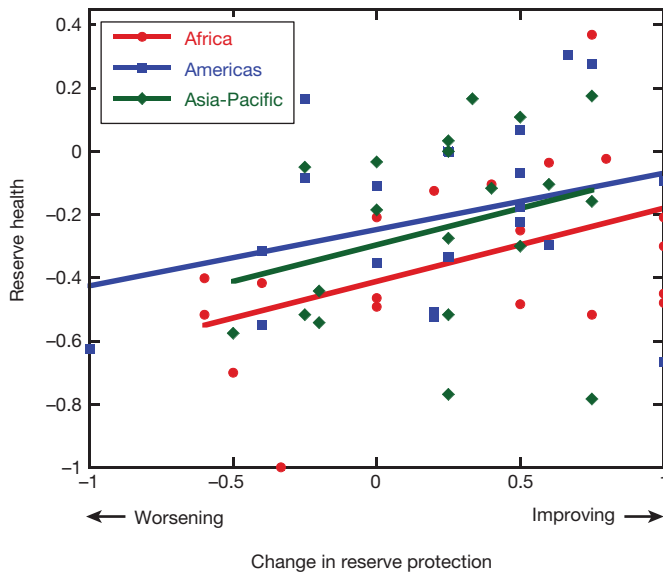
An important predictor of reserve health was improving reserve management. According to our experts, reserves in which actual, on-the-ground protection efforts (see Supplementary Information) had increased over the past 20 to 30 years generally fared better than those in which protection had declined; a relationship that was consistent across all three of the world's major tropical regions (Fig. 3). Indeed, on-the-ground protection has increased in more than half of the reserves over the past 20 to 30 years, and this is assisting efforts to limit threats such as deforestation, logging, fires and hunting within these reserves (Supplementary Table 3), relative to areas immediately outside (Supplementary Table 4).

However, our findings show that protecting biodiversity involves more than just safeguarding the reserves themselves. In many instances, the landscapes and habitats surrounding reserves are under imminent threat<sup>5,6,15</sup> (Fig. 4 and Supplementary Tables 3 and 4). For example, 85% of our reserves suffered declines in surrounding forest cover in the last 20 to 30 years, whereas only 2% gained surrounding forest. As shown by general linear models (Supplementary Table 5), such changes can seriously affect reserve biodiversity. Among the



**Figure 2** | Percentages of reserves that are worsening versus improving for key disturbance-sensitive guilds, contrasted between 'suffering' and 'succeeding' reserves (which are distinguished by having lower ( $< -0.25$ ) versus higher ( $\geq -0.25$ ) values for the reserve-health index, respectively). For disturbance-

favouring organisms such as exotic plants and animals, pioneer and generalist trees, lianas and vines, and human diseases, the reserve is considered to be worsening if the group increased in abundance. For any particular guild, reserves with missing or zero values (no trend) are not included.



**Figure 3** | Effects of improving on-the-ground protection on a relative index of reserve health. This positive relationship held across all three tropical continents (a general linear model showed that the protection term was the most effective predictor of reserve health (Akaike’s information criterion weight, 0.595; deviance explained, 11.4%), with the addition of ‘continent’ providing only a small improvement in model fit (Akaike’s information criterion weight, 0.317; deviance explained, 16.3%).

potential drivers of declining reserve health, three of the most important predictors involved ecological changes outside reserves (declining forest cover, increasing logging and increasing fires outside reserves; Supplementary Fig. 6). The remainder involved changes within reserves (particularly declining forest cover and increasing hunting, as well as increasing logging and harvests of non-timber forest products; Supplementary Table 5).

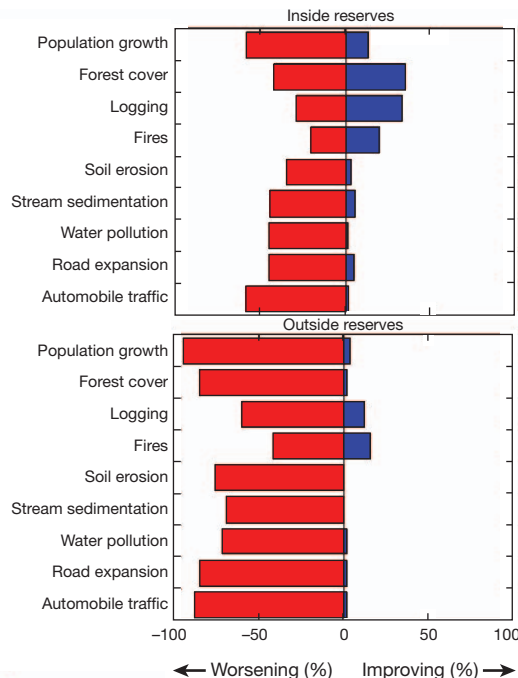
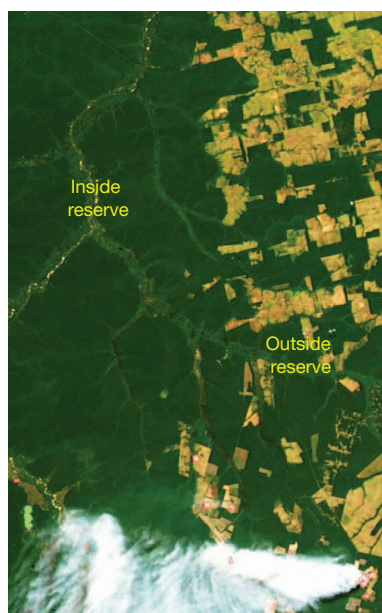
Thus, changes both inside and outside reserves determine their ecological viability, with forest disruption (deforestation, logging and fires), and overexploitation of wildlife and forest resources (hunting

and harvests of non-timber forest products) having the greatest direct negative impacts. Other environmental changes, such as air and water pollution, increases in human population densities and climatic change (changes in total rainfall, ambient temperature, droughts and windstorms) generally had weaker or more indirect effects over the last 20 to 30 years (Supplementary Table 5).

Environmental degradation occurring around a protected area could affect biodiversity in many ways, such as by increasing reserve isolation, area and edge effects<sup>15–19</sup>. However, we discovered that its effects are also more insidious: they strongly predispose the reserve itself to similar kinds of degradation. Nearly all (19 of 21) of the environmental drivers had positive slopes when comparing their direction and magnitude inside versus outside reserves (Fig. 5). Among these, 13 were significant even with stringent Bonferroni corrections ( $P < 0.0071$ ) and 17 would have been significant if tested individually ( $P < 0.05$ ). As expected, the associations were strongest for climate parameters but were also strong for variables describing air and water pollution, stream sedimentation, hunting, mining, harvests of non-timber forest products and fires. To a lesser extent, trends in forest cover, human populations, road expansion and automobile traffic inside reserves also mirror those occurring outside reserves (Fig. 5).

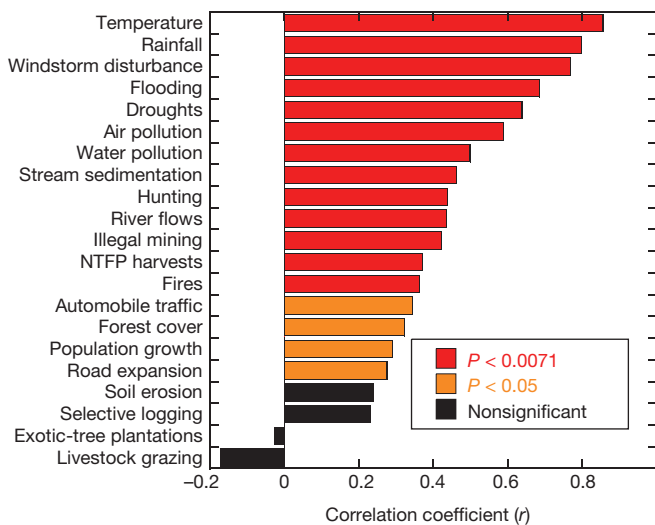
Our findings signal that the fates of tropical protected areas will be determined by environmental changes both within and around the reserves, and that pressures inside reserves often closely reflect those occurring around them. For many reasons, larger reserves should be more resilient to such changes<sup>15–22</sup>, although we found that removing the effects of reserve area statistically did not consistently weaken the correlations between changes inside versus outside protected areas (Supplementary Table 6).

Our study reveals marked variability in the health of tropical protected areas. It indicates that the best strategy for maintaining biodiversity within tropical reserves is to protect them against their major proximate threats, particularly habitat disruption and overharvesting. However, it is not enough to confine such efforts to reserve interiors while ignoring their surrounding landscapes, which are often being rapidly deforested, degraded and overhunted<sup>5,6,13,15</sup> (Fig. 5). A failure to limit interrelated internal and external threats could predispose reserves to ecological decay, including a taxonomically and functionally



**Figure 4** | Comparison of ecological changes inside versus outside protected areas, for selected environmental drivers. The image is an example of the strong distinction in disturbance inside versus outside a reserve. The bars show the percentages of reserves with improving versus worsening conditions.





