



National emphasis on high-level protection reduces risk of biodiversity decline in tropical forest reserves



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ABSTRACT

Tropical protected areas have variable success in protecting their biodiversity. Many are experiencing biodiversity declines because of pressures such as logging, fire and hunting in their immediate surroundings, and inadequate protection inside the reserves. Here we assess how the national socio-economic context in which protected areas are embedded correlates with temporal trends in the condition of their biodiversity. Focussing on 60 protected areas arrayed across the world's major tropical regions, we examine the correlation between the biodiversity 'health' of protected areas and indices of human population size, wealth, governance quality, the environmental ranking of their respective nation, and national emphasis on reserve protection. We hypothesize that, after controlling for variability in socio-economic context, a country's emphasis on implementing high-protection reserves reduces the likelihood of biodiversity decline in its protected areas. We find that, after accounting for spatial non-independence and general socio-economic context, the best predictor of biodiversity trends within a tropical protected area is the country's overall emphasis on reserve quality, as measured by the proportion of IUCN Category I–IV reserves in nations' protected-area networks. This result suggests that national-level policies can have an important influence on the fate of biodiversity in tropical protected areas.

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1. Introduction

According to the World Database on Protected Areas (IUCN and UNEP-WCMC, 2013), as of 2013 there were over 210,000 protected areas worldwide, of which approximately 46% are managed explicitly for biodiversity protection (IUCN Categories I–IV; explained below) (Dudley, 2008). The percentage of the Earth's land area under some form of legal protection has risen sharply from <4% in 1985 to nearly 15.4% by 2014 (Juffe-Bignoli et al., 2014).

Taken at face value, this trend is certainly a positive sign, but biodiversity is still in decline throughout most of the world, and it risks being degraded even further over the coming decades (Pimm et al., 2014). While protected areas can safeguard vegetation and minimize land-use pressures after establishment (Bruner et al., 2001; Geldmann et al., 2013; Carranza et al., 2014a), coverage is still inadequate because many endemic and threatened species are found entirely outside the global protected-area network

(Rodrigues et al., 2004; Venter et al., 2014). Further, many protected areas – especially in the tropics – are failing to protect their biodiversity fully (Western et al., 2009; Laurance et al., 2012; Carranza et al., 2014b). A recent systematic review of protected-area effectiveness based on 76 studies concluded that, on average, the existence of a reserve protects at least some forest habitats, but evidence was inconclusive that they maintain populations of species better than do equivalent areas outside reserves (Geldmann et al., 2013). Patterns of deforestation inside and outside of protected areas are also highly variable among regions (Joppa et al., 2008), although Coetzee et al. (2014) determined via a global meta-analysis that protected areas generally have higher biodiversity values relative to comparable areas outside reserves.

There is now a large and growing literature attempting to identify the conditions that promote effective conservation of biodiversity in protected areas. Quantifying such measures and correlates of success (and failure) are essential to justify continued expansion of the network and conservation investment in general (Parrish et al., 2003). The problem is that few protected areas have robust monitoring designs in place to measure biodiversity trends (Parrish et al., 2003; Ferraro and Pattanayak, 2006; Geldmann et al., 2013), such that many studies are obliged to measure proxies for 'success'.

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For example, deforestation pressures outside 36 protected areas were thought to signal future conservation failures within them (Naughton-Treves et al., 2005), an expectation that was corroborated by observations of declining biodiversity within tropical protected areas where outside pressures were relatively higher (Laurance et al., 2012). On a finer scale, the greatest differences in terms of threatening processes (land clearing, logging, hunting, fire, grazing) inside and outside tropical protected areas correlated most strongly with guard density, the deterrent level focused on illegal activity, border demarcation and the presence of direct-compensation programs for local residents (Bruner et al., 2001). Likewise, a comparison of 40 tropical protected areas to 33 community-managed forests suggested lower deforestation in the latter due to their higher relative community engagement (Porter-Bolland et al., 2012). The intensity of law enforcement and NGO support were the best predictors of great ape survival among 109 resource management areas in Africa (Tranquilli et al., 2012), and enforcement was the most effective contributor to reductions in poaching in Serengeti National Park (Hilborn et al., 2006).

