LETTER

doi:10.1038/nature11318

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[1–3]. 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[4–9]. 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[1–3]. 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[10]. 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[6,11–13], but are largely unable to discern crucial on-the-ground changes in forest biodiversity and ecological functioning[14].

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 ± s.d., 19.1 ± 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
Broadly forest-dependent guilds	
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
Other functional groups	
Ecological specialists	
Species requiring tree cavities	
Migratory species	
Disturbance-favouring guilds	
Lianas and vines	
Pioneer and generalist trees	
Exotic animal species	
Exotic plant species	
Disease-vectoring invertebrates	
Light-loving butterflies	
Human diseases	

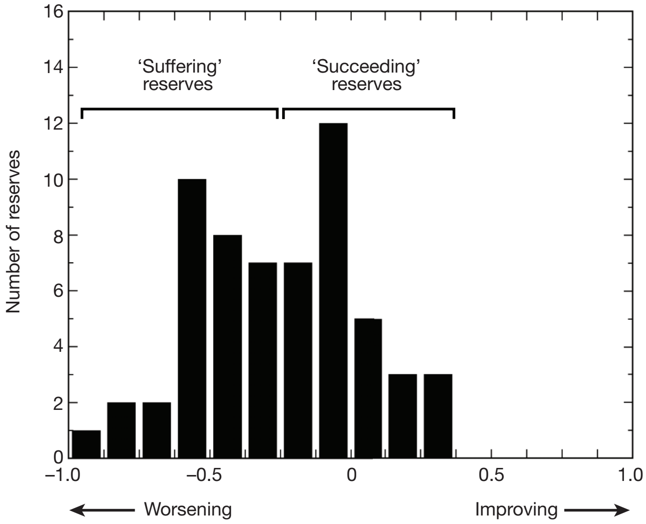

Figure 1 | Distribution of the 'reserve-health index' for 60 protected areas spanning the world's major tropical forest regions. This relative index averages changes in 10 well-studied guilds of animals and plants, including disturbance-avoiding and disturbance-favouring groups, over the past 20 to 30 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[5,6,15] (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

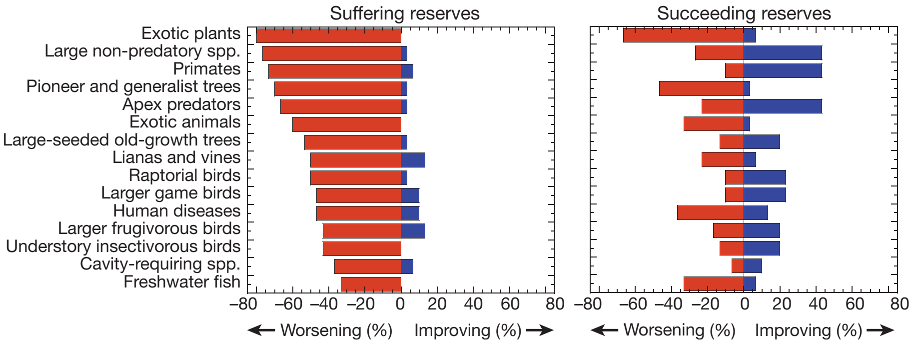

Figure 2 | Percentages of reserves that are worsening versus improving for key disturbance-sensitive guilds, contrasted between 'suffering' and 'succeeding' reserves (which are distinguished by having lower (< -0.25) versus higher (≥ -0.25) values for the reserve-health index, respectively). For disturbance-favouring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

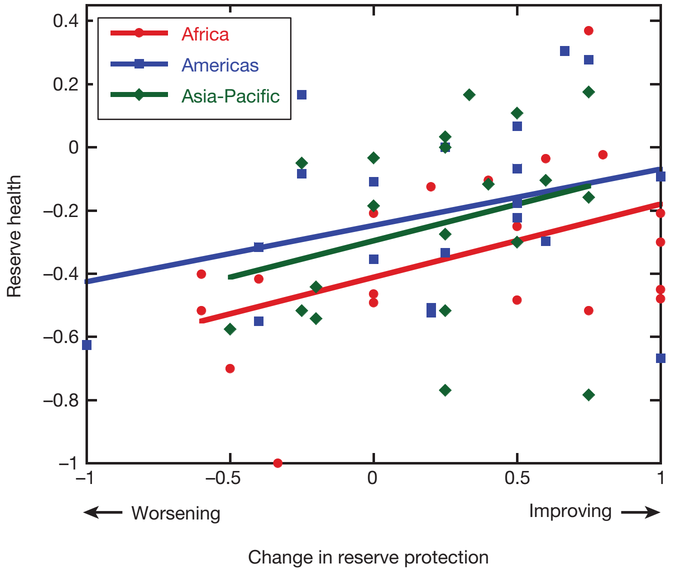

Figure 3 | Effects of improving on-the-ground protection on a relative index of reserve health. This positive relationship held across all three tropical continents (a general linear model showed that the protection term was the most effective predictor of reserve health (Akaike's information criterion 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[15–19]. 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[15–22], 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[5,6,13,15] (Fig. 5). A failure to limit interrelated internal and external threats could predispose reserves to ecological decay, including a taxonomically and functionally