**Figure 5** | Pearson correlations comparing the direction and strength of 21 environmental drivers inside versus outside tropical protected areas. NTFP, non-timber forest products.

sweeping array of changes in species communities (Fig. 2) and an erosion of fundamental ecosystem processes<sup>16,18,23</sup>.

Protected areas are a cornerstone of efforts to conserve tropical biodiversity<sup>3,4,13,21</sup>. It is not our intent to diminish their crucial role but to highlight growing challenges that could threaten their success. The vital ecological functions of wildlife habitats surrounding protected areas create an imperative, wherever possible, to establish sizeable buffer zones around reserves, maintain substantial reserve connectivity to other forest areas and promote lower-impact land uses near reserves by engaging and benefiting local communities<sup>4,15,24–27</sup>. A focus on managing both external and internal threats should also increase the resilience of biodiversity in reserves to potentially serious climatic change<sup>28–30</sup> in the future.

## METHODS SUMMARY

Our interview protocol, rationale, questionnaire and data analyses are detailed in the Supplementary Information. We selected protected areas broadly to span the African, American and Asia-Pacific tropics (Supplementary Fig. 1), focusing on sites with mostly tropical or subtropical forest that had at least 10 refereed publications and 4–5 researchers with long-term experience who could be identified and successfully interviewed.

We devised a robust and relatively simple statistical approach to assess temporal changes in the abundance of each guild and in each potential environmental driver across our reserve network (see Supplementary Information). In brief, this involved asking each expert whether each variable had markedly increased, remained stable or markedly declined for each reserve. These responses were scored as 1, 0 and –1, respectively. For each response, the expert was also asked to rank their degree of confidence in their knowledge. After discarding responses with lower confidence, scores from the individual experts at each site were pooled to generate a mean value (ranging from –1.0 to 1.0) to estimate the long-term trend for each variable.

The means for each variable across all 60 sites were then pooled into a single data distribution. We used bootstrapping (resampling with replacement; 100,000 iterations) to generate confidence intervals for the overall mean of the data distribution. If the confidence intervals did not overlap zero, then we interpreted the trend as being non-random. Because we tested many different guilds, we used a stringent Bonferroni correction ( $P \leq 0.0056$ ) to reduce the likelihood of Type I statistical errors, although we also identified guilds that showed evidence of trends ( $P \leq 0.05$ ) if tested individually. For comparison, we estimated effect sizes (bootstrapped mean divided by s.d., with negative values indicating declines) for changes in guild abundances and for potential drivers inside and outside reserves (Supplementary Tables 2–4).

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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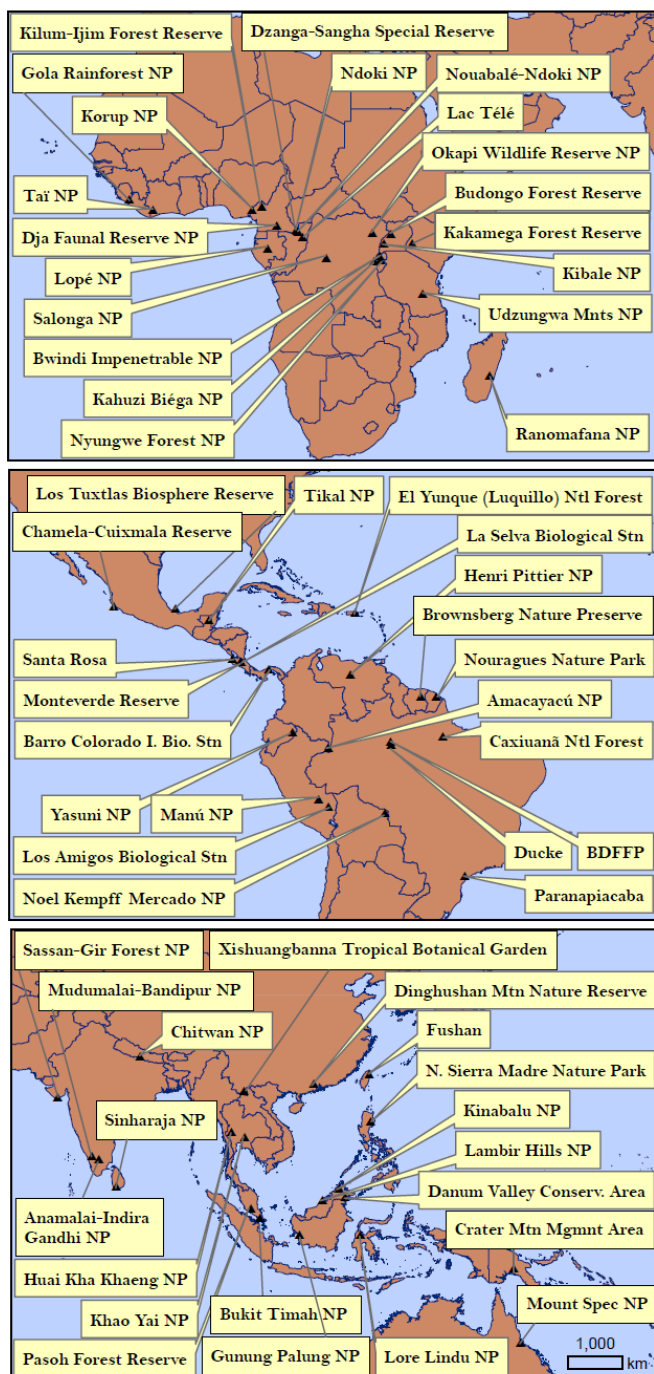
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‡Deceased.

## Supplementary Information

### Methods

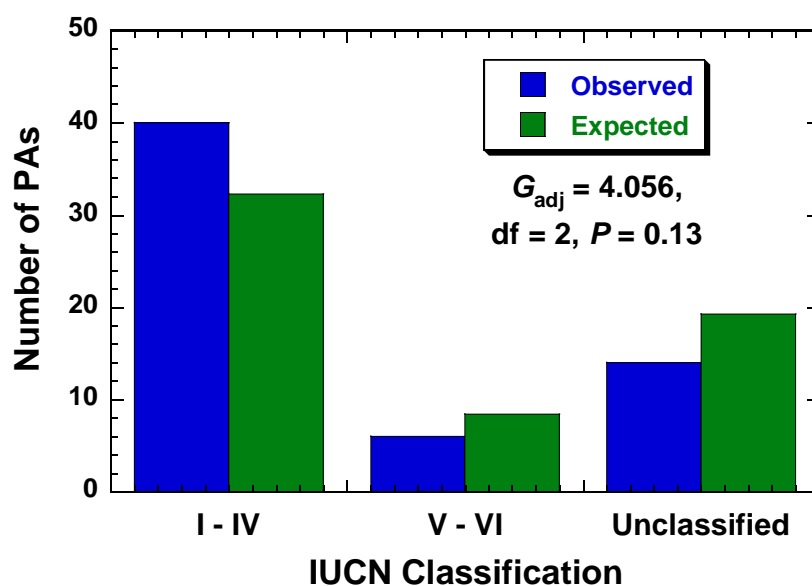
**Supplementary Figure 1** Names and locations of 60 protected areas stratified across the African, American and Asia-Pacific tropics.



### *Representativeness of study sites*

Our 60 tropical protected areas spanned 36 different nations. To provide an indication of the degree to which our sites were ‘typical’, we compared the relative frequency of reserves within ‘high-protection’ (IUCN Categories I-IV), ‘multiple-use’ (IUCN Categories V-VI), and unclassified categories between our sample and all 16,038 protected areas within the same nations from the World Database on Protected Areas ([www.wdpa.org](http://www.wdpa.org)). We excluded China from this comparison because its reserve-classification scheme differs from that of other nations in having virtually no high-protection reserves; the ratio of multiple-use to high-protection reserves in China was 628.3, whereas ratios for all the other 35 nations were  $< 3.4$ . We found no significant difference in the frequencies of reserves in the three different categories between our sample and expected values derived from all 16,038 reserves in the same nations ( $G_{\text{adj}} = 4.056$ , d.f. = 2,  $P = 0.13$ ;  $G$ -test for goodness-of-fit, with Williams’ correction for sample size) (Supplementary Fig. 2). Other kinds of data, such as the budgets and staffing for protected areas, were unavailable for most sites, precluding more in-depth comparisons of this nature.

**Supplementary Figure 2** Number of high-protection (IUCN Categories I-IV), multiple-use (Categories V-VI) and unclassified protected areas in our study compared to expected values derived from all 16,038 protected areas in the same tropical nations.



### *Reserve isolation*

We also assessed the relative geographical isolation of the protected areas in our study, as measured by their distance to the nearest city. We did so because reserve isolation might influence the human pressures that a reserve experiences, and we wished to know whether our reserves were more or less isolated from nearby human populations than is typical of other reserves in the same nations.