A recent study based on validated interviews of 262 expert biologists across the tropics was the first to provide empirical evidence of biodiversity change in a large sample of protected areas (Laurance et al., 2012). They showed that biodiversity was being substantially eroded in about half of the reserves examined, with the remainder largely ‘succeeding’ in sustaining their biodiversity. In fact, a composite reserve ‘health’ index derived from an average trend of the ten best-studied guilds indicated that most (85%) of the protected areas examined had a health index ≤ 0 , indicating a variable but generally worsening overall trend in biodiversity. Further, a simple bivariate linear model suggested that improving on-the-ground protection (management) explained the most variation in reserve health (Laurance et al., 2012).

The suggestion that general management commitment, like the presence of field researchers (Laurance, 2013) and park rangers within a particular reserve improving its biodiversity prospects (Leverington et al., 2010), is tantalizing and merits further investigation. The problem is that such fine-scale budgetary and management details are missing for most parks (Bruner et al., 2004; Coad et al., 2013), and especially for most of the tropical protected areas for which a biodiversity health index exists. At the global scale, at least, there is clear evidence that some socio-economic indicators affect the environmental performance of a country, with increasing relative national ‘wealth’ in particular leading to poorer environmental outcomes (Bradshaw et al., 2010). We therefore asked a similar question of whether the national ‘emphasis’ on protected areas accounts for some of the variation in tropical reserve health. We hypothesize that the more a country ‘invests’ in reserves designed specifically to protect local biodiversity, the lower the likelihood that its protected areas will fail to achieve that protection. We therefore compared the reserve health index of Laurance et al. (2012) to the proportion of reserves within each nation categorized by the IUCN as established primarily for the reasons of biodiversity conservation (Categories I–IV) (Joppa et al., 2008) as an index of national conservation emphasis. We also controlled for other socio-economic differences among countries including country area, human population size, wealth, wealth inequality and corruption, while simultaneously accounting for spatial and national non-independence in the dataset.

2. Methods

2.1. Reserve health

Due to the paucity of long-term biodiversity trend data in tropical protected areas, we used the published data describing the

biodiversity ‘health’ of 60 pan-tropical reserves within 36 countries (Laurance et al., 2012). The health index is an integrated assessment of biodiversity trends across 10 guilds deemed sensitive to environmental changes by local experts (Laurance et al., 2012). Six of these guilds are considered ‘disturbance avoiders’ (apex predators, large non-predatory vertebrates, primates, understory insectivorous birds, large frugivorous birds and large-seed old-growth trees), and the remaining four are generally ‘disturbance-favouring’ guilds (pioneer and generalist trees, lianas and vines, exotic animals and exotic plants) (Laurance et al., 2012). The health index for each reserve is an average of the mean trend values (-1 = declining abundance of disturbance-avoiding guilds or increasing disturbance-favouring guilds, 0 = no change and 1 = increasing disturbance-avoiding/decreasing disturbance-favouring) across the guilds (Laurance et al., 2012).

2.2. Potential correlates

We were primarily interested in investigating the national conditions correlated with protected-area success as measured by this health index. Other socio-economic conditions being equal, we hypothesize that the national emphasis on gazetted high-protection reserves might partially predict the degree to which tropical protected areas are governed and supported. To that end, we compiled the country-level breakdown of protected areas by IUCN protection category from the World Database on Protected Areas (IUCN and UNEP-WCMC, 2013), as an index of such reserve support and governance.

Protected areas of IUCN Category (Dudley, 2008) Ia (Strict Nature Reserve), Ib (Wilderness Area), II (National Park), III (Natural Monument or Feature) and IV (Habitat/Species Management Area) are generally considered those with the highest protection value and commitment (specifically managed for biodiversity protection), compared to categories V (Protected Landscape/Seascape) and VI (Protected Area with Sustainable Use of Natural Resources), which are subject to multiple-use management (Joppa et al., 2008). As such, the proportion of protected areas in the ‘high-protection’ categories (I–IV) might hypothetically predict a non-random component of the variation in protected area health (McDonald and Boucher, 2011). In our case, we calculated this proportion as Ia, Ib, II, IV/total number of protected areas (i.e., excluding Category III from the numerator, because such protected areas are generally small and “... include elements that have been influenced or introduced by humans”). However, the exclusion or inclusion of Category III protected areas made little difference to our conclusions (see Results).