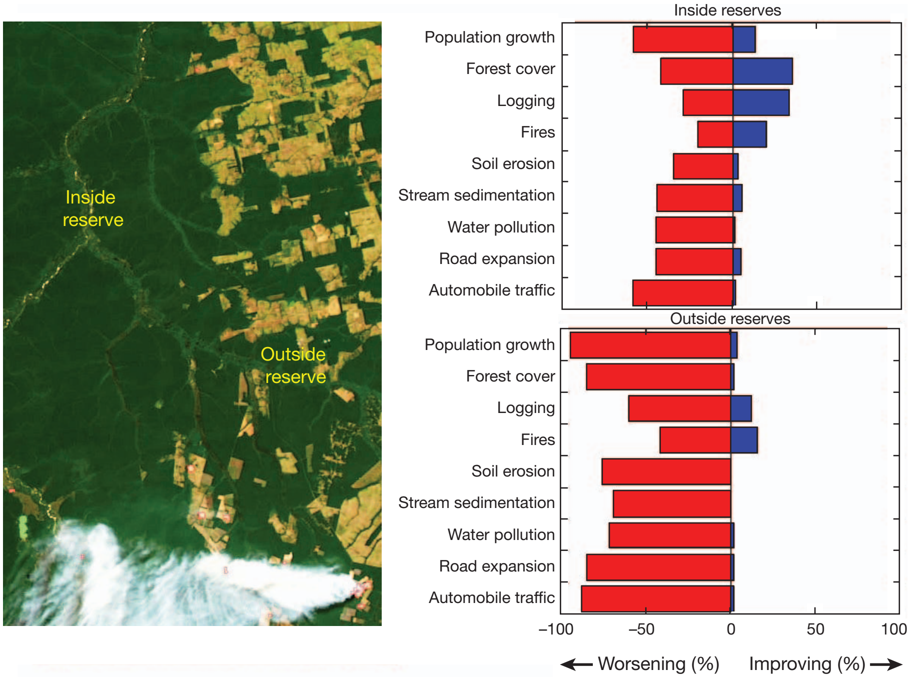

Figure 4 | Comparison of ecological changes inside versus outside protected areas, for selected environmental drivers. The image is an example of the strong distinction in disturbance inside versus outside a reserve. The bars show the percentages of reserves with improving versus worsening conditions.

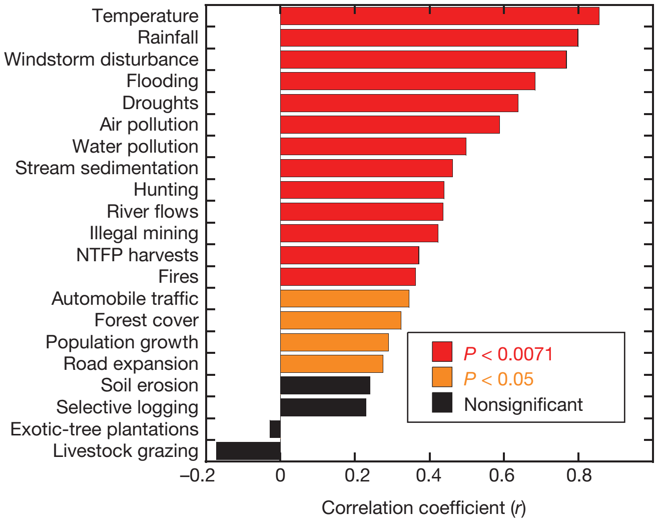

Figure 5 | Pearson correlations comparing the direction and strength of 21 environmental drivers inside versus outside tropical protected areas. NTFP, non-timber forest products.

sweeping array of changes in species communities (Fig. 2) and an erosion of fundamental ecosystem processes[16,18,23].

Protected areas are a cornerstone of efforts to conserve tropical biodiversity[3,4,13,21]. 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[4,15,24–27]. A focus on managing both external and internal threats should also increase the resilience of biodiversity in reserves to potentially serious climatic change[28–30] 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).

Received 24 February; accepted 14 June 2012.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements The study was supported by James Cook University, the Smithsonian Tropical Research Institute, an Australian Laureate Fellowship (to W.F.L.) and NSF grant RCN-0741956. We thank A. Bruner, R. A. Butler, G. R. Clements, R. Condit, C. N. Cook, S. Goosem, J. Geldmann, L. Joppa, S. L. Pimm and O. Venter for comments.

Author Contributions W.F.L. conceived the study and coordinated its design, analysis and manuscript preparation. D.C.U., J.R. and M.K. conducted the interviews; C.J.A.B. assisted with data analysis and some writing; and S.P.S., S.G.L., M.C. and W.L. organized data or collected metadata. The remaining authors provided detailed interviews on protected areas and offered feedback on the manuscript.

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