For each of our 60 protected areas, we overlaid its boundary map onto a mapped surface of travel-time accessibility<sup>1</sup>. This surface estimates, for any point on Earth, the mean travel time in minutes required to reach the nearest city of  $> 50,000$  residents, using conventional local

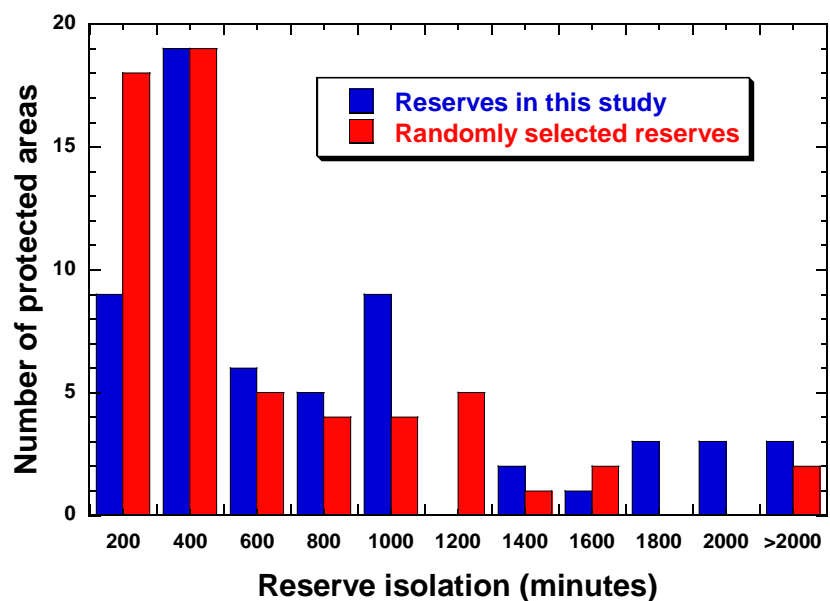


means such as automobiles, boats and hiking. The surface has a spatial resolution of 0.0083 decimal degrees (925 m at the equator), and we averaged the measurements for every pixel within each reserve to estimate its average isolation.

We then randomly selected 60 reserves for comparison. We stratified the randomly selected reserves across the same 36 nations in which our protected areas occur (choosing for each nation an equal number of random reserves as that found in our original sample). The randomly selected reserves were chosen from the World Database on Protected Areas ([www.wdpa.org](http://www.wdpa.org)), using a Mersenne Twist random number generator with a random seed value. Marine protected areas were excluded from the random sample by considering only reserves whose centre-most point fell on land.

We found considerable overlap between the isolation of our reserves (mean  $\pm$  SD = 741  $\pm$  761 minutes to the nearest city) and the randomly selected reserves (505  $\pm$  479 minutes) (Supplementary Fig. 3). The isolation values did not differ significantly on average, either when using a Mann-Whitney  $U$ -test ( $P = 0.071$ ) or a two-way ANOVA that contrasted log-transformed isolation values between our sample and the random sites and also among the three major tropical regions (Africa, Americas, Asia-Pacific). This latter analysis revealed no significant difference between our reserves and the random sites ( $F_{1,114} = 3.19$ ,  $P = 0.077$ ), but some difference among the three major regions ( $F_{2,114} = 3.33$ ,  $P = 0.039$ ). In pairwise comparisons, reserves in Africa were more isolated ( $P < 0.05$ ; Tukey's test) than those in the Asia-Pacific, with reserves in the Americas being intermediate and not significantly different from those in the other two regions.

**Supplementary Figure 3** Comparison of the relative isolation (travelling time to the nearest city of > 50,000 residents) between the 60 tropical forest protected areas in our study and a random sample of 60 protected areas stratified across the same 36 nations.





### *Design of interviews*

We initially tested whether we could use research publications to assess the knowledge-base at our research sites, using two of the best-studied sites in the tropics, Barro Colorado Island in Panama and La Selva Biological Station in Costa Rica. Despite perusing the entire publication lists for both sites (up to early 2008), we found that recognized experts provided more comprehensive, up-to-date and time-efficient assessments. Moreover, the number of available refereed publications varied enormously among our 60 selected sites, from just 10 to > 3,300 papers. A reliance solely on publications would have imparted an obvious sampling bias when attempting to compare different sites, whereas experts are able to integrate a much wider range of knowledge based on personal observations, communications with other researchers and critically evaluating the relevant technical literature for their site.

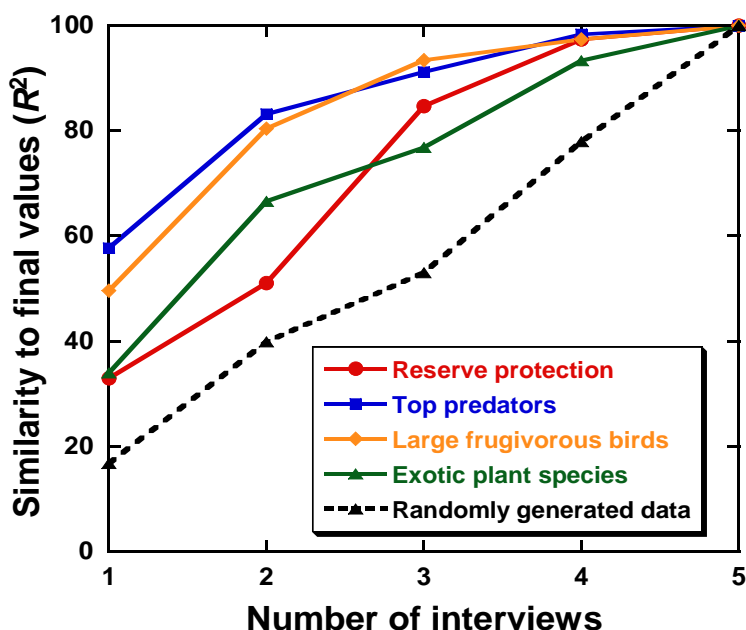
Our 10-page interview form, coupled with a telephone or face-to-face interview, allowed us to plumb in detail the accumulated knowledge of our long-term experts. The form (attached below as Appendix 1) includes 120 individual questions, 60 of which have five-part answers. We carefully designed our interview form after consulting the relevant survey-method literature<sup>2-5</sup> and with social-science experts who routinely conduct such surveys. Two of the most important potential biases to avoid are (a) diluting high-confidence responses with low-confidence responses, and (b) interviewing ‘clusters’ of closely affiliated, like-minded experts<sup>2,3</sup>. To minimize the first concern, we asked our experts to rank their level of confidence for each question they were asked (‘speculative’, ‘good’, ‘high’). We discarded all speculative responses prior to analysis. To minimize the second concern, we used both technical publications and communications with an array of different individuals to identify our experts. These experts were predominantly ecologists, zoologists, and botanists with long-term field and empirical data-collection experience in their respective protected area.

Another concern in surveys such as ours is that respondents might provide biased responses either because they fear political or professional retribution<sup>2,3</sup> or are personally invested in seeing the protected area succeed<sup>4</sup>. To minimize this concern, we offered all respondents complete anonymity, should they wish. We established the following conditions: if an outside party wishes to communicate with an expert for a particular reserve, they should contact the lead author of this study (William Laurance, email: [bill.laurance@jcu.edu.au](mailto:bill.laurance@jcu.edu.au)) who will then forward the request to the relevant expert. That expert can then either respond or ignore the request at their discretion. In practice, anonymity was not a concern for most of our experts, all of whom were offered, and most of whom accepted, co-authorship of this study (however, to err on the side of caution, none is explicitly associated with any particularly protected area in this study). We also considered and rejected the notion that these experts might have provided overly positive responses because they wanted to see the reserve succeed. In practice, many respondents (virtually all of whom were independent researchers, not park employees) expressed at least some concerns about the condition of their reserve. Further, our interview protocol was so exhaustive, specific and objective (with both written and verbal components and interviews of 4-5 different researchers per reserve) that it would have been difficult for any individual to obfuscate important changes in the reserve.

A final concern we had was whether 4-5 interviews were sufficient to identify the key trends at our different sites. To test this we conducted a ‘saturation analysis’<sup>5</sup>, which is designed to determine how much new information is being provided by each additional interview (Supplementary Fig. 4). First, we arbitrarily selected four of our response variables that varied widely. Second, for each of our 21 reserves for which we had 5 interviews, we pooled the

interview data to generate mean scores for each variable. Third, we compared the mean score across these reserves from 1, 2, 3, and then 4 interviews to those generated by 5 interviews, using linear regression. As shown by the rapid and nonlinear rise in  $R^2$  for each variable, the mean scores for each reserve rapidly converge on the final values after just 2-4 interviews. We conclude from this assessment that our regime of 4-5 interviews per site was sufficient to capture the most important aspects of available expert knowledge.

**Supplementary Figure 4** Saturation curves for four representative response variables, compared to values achieved with randomly generated data.