As another metric of a country’s emphasis on biodiversity conservation, we included two different composite rankings of environmental ‘performance’: an absolute environmental ranking (not accounting for resource availability), and a proportional ranking (i.e., relative to existing natural resource availability) (Bradshaw et al., 2010). The composite rankings are based on natural forest loss, habitat conversion, marine-species captures, fertilizer use, water pollution, carbon emissions and number of threatened species (Bradshaw et al., 2010).

Of course, the caveat of ‘all other things being equal’ means that we are obliged to control for other, country-specific geographical and socio-economic conditions. We therefore compiled the land area of each of the 36 countries as a control variable because total available area will dictate to some extent how many protected areas a country can harbour. We also included the total area under some form of protection per country as an additional control variable. We used this approach instead of including per-capita (e.g., per capita GNI) or proportional measures (e.g., proportion of area protected) because of the typical inflation of variances near proportional extremes and the conflation of influence when two

variables are combined. However, partialling the variance using control variables as we have done here is functionally equivalent to testing per capita or proportional variables directly (we also tested proportional variables separately – see Results).

We also included human population size (controlling for country area as described above) because population pressures on natural resources can degrade ecological integrity (Mayaka, 2002; Andrade and Rhodes, 2012; Bradshaw and Brook, 2014), and at a global scale, there is a clear historical relationship between human population size and threats to biodiversity and/or environmental degradation (Kirkland and Ostfeld, 1999; Thompson and Jones, 1999; Bradshaw et al., 2010). Further, high human populations surrounding protected areas directly compromise their biodiversity (Wittemyer et al., 2008).

Although wealth is either linearly or not related to country-level environmental performance (Bradshaw et al., 2010), others have hypothesized that increasing wealth, especially in developing nations, increases adult literacy rates, overall education levels and therefore, active community engagement in protected area management and a possible increase in compliance of protected-area policies (Reed, 2008; Sultana and Abeyasekera, 2008; Andrade and Rhodes, 2012; Waldron et al., 2014). Increasing wealth might also act as a disincentive to exploit natural resources such as game, firewood and area to farm due to the reduced need to do so (Brashares et al., 2004). We therefore included the 2005 purchasing power parity-adjusted gross national income (GNI) for each country (controlling for a country's population size as described above) as an indicative wealth indicator over the period of investigation (last 20–30 years). Ideally, we would have used a more environmentally inclusive index of national wealth, such as the genuine progress indicator (GPI); however, GPI has only been calculated for a few tropical countries (Kubiszewski et al., 2013) and so we could not apply it here. Another dimension of wealth not encapsulated in standard market activity is the inequality of wealth distribution amongst a country's citizenry. This is because wealth inequality has a negative effect on social outcomes and institutional integrity (Ross et al., 2005; Holland et al., 2009), such as the social engagement and institutional oversight and enforcement associated with protected area management. For example, the Gini coefficient (Milanovic, 2011) of wealth inequality (ranging from 0 = perfect equality to 100 = perfect inequality) was correlated with species threat among 50 countries (Holland et al., 2009), although it was only weakly correlated with deforestation rates for countries within Biodiversity Hotspots (Jha and Bawa, 2006). We therefore calculated an average Gini from 1990 to 2011 with data from the World Bank Indicators database (data.worldbank.org/indicator/SI.POV.GINI).

Finally, political corruption ('unlawful use of public office for private gain') (Transparency International, 2002; Smith et al., 2003) is expected to increase biodiversity loss (Smith et al., 2003). While there is evidence that it increases deforestation, pollution, and land degradation (Jepson et al., 2001; Ewers, 2006; Li and Reuveny, 2006; Morse, 2006), others have found no relationship between corruption and change in natural forest cover or environmental performance (Smith et al., 2003; Bradshaw et al., 2010). We therefore included the governance quality ranking from Bradshaw et al. (2010) for each country in our sample. The ranking is derived from data available from the Worldwide Governance Indicators project (Kaufmann et al., 2007), and is an average of six dimensions of governance from 2002 to 2006 (Bradshaw et al., 2010).

2.3. Analysis

Given the small sample size (60 parks in 36 countries), we avoided constructing overly complex models by analysing

preliminary general linear mixed-effects models (GLMM) (Gaussian error distribution and identity links based on the log-transformed predictors; log-link Gaussian models failed to converge) grouped by 'themes' of potential correlates. We applied the lmer function from the lme4 package in R (Bates et al., 2013), with the random effect 'continent' (Americas, Africa or Asia) to account for broad-scale spatial non-independence. Although including all data in this way ignores other non-independence issues (e.g., multiple parks within countries; see below), it identifies which correlates are likely to provide some explanatory power before constructing the final model set.

To construct the final model set, we employed three model-set phases testing different 'themes' of variables. The first phase was a GLMM set including the country-level protected-area parameters (number of protected areas, total area protected, number of high-protection areas) as well as the area of each country. This did not provide strong support for the area of each country protected, and this variable was also strongly correlated (Spearman's $|\rho| \geq 0.5$) with the four other parameters (Table S1). The second-phase model set included area, and the wealth and governance quality parameters, but as expected, the Gini coefficient and governance quality index were not strongly supported. The third-phase model set included population size and the two composite environmental rankings. Here, neither of the two environmental ranking scores had strong support.

The final GLMM set therefore included country area, population size, gross national income, number of protected areas and number of high-protection areas (IUCN Categories Ia, b + II + IV) in various combinations (11 models including the intercept-only model; Table S2). The model set was further complicated by the directionality of the 'health' response variable: most protected areas (82%) had a declining (negative) health index, two (3%) had a health index = 0, and the remaining nine (15%) had an increasing (positive) health index. We therefore included a binary 'direction' factor (increasing or not increasing) as an interaction term with the included variables. This demonstrated strong support for a functionally different relationship between the predictor variables and the health response depending on direction (Table S2), and an examination of the relationship between health and protected area statistics revealed that protected areas with positive health indices were outliers (see Results). For this reason, we only subsequently modelled the protected areas where health was declining (negative) so that we could calculate model-averaged, standardized coefficients easily for each contributing variable.

A necessary condition of all linear models is that all samples are independent, which is clearly not the case for multiple protected areas within the same country. We accounted for this non-independence in two ways: (1) resampling a single protected area per country (for countries with >1 protected area) and applying the linear models to that sample, and (2) accounting for any further non-independence by coding 'continent' (South America, Africa or Asia) as a random effect in a generalised linear mixed-effects model (GLMM) format (Laurance et al., 2014a). We applied the lmer function from the lme4 package in R (Bates et al., 2013) to each resampled dataset for 1000 iterations. We also calculated the marginal R^2 of each resampled GLMM (R_m) as a measure of goodness of fit (Nakagawa and Schielzeth, 2013). We present the 2.5 and 97.5 percentiles of the Akaike's information criterion (AIC) weights (w_{AIC}) and R_m over all 1000 top-ranked models (Herrando-Pérez et al., 2014).

We calculated standardized coefficients $\beta_x(s_x/s_y)$, where s_x and s_y are the standard deviations of predictor x and the response y for each term x in each model of the set, and then averaged these across all models based on w_{AIC} (re-calculating $\sum w_{AIC} = 1$ over the models in which each term appeared) (Bradshaw et al., 2014). We also calculated model-averaged t statistics (β_x/SE_x) as

an indication of each predictors influence on the response (see Results and [Supplementary Information](#)). The value of these model-averaged, standardized effect sizes provided a relative rank of the importance of each predictor for each iteration, while simultaneously controlling for non-independence issues. We then calculated the median and 95 percentiles of the model-averaged, standardized coefficients over all iterations as an index of the relative contribution of each variable considered.

3. Results

Many countries (22/60 = 37%) had only one protected area represented in the sample, although two countries had up to four protected areas (Brazil and Malaysia) ([Fig. 1A](#)). To visualise the relationships, the percentage of 'high-protection' reserves (IUCN categories Ia, b + II + IV) varied from >80% (Thailand & India) to zero (Papua New Guinea & DRC) ([Fig. 1B](#)), and the percentage of the land area protected ranged from >50% (Venezuela) to <4% (Papua New Guinea & Madagascar) ([Fig. 1D](#)) among the 36 countries represented in the sample. Most protected areas (85%) had a health index ≤ 0 (declining [82%] or stable [3%] biodiversity) ([Fig. 1C](#)). Unfortunately our data cannot account for the starting conditions of each reserve. While many would have been near-pristine at the time of establishment, many others have started from highly disturbed baselines resulting from overgrazing, mining, farming and fire (e.g., Guanacaste Conservation Area in Costa Rica; Brownsberg Nature Park in Suriname). Other national parks have been established from forest reserves with previously

poorly enforced access (e.g., Bwindi Impenetrable National Park in Uganda). This potentially explains why 15% of the sample reserves had increasing (recovering) biodiversity trends.