### *Statistical analyses*

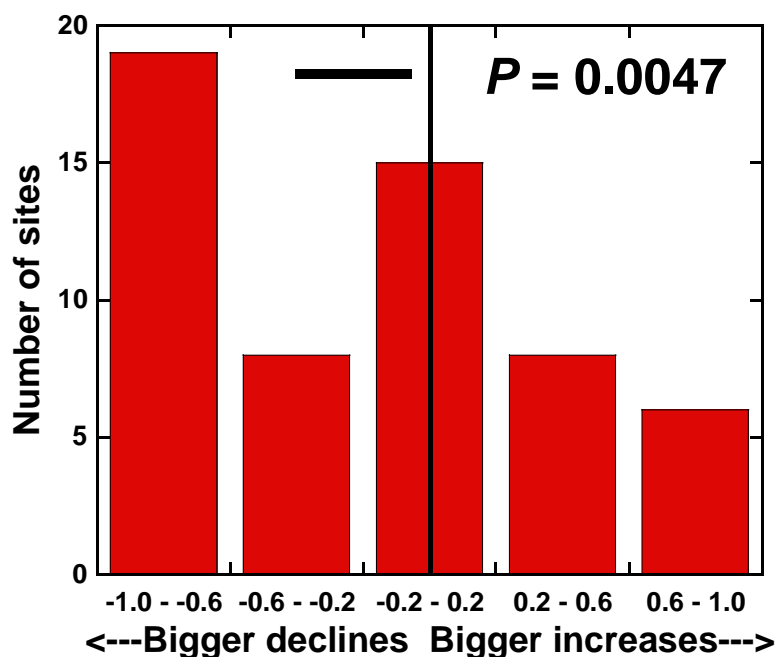
For ease of interpretation, we devised a robust and relatively simple statistical approach to assess temporal changes in each guild and potential environmental driver. We illustrate our strategy using the abundance of a single guild, apex predators, as an example. For each reserve, each expert was asked to indicate whether the overall abundance of apex predators had declined by at least 10-25%, remained roughly stable, or increased by at least 10-25%, over the past 20-30 years. These responses were scored as -1, 0, and 1, respectively<sup>A</sup>. If an expert had no knowledge

<sup>A</sup> We originally collected quantitative data on each guild or environmental driver, using an ordinal scale (-3 = decline of > 50%; -2 = decline of 25-50%; -1 = decline of 10-25%; 0 = no change; 1 = increase of 10-25%; 2 = increase of 25-50%; 3 = increase of > 50%). However, we elected to simplify these data into a three-point scale (+1, 0, -1) because the validity of means and standard deviations derived from ordinal data has been questioned<sup>6</sup> and because the three-point and ordinal scales yielded virtually identical results. For example, calculated effect sizes for our guilds (using the 27 guilds with adequate sample sizes; Supplementary Table 2) based on the three-point and ordinal scales were strongly, positively and linearly related ( $F_{1,25} = 744.5$ ,  $R^2 = 96.8\%$ ,  $P < 0.00001$ ; least-squares regression analysis).

for this particular variable or indicated that their view was speculative, their response was discarded. Among the experts with good or high confidence, we combined scores to generate a mean value (ranging from -1.0 to 1.0) to estimate the long-term trend in abundance of apex predators at their study site.

The means for all 60 sites were then pooled into a single data distribution (Supplementary Fig. 5). We used bootstrapping (random resampling with replacement; 100,000 iterations) to generate confidence intervals for the overall mean of the data distribution. If the confidence intervals for the mean did not overlap zero, we then interpreted the trend as non-random. Because we tested a number of different guilds, we used a stringent Bonferroni correction ( $P = 0.0056$ ) to reduce the likelihood of Type I statistical errors. Given that our study has important implications for nature conservation, we also identify guilds that would have shown non-random trends ( $P \leq 0.05$ ) had we tested them individually.

**Supplementary Figure 5** Example of a data distribution for 60 tropical protected areas (arbitrarily divided into increments of 0.4), for plotting changes in the abundance of apex predators. The horizontal black line shows the 95% confidence interval for the mean value, and the  $P$  indicates the probability of a non-random deviation from zero.



We also assessed effect sizes for changes in guild abundances (Supplementary Table 2) by estimating the mean value for each guild (from bootstrapping), and then dividing this by the standard deviation of that guild. With this procedure, negative values indicate a decline in guild abundance, and positive values an increase. We used a similar procedure to identify changes in our potential environmental driver variables inside (Supplementary Table 3) and outside (Supplementary Table 4) protected areas.

Our reserve-protection index provided a simple assessment of the degree to which practical, on-the-ground enforcement measures—resulting broadly from the number of park guards and their associated infrastructure, vehicles, supporting legal framework, and level of professional motivation—had changed over the past 20-30 years inside the protected area. Each researcher was asked whether the level of actual protection in their reserve had improved, remained constant, or declined over time (scored as +1, 0, and -1, respectively), and the mean value was calculated for each reserve.

We relied on bivariate tests to assess relationships between potential environmental drivers and our reserve-health index. Multivariate analyses were not possible because, for some reserves, data were unavailable for some response variables and drivers. These missing values varied among the reserves, making it impossible to create a complete matrix of drivers and response variables needed for multivariate analyses. We used Spearman rank correlations (with Bonferroni corrections to limit the likelihood of spurious correlations, using a recommended experiment-wise error rate of 0.15 in all cases<sup>7</sup>) to identify potential relationships between the drivers and reserve health, and general linear models to test the efficacy of predictors. We evaluated our general linear models using Akaike's information criterion corrected for finite samples ( $AIC_c$ ), an information-theoretic index of bias-corrected model weight<sup>8</sup>. We assessed each model's probability using  $AIC_c$  weights ( $wAIC_c$ ); the closer to 1, the stronger the relative evidence for that model. The percent deviance explained (%DE) measures the models' structural goodness-of-fit. The evidence ratio (ER) is the ratio of the  $wAIC_c$  for each model over its null (intercept-only model); models with higher ER values have greater support relative to the null.

### ***Validation of interview data***

We explored several strategies for independently testing our interview data. For example, we repeatedly attempted to access time-series data on the abundances of selected vertebrate species being compiled for the Living Planet Index ([http://en.wikipedia.org/wiki/Living\\_Planet\\_Index](http://en.wikipedia.org/wiki/Living_Planet_Index)), an initiative of WWF and the Zoological Society of London. However, the datasets in this index, at least for the 60 protected areas in our study, are currently too sparse and preliminary to provide a sound basis for comparison (B. Collen, pers. comm.). We also explored data on investments in the management of Amazonian protected areas, but found little usable overlap with our study sites (C. A. Peres, pers. comm.). We did find more overlap between our study sites and a pantropical assessment of fire incidence in and around protected areas<sup>9</sup>, but this study provided only a single estimate of fire frequency, not a time series, and so could not be used to test the trend data from our investigation.

We finally elected to do an extensive meta-analysis of available time-series studies, using data from published or in-press research articles, refereed book chapters, and technical research reports. We established four *a priori* criteria to include studies. They had to (1) focus on one of the 60 protected areas in our study, (2) yield clearly interpretable data on one of the guilds or potential driver variables we evaluated, (3) provide a time-series of measurements that overlapped at least partially with our study period (the last 20-30 years), and (4) have been published recently, ideally after 2009. This final criterion was designed to limit the exposure of our experts to the scientific work in question (about 85% of our interviews were conducted between mid 2008 and late 2009), thereby providing a more independent test of our findings. We used several strategies, including the internet, searches of our own extensive technical-literature databases<sup>10</sup>, consultation with other relevant experts, and personal knowledge, to identify potentially suitable time-series.



We identified 59 independent datasets that met our four selection criteria and provided a direct basis for comparison with our interviews (Supplementary Table 1). These studies used a variety of repeated-sampling approaches, such as mark-recapture studies, track counts, automatic-camera censuses, plot-based monitoring, and remote sensing, to assess temporal changes in their response variables. The datasets, which span 27 different protected areas, are approximately evenly distributed across the three major tropical regions (21 in Africa, 20 in the Americas, 16 in the Asia-Pacific). Nearly half of these studies (28 of 59) focused on one of six well-studied guilds (primates, large non-predatory vertebrates, top predators) or potential driver variables (forest cover inside reserves, forest cover outside reserves, hunting inside reserves), but the remainder were diverse in nature. Altogether, 15 guilds and 13 driver variables were represented by at least one independent dataset.

To provide a direct basis for comparison with our study, we used a simple three-way system (increase, no significant change, decrease) to classify the trend in each independent dataset, following the conclusions of the original researchers. Using this approach, the null hypothesis is that one third of the 59 independent datasets would agree with the trends in our interview data, based simply on chance. We found, however, that the independent datasets agreed with our findings in 51 of the 59 comparisons (86.4%). This number is strikingly higher than that from random expectation ( $G_{\text{adj}} = 36.50$ , d.f. = 1,  $P < 0.0001$ ;  $G$ -test for goodness of fit, adjusted for sample size).

In assessing the eight datasets that disagreed with our findings (Supplementary Table 1), we discerned only one obvious pattern: four described trends that occurred recently, and thus might not have been known to the experts we interviewed, or were regarded as not being representative of longer-term trends. For example, one involved recent chytrid-fungus-related declines of stream-dwelling amphibians at Manu National Park in Peru<sup>11</sup> that were detected only in 2009. Two others resulted from recent (2005-2009) efforts to improve protection of Lope Reserve, Gabon, which have led to a recent increase there in the abundance of elephants and other large non-predatory vertebrates<sup>12</sup>.