Examining the simple (raw) bivariate relationships between protected area health index and the percentage of high-protection reserves ([Fig. 2A](#)) and the density of high-protection reserves (km^{-2} country area) ([Fig. 2B](#)) suggested a positive relationship, such that higher emphasis on high-protection reserves was correlated with better health. The relationship was compromised by reserves with positive (increasing) health indices ([Fig. 2](#)), and there was a strong effect of 'direction' on the model fits ([Table S3](#)), so we included only those protected areas with negative (declining) health indices in the main analysis.

The main resampled-GLMM approach revealed that the population-only model was the most frequently top-ranked, although substantially more variance was explained by including the number of high-protection reserves ([Table 1](#)). However, the model-averaged, standardized coefficients demonstrated that the number of high-protection reserves was one of the two most important predictors of increasing health of reserves ([Fig. 3](#)). The gross national income of the country (partialled by the inclusion of population so that it was comparable among countries) was the only other supported predictor; as it increased, reserve health declined ([Fig. 3](#)). The total number of protected areas by itself did not influence average reserve health ([Fig. 3](#)). We also verified the gross national income and corruption contributions by including longer-term (GNI: 1990–2013; World Governance Indicators

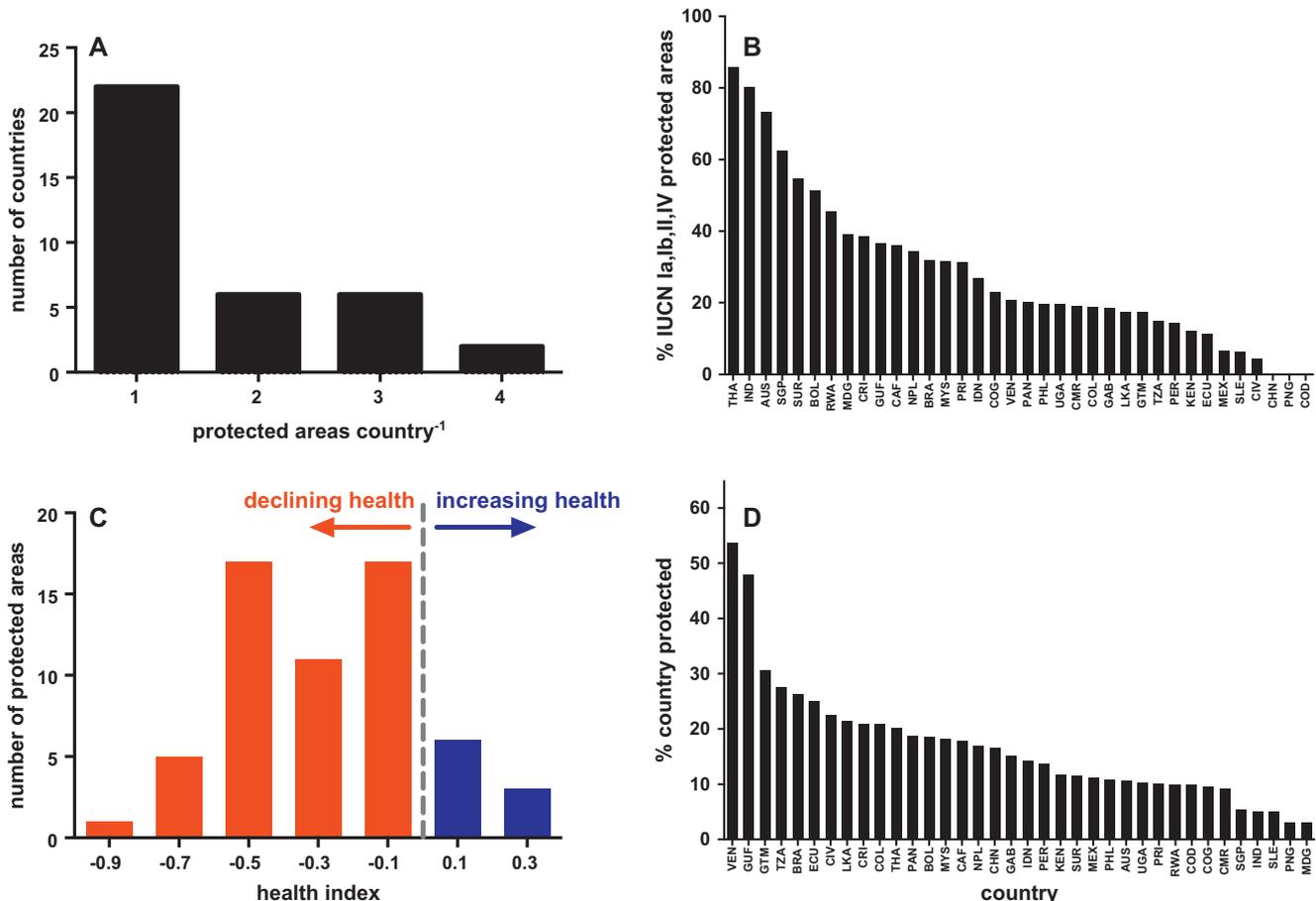