Notably, none of the eight disagreements was fundamental in nature—our experts never reported a trend *opposite* to that shown by the independent test. For example, in Budongo Forest, Uganda, our experts collectively indicated that primate abundance had increased somewhat over the last 2-3 decades, whereas standardized field-monitoring data (35 transects of 2 km in length that were repeatedly censused from 1992-2009) revealed that individual species abundances varied considerably over time, with no clear trend in overall abundance<sup>13</sup>. Similarly, our experts reported that ambient temperature had increased over time at Los Tuxtlas Biosphere Reserve in Mexico, whereas an independent analysis based on long-term records (1925-2006) from 24 nearby meteorological stations revealed just a slight rise in mean temperature (0.016° C per decade) that was not statistically significant<sup>14</sup>.

Overall, these validation tests give us considerable confidence in the efficacy of our interview data (see refs. 15-17 for relevant discussions). The available comparisons do not span all of the protected areas, guilds, or potential driver variables we assessed evenly, but this simply illustrates the highly sparse and patchy nature of suitable time-series analyses. Indeed, the 59 datasets we compiled after extensive efforts represent just a tiny fraction (1.6%) of the 3,589 assessments of trends in guilds and potential drivers captured by our interview data (our interviews provided 1,262 assessments of guild trends and 2,327 assessments of trends in environmental drivers, across our network of 60 protected areas). It was precisely this deficit that prompted us to undertake this interview-based investigation, to provide a much more systematic

and far-reaching comparison of the fate of tropical protected areas than has previously been possible.

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**Supplementary Table 1.** Independent tests of identified trends in guild abundances and potential environmental drivers from expert interviews, using available time-series data from scientific publications and technical reports. For each test, we indicate whether or not the independent data validated the overall trend identified by our expert interviews. ‘Time interval’ indicates the span of years covered by each empirical dataset. References for each test are listed below.

No.	Protected area	Region	Guild or driver trend based on interviews	Trend validated?	Time interval	Reference
1	Budongo	Africa	Primates increased in abundance	No	1992-2009	1
2	Bwindi	Africa	Harvests of NTFPs declined inside park	Yes	1991-2003	2
3	Kakamega	Africa	Primates increased in abundance	Yes	1997-2010	3, 4
4	Kakamega	Africa	Understory birds declined in abundance	Yes	1912-2003	5
5	Kakamega	Africa	Forest cover declined inside reserve	Yes	1912-2003	5
6	Kahuzi-Biega	Africa	Primates declined in abundance	Yes	1978-2004	6
7	Kibale	Africa	Primates declined in abundance	No	1975-2006	7
8	Kibale	Africa	Ambient temperature increased inside reserve	Yes	1975-2006	8
9	Kibale	Africa	Rainfall increased inside reserve	Yes	1900-2006	8
10	Kilum-Ijim	Africa	Large-seeded old-growth trees declined in abundance	Yes	1998-2006	9
11	Kilum-Ijim	Africa	Harvests of NTFPs increased inside reserve	Yes	1998-2006	9
12	Lope	Africa	Large non-predatory vertebrates declined	No	2005-2009	10
13	Lope	Africa	Hunting increased inside reserve	No	2005-2009	10
14	Nouabale-Ndoki	Africa	Large non-predatory vertebrates declined	Yes	2006-2011	11
15	Nouable-Ndoki	Africa	Hunting increased inside reserve	Yes	2006-2011	11

16	Nouable-Ndoki	Africa	Hunting increased outside reserve	Yes	2006-2011	12
17	Ngungwe	Africa	Human populations increased outside reserve	Yes	1991-2007	13
18	Okapi	Africa	Large non-predatory vertebrates declined in abundance	Yes	1995-2006	14
19	Udzungwa	Africa	Primates increased in abundance	No	2004-2009	15
20	Udzungwa	Africa	Pioneer/generalist trees were stable in abundance	Yes	1986-2007	16
21	Udzungwa	Africa	Large-seeded old-growth trees were stable in abundance	Yes	1986-2007	17
22	Udzungwa	Africa	Forest cover remained stable inside the reserve	Yes	1983-2009	17
23	Udzungwa	Africa	Forest cover declined outside reserve	Yes	1983-2009	17
24	Barro Colorado Island	Americas	Lianas increased in abundance	Yes	1995-2007	18
25	Brownsberg	Americas	Illegal mining increased inside reserve	Yes	1971-2005	19
26	Chamela-Cuixmala	Americas	Top predators declined in abundance	No	1995-2008	20
27	La Selva	Americas	Terrestrial amphibians declined in abundance	Yes	1970-2005	21
28	La Selva	Americas	Terrestrial lizards/larger reptiles declined in abundance	Yes	1970-2005	21
29	La Selva	Americas	Understory insectivorous birds declined in abundance	Yes	1960-1999	22
30	Los Amigos	Americas	Top predators increased in abundance	Yes	2004-2008	23
31	Los Amigos	Americas	Large non-predatory vertebrates increased in abundance	Yes	2004-2008	23



32	Los Amigos	Americas	Primates increased in abundance	Yes	2004-2008	23
33	Los Amigos	Americas	Omnivorous mammals increased in abundance	Yes	2004-2008	23
34	Los Amigos	Americas	Game birds increased in abundance	Yes	2004-2008	23
35	Los Amigos	Americas	Larger frugivorous birds increased in abundance	Yes	2004-2008	23
36	Los Amigos	Americas	Hunting declined inside reserve	Yes	2004-2008	23
37	Los Amigos	Americas	Forest cover declined outside reserve	Yes	2002-2010	23
38	Los Amigos	Americas	Illegal mining increased outside reserve	Yes	2002-2010	24
39	Los Tuxtlas	Americas	Ambient temperature increased inside reserve	No	1925-2006	25
40	Luquillo	Americas	Exotic plants increased in abundance	Yes	1936-2003	26
41	Manu	Americas	No change in stream-dwelling amphibian abundance	No	1999-2009	27
42	Manu	Americas	No change in terrestrial amphibian abundance	Yes	1999-2009	27
43	Nouragues	Americas	Illegal mining increased inside reserve	Yes	2000-2008	28
44	Anamalai	Asia-Pacific	Primates increased in abundance	Yes	1996-2010	29
45	Khao Yai	Asia-Pacific	Top predators declined in abundance	Yes	1999-2007	30
46	Lambir	Asia-Pacific	Large non-predatory vertebrates declined in abundance	Yes	1984-2007	31
47	Lambir	Asia-Pacific	Primates declined in abundance	Yes	1984-2007	31
48	Lambir	Asia-Pacific	Omnivorous mammals declined in abundance	Yes	1984-2007	31

49	Lambir	Asia-Pacific	Larger frugivorous birds declined in abundance	Yes	1984-2007	31
50	Lambir	Asia-Pacific	Raptorial birds declined in abundance	Yes	1984-2007	31
51	Lambir	Asia-Pacific	Hunting increased inside reserve	Yes	1984-2007	31
52	Lore Lindu	Asia-Pacific	Forest cover declined inside reserve	Yes	1972-2007	32
53	Mudumalai-Bandipur	Asia-Pacific	Exotic plants increased in reserve	Yes	1997-2008	33
54	Mudumalai-Bandipur	Asia-Pacific	Fires increased inside reserve	Yes	1989-2005	34
55	Northern Sierra Madre	Asia-Pacific	Forest cover declined inside reserve	Yes	1972-2002	35
56	Northern Sierra Madre	Asia-Pacific	Forest cover declined outside reserve	Yes	1972-2002	35
57	Northern Sierra Madre	Asia-Pacific	Logging increased inside reserve	Yes	2003-2009	36
58	Xishuangbanna	Asia-Pacific	Forest cover declined outside reserve	Yes	1976-2003	37
59	Xishuangbanna	Asia-Pacific	Exotic tree plantations increased around reserve	Yes	1976-2003	37

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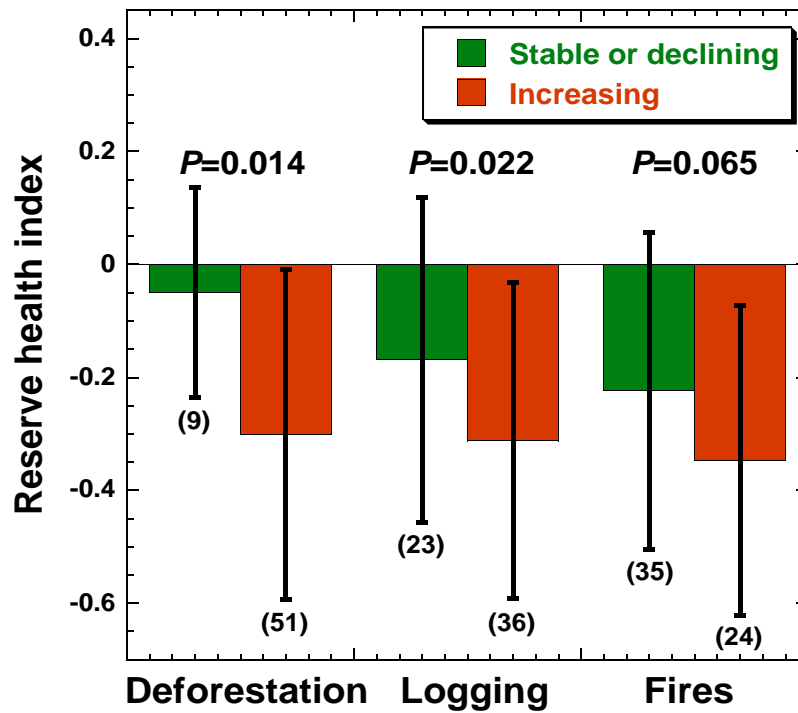
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## Supplementary Analyses

**Supplementary Figure 6** Effects of surrounding disturbances on reserve health (mean  $\pm$  SD). Health values declined less in reserves where deforestation, logging or fires were stable or declined, relative to those where these disturbances increased over time.  $P$  values shown are for Mann-Whitney  $U$ -tests. Sample sizes are in parentheses.



**Supplementary Table 2** Trends in the abundance of 27 animal and plant guilds within 60 tropical protected areas, ranked by effect size (negative values indicate declines in guild abundance, and positive values an increase). *P* values shown in bold are non-random using a stringent Bonferroni correction ( $P \leq 0.0056$ ), whereas those in italics are non-random at  $P \leq 0.05$ . The *P* values, estimated mean, and upper and lower 95% confidence limits (CLs) for each guild were estimated by bootstrapping (with 100,000 iterations). Four guilds (aquatic invertebrates, army/driver ants, disease-vectoring invertebrates, dung beetles) were too poorly known to reliably assess overall trends in their abundance.

<b>Guild</b>	<b>P</b>	<b>Effect size</b>	<b>Mean</b>	<b>SD</b>	<b>Lower CL</b>	<b>Upper CL</b>	<b>No data (%)</b>
Ecological specialists	<b>&lt;0.00001</b>	-1.053	-0.425	0.4035	-0.600	-0.250	50.0
Stream amphibians	<b>0.00002</b>	-1.012	-0.3495	0.3452	-0.525	-0.17391	56.7
Freshwater fish	<b>&lt;0.00001</b>	-0.893	-0.4411	0.4938	-0.63441	-0.24775	41.7
Terrestrial amphibians	<b>0.00157</b>	-0.796	-0.2786	0.3497	-0.45455	-0.10256	53.3
Non-venomous snakes	<b>0.00127</b>	-0.761	-0.2968	0.3903	-0.4881	-0.10556	51.7
Bats	<b>0.00190</b>	-0.666	-0.1772	0.266	-0.2973	-0.05714	46.7
Lizards & larger reptiles	<b>0.00382</b>	-0.564	-0.2877	0.5097	-0.49495	-0.08036	40.0
Venomous snakes	<i>0.01511</i>	-0.53	-0.2261	0.4263	-0.42929	-0.02299	48.3
Large non-predatory spp.	<b>0.00022</b>	-0.48	-0.2871	0.5985	-0.44583	-0.12845	5.0
Epiphytes	<b>0.00557</b>	-0.439	-0.151	0.3439	-0.26798	-0.03398	26.7
Lg-seed old-growth trees	<b>0.00086</b>	-0.436	-0.2033	0.4658	-0.33041	-0.07615	8.3
Spp. requiring tree cavities	<i>0.01852</i>	-0.389	-0.1794	0.4616	-0.34804	-0.01068	31.7
Migratory species	<i>0.04674</i>	-0.368	-0.1463	0.3973	-0.31707	0.02451	41.7
Understory insectiv. birds	<i>0.01112</i>	-0.368	-0.1482	0.4023	-0.27516	-0.02128	20.0
Apex predators	<b>0.00469</b>	-0.361	-0.2151	0.5958	-0.37557	-0.05455	6.7
Raptorial birds	<i>0.02587</i>	-0.314	-0.1385	0.4414	-0.27733	0.00043	20.0
Light-loving butterflies	0.16	-0.299	-0.1082	0.3617	-0.3125	0.09615	55.0
Larger frugivorous birds	<i>0.03055</i>	-0.276	-0.1269	0.4598	-0.26042	0.00654	13.3
Primates	<i>0.02777</i>	-0.269	-0.1489	0.553	-0.30121	0.00333	8.3
Rodents	0.13	-0.188	-0.0975	0.5195	-0.26871	0.07364	23.3
Larger game birds	0.13	-0.166	-0.0884	0.5312	-0.24691	0.07014	15.0
Opportunistic omnivores	0.12	-0.164	-0.0996	0.6067	-0.27075	0.07164	10.0
Human diseases	<b>0.00115</b>	0.438	0.2288	0.5227	0.08025	0.37727	11.7
Lianas & vines	<b>0.00116</b>	0.467	0.2016	0.4316	0.07516	0.32801	15.0
Exotic animal species	<b>&lt;0.00001</b>	0.904	0.3475	0.3842	0.24214	0.45283	11.7
Pioneer & generalist trees	<b>&lt;0.00001</b>	1.028	0.4592	0.4465	0.3366	0.5817	15.0
Exotic plant species	<b>&lt;0.00001</b>	1.169	0.4823	0.4126	0.375	0.58951	6.7

**Supplementary Table 3** As in Supplementary Table 1 except for potential environmental drivers inside protected areas, and with a different Bonferroni correction ( $P \leq 0.0071$ ).

<b>Driver variable</b>	<b>P</b>	<b>Effect size</b>	<b>Mean</b>	<b>SD</b>	<b>Lower CI</b>	<b>Upper CI</b>	<b>No data (%)</b>
Reserve health	<0.00001	-0.910	-0.2313	0.2686	-0.3372	-0.1879	0
River & stream flows	0.01052	-0.301	-0.1048	0.3484	-0.1944	-0.0153	1.7
Exotic plantations	0.03395	-0.237	-0.0486	0.2048	-0.1006	0.0033	0
Selective logging	0.13	-0.147	-0.0649	0.4399	-0.1761	0.0464	0
Natural-forest cover	0.25	-0.085	-0.0381	0.4501	-0.1519	0.0758	0
Illegal mining	0.35	-0.047	-0.0116	0.2452	-0.0750	0.0517	1.7
Fires	0.44	-0.024	-0.0076	0.3169	-0.0883	0.0731	0
Rainfall	0.40	0.038	0.0156	0.4085	-0.0994	0.1305	10.0
Hunting	0.11	0.157	0.0982	0.6249	-0.0597	0.2561	0
NTFP harvests	0.02816	0.247	0.1193	0.4828	-0.0031	0.2417	0
Soil erosion	<0.00001	0.517	0.1800	0.3483	0.0893	0.2708	3.3
Reserve-protection effort	0.00005	0.520	0.2500	0.4806	0.1286	0.3714	0
Flooding	<0.00001	0.539	0.1489	0.2762	0.0760	0.2217	5.0
Windstorms	<0.00001	0.561	0.1580	0.2819	0.0759	0.2402	15.0
Roads	<0.00001	0.599	0.1294	0.2160	0.0747	0.1842	0
Stream sedimentation	<0.00001	0.633	0.2497	0.3945	0.1404	0.3591	10.0
Human population density	<0.00001	0.668	0.2286	0.3425	0.1417	0.3156	0
Water pollution	<0.00001	0.709	0.2205	0.3111	0.1396	0.3014	3.3
Ambient temperature	<0.00001	0.745	0.2687	0.3609	0.1633	0.3742	16.7
Livestock grazing	<0.00001	0.765	0.2233	0.2919	0.1497	0.2969	0
Drought severity/intensity	<0.00001	0.851	0.3200	0.3759	0.2218	0.4181	5.0
Air pollution	<0.00001	0.892	0.2946	0.3303	0.2068	0.3824	6.7
Automobile traffic	<0.00001	0.906	0.2806	0.3095	0.2022	0.3589	0

**Supplementary Table 4** As in Supplementary Table 1 except for potential environmental drivers outside of protected areas (within a 3 km-wide zone around the protected area), and with a different Bonferroni correction ( $P \leq 0.0071$ ).