Fig. 1. Characteristics of protected areas in the sample of 60 reserves. (A) Number of protected areas per country (36 countries in total); (B) percentage of high-protection (IUCN categories Ia, b + II + IV) reserves by country; (C) distribution of the protected area 'health' index (Laurance et al., 2012); (D) percentage of the country under some form of protection by country. Three-character ISO country codes are described at <http://countrycode.org>.

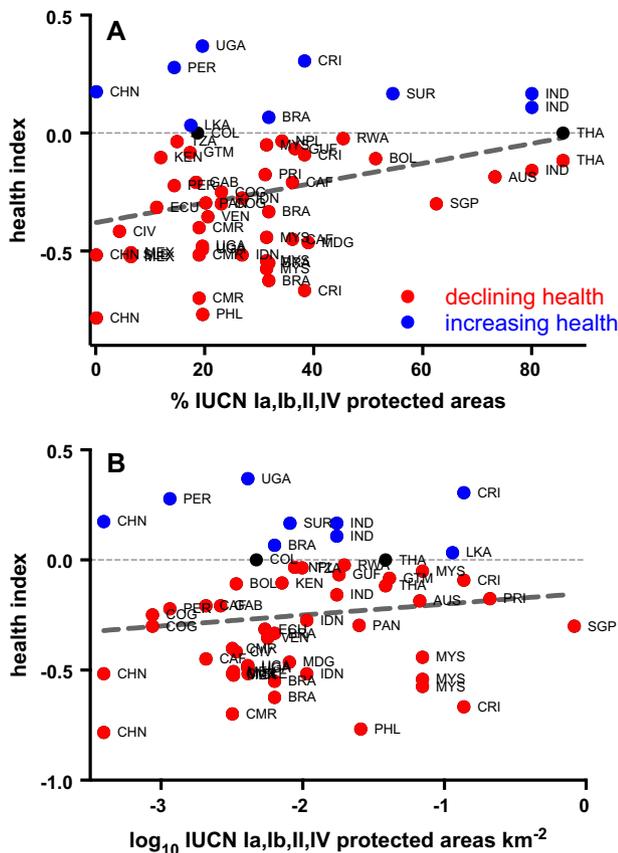


Fig. 2. Relationship between a protected area's health index and (A) the percentage of high-protection (IUCN categories Ia, b + II + IV) reserves by country in which the reserve is found ($R^2 = 0.11$) and (B) the \log_{10} density of high-protection reserves per unit country area in which the reserve is found ($R^2 = 0.01$). Indicative trend lines are fitted through the entire dataset in each case. Three-character ISO country codes are described at <http://countrycode.org>.

Table 1

General linear mixed-effects model rankings over 1000 single-country resamples of the dataset (declining-health protected areas only). Shown are the proportion of times a model was top-ranked, and the range of Akaike's information criterion weight (w_{AIC}) and the fixed-effects component R^2 (R_m). Predictors include human population size (POP), country area in km^2 (AREA), purchasing power parity-adjusted gross national income (GNI), number of protected areas (PA) and number of high-protection reserves (IUCN categories Ia, b + II + IV). The full eleven-model set on which the simulation was based is listed in Table S2.