	<b>P</b>	<b>Effect size</b>	<b>Mean</b>	<b>SD</b>	<b>Lower CI</b>	<b>Upper CI</b>	<b>No data (%)</b>
Natural-forest cover	<b>&lt;0.00001</b>	-1.470	-0.5907	0.4019	-0.6925	-0.489	1.7
River & stream flows	<i>0.03883</i>	-0.248	-0.1005	0.4052	-0.2115	0.0106	8.3
Rainfall	0.27	-0.088	-0.0337	0.3819	-0.1431	0.0756	11.7
Fires	<b>0.00433</b>	0.348	0.1412	0.4054	0.0350	0.2474	3.3
Hunting	<b>0.00153</b>	0.398	0.2257	0.5674	0.0778	0.3736	3.3
Livestock grazing	<b>0.00094</b>	0.432	0.1919	0.4442	0.0747	0.3092	5.0
Windstorms	<b>&lt;0.00001</b>	0.593	0.1432	0.2417	0.0677	0.2188	21.7
Flooding	<b>&lt;0.00001</b>	0.605	0.2492	0.4115	0.1358	0.3626	10.0
Illegal mining	<b>&lt;0.00001</b>	0.626	0.2687	0.4295	0.1541	0.3833	6.7
NTFP harvests	<b>&lt;0.00001</b>	0.720	0.3152	0.4378	0.1927	0.4377	11.7
Selective logging	<b>&lt;0.00001</b>	0.729	0.3613	0.4956	0.2325	0.4901	3.3
Exotic plantations	<b>&lt;0.00001</b>	0.749	0.3416	0.4561	0.2199	0.4633	6.7
Ambient temperature	<b>&lt;0.00001</b>	0.818	0.3221	0.3940	0.2067	0.4375	18.3
Air pollution	<b>&lt;0.00001</b>	0.966	0.3716	0.3846	0.2682	0.4750	10.0
Drought severity/intensity	<b>&lt;0.00001</b>	0.978	0.3747	0.3830	0.2674	0.4820	15.0
Water pollution	<b>&lt;0.00001</b>	1.218	0.4936	0.4054	0.3898	0.5975	5.0
Stream sedimentation	<b>&lt;0.00001</b>	1.234	0.5417	0.4390	0.4219	0.6616	18.3
Soil erosion	<b>&lt;0.00001</b>	1.356	0.5638	0.4158	0.4576	0.6699	10.0
Roads	<b>&lt;0.00001</b>	1.671	0.6601	0.3950	0.5607	0.7594	1.7
Automobile traffic	<b>&lt;0.00001</b>	1.845	0.7012	0.3801	0.6078	0.7945	3.3
Human population density	<b>&lt;0.00001</b>	2.294	0.7943	0.3462	0.7097	0.8789	1.7



**Supplementary Table 5** Assessing effects of potential environmental drivers on the reserve-health index, using Spearman rank correlations and general linear models (GLMs). For the correlations,  $P$  values in bold have a Bonferroni-corrected value of  $P \leq 0.0071$ . For the GLMs, the strongest models are those with weights of the Akaike's information criterion corrected for sample size ( $wAIC_c$ ) that are closest to 1. The percent deviance explained (%DE) measures the models' structural goodness-of-fit, whereas models with higher ER values have greater support relative to the null (intercept-only) model. Models with blanks could not be fitted with plausible error structures.

Potential driver	Correlations		General Linear Models			
	$R_s$	$P$	$wAIC_c$	ER	%DE	n
Natural forest cover-outside	0.487	<b>0.0001</b>	0.989	85.9	16.9	59
Natural forest cover-inside	0.432	<b>0.0006</b>	0.998	502.5	21.7	60
Livestock grazing-inside	0.178	0.174	0.786	3.7	7.7	60
Automobile traffic-inside	0.15	0.251	0.393	0.6	2.2	60
Air pollution-inside	0.052	0.706	0.842	5.2	13.3	56
Stream sedimentation-outside	0.052	0.722	0.189	0.2	10.3	49
Ambient temperature-inside	0.046	0.749	0.887	7.5	21.2	50
Road expansion-outside	0.036	0.784	0.309	0.4	1	59
Droughts-inside	0.011	0.937	0.529	1.1	7.3	57
Illegal mining-outside	0.003	0.980	0.703	1.7	7.5	56
Road expansion-inside	-0.017	0.897	0.252	0.3	0.1	60
Automobile traffic-outside	-0.029	0.829	0.224	0.3	0.6	58
Windstorms-inside	-0.049	0.735	-----	-----	-----	51
Rainfall-outside	-0.054	0.700	0.576	1.3	12.2	53
Windstorms-outside	-0.064	0.667	-----	-----	-----	47
Rainfall-inside	-0.071	0.609	0.825	4.6	15.1	54
Ambient temperature-outside	-0.086	0.555	0.438	0.7	14.6	49
Soil erosion-outside	-0.089	0.520	0.205	0.3	4.5	54
Illegal mining-inside	-0.107	0.418	-----	-----	-----	59
Water pollution-inside	-0.111	0.405	0.724	2.6	8.9	58
Water pollution-outside	-0.129	0.335	0.772	3.4	9.7	57
Stream sedimentation-inside	-0.141	0.310	0.579	1.3	11.2	54
Exotic-tree plantations-outside	-0.143	0.288	0.138	0.2	0.7	56
Livestock grazing-outside	-0.155	0.246	0.701	2.3	8.5	57
Floods-outside	-0.158	0.249	-----	-----	-----	54
Stream/river flows-outside	-0.164	0.227	0.183	0.2	2.9	55
Human populations-inside	-0.171	0.190	0.4	0.7	2.3	60
Air pollution-outside	-0.181	0.185	0.92	11.3	16.8	54
Stream/river flows-inside	-0.19	0.150	0.757	3.1	8.3	59

Human populations-outside	-0.202	0.122	0.654	1.9	5.7	59
Hunting-outside	-0.205	0.119	0.777	3.5	8.7	58
Soil erosion-inside	-0.213	0.109	0.677	2.1	8.2	58
Exotic-tree plantations-inside	-0.216	0.097	0.622	1.6	5.2	60
Drought-outside	-0.223	0.113	0.977	40.3	24	51
NTFP harvests-outside	-0.239	0.081	0.928	12.5	18.2	53
Floods-inside	-0.253	0.058	-----	-----	-----	57
Fires-outside	-0.279	<i>0.0323</i>	0.955	21.2	14.1	58
Fires-inside	-0.288	<i>0.0254</i>	0.94	15.7	12.1	60
NTFP harvests-inside	-0.353	<b>0.0057</b>	0.971	33.8	14.3	60
Selective logging-outside	-0.373	<b>0.0036</b>	0.862	6.2	10.5	58
Selective logging-inside	-0.397	<b>0.0017</b>	0.973	36.1	14.5	60
Hunting-inside	-0.452	<b>0.0003</b>	0.998	498.1	21.7	60

**Supplementary Table 6** Pearson correlations between potential environmental drivers inside versus outside of protected areas, and partial Pearson correlations showing the relationship between these two variables once the effects of reserve area were removed statistically. *P* values in bold have a Bonferroni-corrected value of  $P \leq 0.0071$ .

<b>Driver</b>	<b><i>R</i></b>	<b><i>P</i></b>	<b>n</b>	<b>Partial <i>R</i></b>
Livestock grazing	-0.1722	0.20	57	-0.1643
Exotic-tree plantations	-0.0274	0.84	56	-0.0069
Selective logging	0.2300	0.0825	58	0.2123
Soil erosion	0.2401	0.0803	54	0.2418
Road expansion	0.2749	0.0351	59	0.2814
Population growth	0.2896	0.0261	59	0.3002
Natural forest cover	0.3232	0.0125	59	0.3340
Automobile traffic	0.3445	0.0081	58	0.3529
Fires	0.3623	<b>0.0052</b>	58	0.3518
NTFP harvests	0.3707	<b>0.0063</b>	53	0.3707
Illegal mining	0.4224	<b>0.0012</b>	56	0.4351
River & stream flows	0.4355	<b>0.0009</b>	55	0.4321
Hunting	0.4381	<b>0.0006</b>	58	0.4314
Stream sedimentation	0.4615	<b>0.001</b>	48	0.4608
Water pollution	0.4978	<b>0.0001</b>	57	0.5145
Air pollution	0.5874	<b>&lt;0.0001</b>	54	0.5851
Drought severity/intensity	0.6374	<b>&lt;0.0001</b>	50	0.6374
Flooding	0.6833	<b>&lt;0.0001</b>	54	0.6995
Windstorm disturbance	0.7667	<b>&lt;0.0001</b>	47	0.7474
Rainfall	0.7979	<b>&lt;0.0001</b>	52	0.8060
Ambient temperature	0.8547	<b>&lt;0.0001</b>	48	0.8496

**Appendix 1** A non-interactive version of the 10-page interview form used in this study. The present study focuses on changes in the abundance of guilds, as well as the potential drivers of environmental change in our network of protected areas. Data on changes in species richness and composition of guilds are not included in the present analysis, because our experts generally had lower confidence in these trends.

## EXPERT QUESTIONNAIRE ON ENVIRONMENTAL CHANGES AT TROPICAL RESEARCH SITES

### Objectives

This is the first-ever effort to systematically assess environmental changes across a large and representative cross-section of the world's tropical protected areas and research sites. This survey is being based on a detailed assessment of expert opinion, using a standardized questionnaire.

The goals of the study are to determine the degree to which environmental changes and their drivers vary across different sites, and the degree to which they are similar. This study is also designed to assess whether tropical scientists are experiencing a "shifting baseline" because their study areas and their biota are changing in subtle or insidious ways.

The data being collected are qualitative and comparative in nature, and thus will not compromise in any way the ability of any investigator to publish his or her research findings about a particular research site.