Model	Proportion top-ranked	w_{AIC}	R_m (%)
~POP	0.582	0.205–0.424	5.9–19.3
~AREA + POP + (Ia, b + II + IV)	0.163	0.202–0.353	16.2–29.5
~AREA + POP + GNI + (Ia, b + II + IV)	0.134	0.201–0.441	24.9–43.4
~1 (null, intercept-only)	0.078	0.201–0.353	–
~AREA + POP + PA + (Ia, b + II + IV)	0.043	0.207–0.330	21.7–29.8

2006–2013) average indices; neither of these longer-term averages provided much explanatory power to reserve health, but the importance of high-conservation reserves was maintained (Fig. S1).

Although including all protected areas revealed the same trend in the model-averaged, standardized coefficients, the inclusion of the positive-health reserves weakened the relationship as expected (confidence bounds overlapping zero; Table S4; Fig. S2). This confirms the problem of including the protected areas where health was increasing (positive index). The inclusion of Category III protected areas in the 'high-protection' reserves made no qualitative

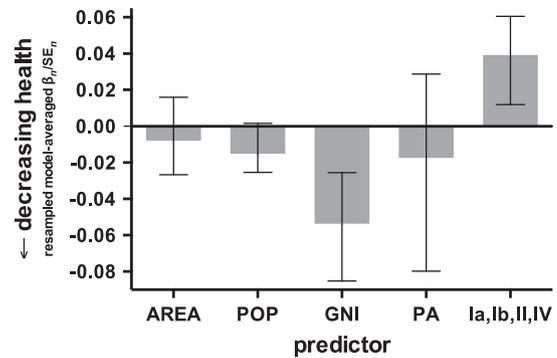


Fig. 3. Resampled (1000 times), model-averaged, standardized coefficients for country area (AREA), human population size (POP), purchasing power parity-adjusted gross national income (GNI), number of protected areas (PA) and number of high-protection reserves (IUCN categories Ia, b + II + IV) for predicting protected area health.

difference to the model ranking (Table S5) or model-averaged, standardized coefficient rankings (Fig. S3). Treating predictors as proportional gave qualitatively similar results (Tables S6–S11; Fig. S4).

4. Discussion

Our results demonstrate that a national emphasis on biodiversity conservation, as implied by the proportion of tropical forest reserves designed specifically for biodiversity protection (IUCN Categories I–IV), was the most important correlate of reserve health among the variables we examined. As a crude metric that can be applied to any country, this relative index of a country's emphasis on protected-area quality appears to correlate with real biodiversity outcomes. Considering that a reserve's health index is not related to reserve size in our sample, nor is the average size of a country's individual protected areas correlated with the proportion of the national territory protected (Fig. S5), we are confident our results are not merely a reflection of ecological differences in the sample of protected areas. This is an important advance in the field given the equivocal, meta-analytical findings of protected-area effectiveness for conserving species' populations (Geldmann et al., 2013; Coetzee et al., 2014). Because area of the globe under some form of protection still falls short of meeting the Convention of Biological Diversity's 2020 targets (Watson et al., 2014), and protection coverage is sporadic and spatially and taxonomically inequitable (Pimm et al., 2014; Venter et al., 2014), demonstrating that reserves can work provided the political will exists is a fundamental step in the right direction.

National context is only one component of success – how each individual protected area is managed is of course even more important. A meta-analysis of 55 published case studies from developing countries examined whether the degree of compliance with protected-area regulations by local communities could be predicted. Using protected area age, land area, whether or not it had a buffer zone, its IUCN protection category, national per-capita gross domestic product, local human population density and amount of local community participation in management, Andrade and Rhodes (2012) concluded that local community participation was the only variable correlated with the compliance of protected-area polices. However, they applied stepwise approaches to build cumulative logistic models, thus possibly overlooking (Whittingham et al., 2006; Mundry and Nunn, 2009) important explanatory variables. Neither was their response variable a direct measure of biodiversity condition or trends. While we do not dispute the argument that community participation in

protected area management can increase biodiversity outcomes (Struhsaker et al., 2005; Ferraro and Pattanayak, 2006; Reed, 2008; Andrade and Rhodes, 2012), dismissing the gross socio-economic context in which it occurs is probably an oversight.

We do acknowledge, however, that equating the proportion of IUCN I–IV-category protected areas with national conservation emphasis might at least be partially confounded. The reasons for different protected-area categorizations are varied, although some biases exist. For example, some researchers have demonstrated that countries with relatively older protected-area systems tend to have more high-protection (I–IV) reserves because they were often established prior to the inclusion of local people's needs (Bertzky et al., 2012). However, others have found little evidence that the amount of land protected in a country is associated with the type of landscapes within it (urbanization, population density, agriculture, number of threatened species) (McDonald and Boucher, 2011). A higher proportion of I–IV reserves might also arise for many other political or socio-economic reasons not examined here for lack of data. For example, McDonald and Boucher (2011) did find evidence that (i) a country's land protection movement is a historical and political process, (ii) the form of government and level of primary education are related to the amount of land protection and the proportion of high-conservation protected areas; and (iii) larger economies lead to a higher amount of protected land. We are confident, however, that the random sample of mainly developing tropical nations reduces potentially confounding influence. Indeed, an examination of relative protected area-network age by country indicates that there is no particular age bias in terms of the proportion of high-conservation reserves in our sample (Fig. S6). Further, our sample was based on perhaps the better-known tropical reserves, which one might predict would have better protective measures in place compared to lesser-known reserves. The addition of such reserves could in fact result in even stronger negative trends.

Our finding that national wealth as crudely measured by gross national income (controlled for population size) and population size (controlled for area) were both negatively correlated with reserve health corroborates previous findings at both global (Kirkland Jr. and Ostfeld, 1999; Thompson and Jones, 1999; Bradshaw et al., 2010) and individual reserve scales (Mayaka, 2002; Sultana and Abeyasekera, 2008). Indeed, that absolute wealth was the principal correlate of increasing environmental degradation among nations (Bradshaw et al., 2010) suggests that any environmental gains arising from increasing per capita wealth – known as the environmental Kuznets curve (Stern et al., 1996) – are offset by the environmental damage resulting from growing economies (Bradshaw et al., 2010). Even though larger economies tend to have a higher proportion of their area protected (McDonald and Boucher, 2011), increasing wealth has the opposite effect on environmental performance. The variables without discernible influence on reserve health were also telling; neither governance quality nor a country's environmental performance ranking correlated with biodiversity trends within reserves. While it is not surprising that governance quality had little effect given its equivocal correlation with biodiversity trends worldwide (Jepson et al., 2001; Smith et al., 2003; Ewers, 2006; Li and Reuveny, 2006; Morse, 2006; Smith et al., 2007; Bradshaw et al., 2010), the lack of correlation between a country's environmental ranking and the health status of reserves within them supports the finding that biodiversity trends within and outside protected areas differ markedly among regions (Joppa et al., 2008).

Of course, establishing and maintaining even well-managed protected areas will not avoid massive continued biodiversity loss given the poor performance of many protected areas, the severe lack of representative coverage, and degradation continuing to occur outside reserves (Pressey, 1994; Margules and Pressey, 2000; Hoffmann et al., 2010; Andrade and Rhodes, 2012;

Laurance et al., 2012; Porter-Bolland et al., 2012; Pimm et al., 2014; Watson et al., 2014). In addition to increasing area coverage, we should focus on designing reserves better to provide economic and social benefits to local people (Naughton-Treves et al., 2005), and to be well-connected and representative within the landscapes they are embedded (DeFries et al., 2005; Naughton-Treves et al., 2005; DeFries et al., 2007; Nagendra, 2008; Porter-Bolland et al., 2012). Outside reserves, protecting existing habitat fragments, restoring deforested and degraded ecosystems, and engaging smarter agricultural practices that integrate biodiversity into their designs in other areas will be key elements for reducing extinction rates (Laurance et al., 2014b; Mendenhall et al., 2014). Another priority is improving technology and energy provision that limit agricultural expansion at the expense of primary forests and other intact ecosystems (Hoffmann et al., 2010; Brook and Bradshaw, 2015). Nonetheless, our results suggest that an increasing national investment in establishing biodiversity-focussed protected areas will likely reduce the risk of further biodiversity erosion at national scales.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.05.019>.

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