This study is being led by Dr William Laurance of the Smithsonian Tropical Research Institute in Panama, with the assistance of Margareta Kalka and Julio Rendeiro. All individuals who provide detailed responses to this questionnaire as well as intellectual input on the manuscript will be offered co-authorship on at least one publication resulting from this work. Individuals who are especially helpful will be higher in the authorship list.

A critical assumption of expert questionnaires such as this is that the data being collected are reliable. Therefore, please do not respond to any question unless you have at least moderately good, direct or indirect knowledge of the issue at hand.

### Expert information

- (1) Full name
- (2) Education level
- (3) Field of expertise
- (4) Gender \_\_\_\_\_
- (5) Nationality
- (6) Work address
- (7) Email
- (8) Phone
- (9) First year of research at site
- (10) Is your knowledge of the site \_\_\_\_\_
- (11) Please rate your overall knowledge of the site \_\_\_\_\_
- (12) How long has it been since you visited the site?      months

### Protected Area Information

- (13) Complete name of Protected Area (PA)
- (14) Longitude      dd      Latitude      dd of PA
- (15) Size of PA      ha
- (16) Name of Research Station within PA

## Expert Questionnaire on Environmental Changes at Tropical Research Sites

- (17) Does the **Focal Research Area (FRA)** encompass the PA? —  
If answered **Yes**, please skip to Question 23  
If answered **No**, continue to Question 18
- (18) Please describe the specific locality of the FRA within the PA (i.e. ne, nw, sw, se, center )
- (19) What is the *closest* distance from the FRA to the border of the PA?      km
- (20) Size of FRA      ha
- (21) Elevation Range of FRA      m
- (22) Please identify your geographical FRA within the PA
- (23) Does the 3 km area bordering the FRA lie mostly within a protected area? —
- (24) Is the fragmentation of the FRA \_\_\_\_\_
- (25) Within a 3km radius, is the FRA \_\_\_\_\_
- (26) Please describe area surrounding the PA (land use, disturbance, human settlement, etc)
- (27) How is protection enforced within the PA?
- (28) What is the protection status of the FRA?
- (29) How has the *level of protection* changed during your time associated with the FRA \_\_\_\_\_
- (30) Please comment

**Part 1: Changes in Animal and Plant Communities**

FEEL FREE TO SKIP QUESTIONS FOR WHICH YOU HAVE LITTLE OR NO KNOWLEDGE.

FOR EACH QUESTION TO WHICH YOU RESPOND, PLEASE PROVIDE DETAILS OF CHANGE, AND FEEL FREE TO ELABORATE ABOUT THE KNOWN OR POSSIBLE DRIVERS OF THE CHANGE.

Over the past 2-3 decades, have any of the following groups changed in (1) Overall Abundance (A) or (2) Species Richness (SR) (native species only) at your FRA (within the PA)?

**MAMMALS**

(31) **Top mammalian predators** (e.g. jaguars, pumas, tigers, giant otters)

Abundance	Species Richness	Knowledge Level
_____	_____	_____
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

(32) **Large, non-predatory species** (e.g. forest elephants, tapirs)

Abundance	Species Richness	Knowledge Level
_____	_____	_____
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

(33) **Primates**

Abundance	Species Richness	Knowledge Level
_____	_____	_____
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## Expert Questionnaire on Environmental Changes at Tropical Research Sites

**(34) Omnivorous/opportunistic mammals**

(e.g. bearded pigs, peccaries, opossums, coati mundis, all &gt;1 kg in weight)

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

**(35) Rodents (< 1 kg in weight)**

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

**(36) Bats**

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## BIRDS

**(37) Understory birds (e.g. many forest-interior insectivores)**

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

**(38) Larger game birds (e.g. cracids, guans, curassows, pheasants)**

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

**(39) Larger frugivorous birds (e.g. toucans, hornbills)**

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

**(40) Raptors (e.g. eagles, hawks, falcons, owls)**

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## AMPHIBIANS AND REPTILES

**(41) Stream-dwelling amphibians**

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		



## Expert Questionnaire on Environmental Changes at Tropical Research Sites

## (42) Terrestrial amphibians

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## (43) Lizards and larger reptiles

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## (44) Venomous snakes

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## (45) Non-venomous snakes

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## TERRESTRIAL INVERTEBRATES

## (46) Light-loving butterflies

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## (47) Army ants (driver ants)

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## (48) Leaf-cutter ants (Neotropics only)

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## (49) Dung beetles

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

## (50) Disease-vectoring invertebrates (e.g. mosquitoes, sandflies, ticks)

<u>Abundance</u>	<u>Species Richness</u>	<u>Knowledge Level</u>
------------------	-------------------------	------------------------



## Expert Questionnaire on Environmental Changes at Tropical Research Sites

**Please specify** any above mentioned changes

**Possible drivers** of changes

**GENERAL GROUPS**

(59) **Migratory species** (e.g. bird and mammal frugivores or nectarivores, migratory fish)

Abundance	Species Richness	Knowledge Level
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

(60) **Ecological specialists** (e.g. foraging specialists, species with complex mutualisms)

Abundance	Species Richness	Knowledge Level
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

(61) **Species dependent on tree cavities** (parrots, certain possums, bats,...)

Abundance	Species Richness	Knowledge Level
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

(62) **Exotic animal species** (not native to FRA habitat)

Abundance	Species Richness	Knowledge Level
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

(63) **Exotic plant species** (not native to FRA habitat)

Abundance	Species Richness	Knowledge Level
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

(64) **Human diseases** (e.g. malaria, leishmaniasis, dengue fever, Chagas)

Abundance	Species Richness	Knowledge Level
<i>Please specify any above mentioned changes</i>		
<i>Possible drivers of changes</i>		

**Part 2: Other Ecological/Anthropogenic Changes**

Over the past 2-3 decades, have any of the following changes occurred

- (a) *within* the focal research area (FRA) ,
- (b) in the 3km area bordering the FRA, and
- (c) in the general area outside the protected area (PA)

(65) For the area outside the PA, please approximate distance (km) from border of PA \_\_\_\_\_

(66) **Natural forest cover**

Within FRA	Within 3km of FRA	Within area outside PA	Knowledge level	Likely impact on research
<i>Details and possible drivers</i>				

## Expert Questionnaire on Environmental Changes at Tropical Research Sites

**(67) Hunting**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(68) Selective logging**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(69) Fires**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(70) Air pollution**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(71) Water pollution**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(72) Pastoralism/livestock grazing**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(73) Illegal mining**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(74) Automobile traffic**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(75) Harvest of natural products** (e.g. fuelwood, tree bark, leaves, fungi, etc.)

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(76) Exotic tree plantations**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(77) River/stream flows** (e.g. from upstream dams or water harvesting)

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(78) Flooding frequency or intensity**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers _____				

**(79) Stream/river sedimentation**

## Expert Questionnaire on Environmental Changes at Tropical Research Sites

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(80) Soil erosion**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(81) Windstorm disturbance**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(82) Drought**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(83) Rainfall**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(84) Temperature**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(85) Forest dynamics, i.e. tree mortality and recruitment (accelerated/decelerated)**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(86) Seed dispersal**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(87) Seedling predation**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(88) Road construction**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(89) Human Population**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**(90) Other**

Within FRA _____	Within 3km of FRA _____	Within area outside PA _____	Knowledge level _____	Likely impact on research _____
Details and possible drivers				

**Part 3: Additional Questions**

## Expert Questionnaire on Environmental Changes at Tropical Research Sites

What do you think will be the **biggest future threats** to your site, and could you identify possible solutions?

(91) **First biggest threat**

*Possible solution*

(92) **Second biggest threat**

*Possible solution*

(93) **Third biggest threat**

*Possible solution*

(94) Can you recommend other experts on this site? ——

(95) **Expert 1**

Name	Expertise	Email
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(96) **Expert 2**

Name	Expertise	Email
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(97) **Expert 3**

Name	Expertise	Email
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(98) **Expert 4**

Name	Expertise	Email
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(99) **Expert 5**

Name	Expertise	Email
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(100) **Expert 6**

Name	Expertise	Email
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(101) **Expert 7**

Name	Expertise	Email
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(102) **Expert 8**

Name	Expertise	Email
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(103) Do you have knowledge of long-term changes of other tropical research sites, and if so, would you be willing to be interviewed about them for our survey? ——

(104) **Site 1**

Name	Country
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(105) **Site 2**

Name	Country
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(106) **Site 3**

Name	Country
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(107) Would you be interested in remaining further involved with this study and in co-authorship of a resulting publication? ——

(108) Comment

Please provide publications describing environmental changes at this site.

(109) **Publication 1**

Author name	Article title	Journal title	Year
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(110) **Publication 2**

Author name	Article title	Journal title	Year
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Expert Questionnaire on Environmental Changes at ~~10~~ Tropical Research Sites

**(111) Publication 3**

Author name	Article title	Journal title	Year
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(112) Comment

*Thank you very much for your time and we greatly appreciate your participation in this study.*