Global Change Biology

Global Change Biology (2015), doi: 10.1111/gcb.13089

Why do we lose protected areas? Factors influencing protected area downgrading, downsizing and degazettement in the tropics and subtropics

WILLIAM S. SYMES[1], MADHU RAO[1,2], MICHAEL B. MASCIA[3] and L. ROMAN CARRASCO[1]

[1]*Department of Biological Sciences, National University of Singapore, Singapore, Singapore,* [2]*Wildlife Conservation Society, Singapore, Singapore,* [3]*Moore Center for Science & Oceans, Conservation International, Arlington, VA, USA*

Abstract

Protected areas (PAs) are an essential tool for the conservation of biodiversity globally. Previous studies have focussed on the effectiveness of PAs and the design of optimal PA networks. However, not all PAs remain intact permanently; many PAs undergo downgrading, downsizing and/or degazettement (PADDD), a fact largely ignored until recently. The drivers of enacted PADDD events and the factors influencing its spatial occurrence are poorly understood, potentially undermining the efficacy of PAs and PA networks. Here we examine the spatial relationship between PADDD and economic, demographic and structural variables, using a 110-year data set of 342 enacted PADDD events across 44 countries in the tropics and subtropics. We find that the probability of an enacted PADDD event increases with the size of the PA and through a synergistic interaction between PA size and local population densities. Our results are robust to the under-reporting of enacted PADDD events that occur among smaller PAs and in regions with lower population density. We find an economic motive for PADDD events, given that the opportunity costs associated with larger PAs are higher, on average, than smaller PAs. Our findings suggest a need for conservation practitioners to better consider PA characteristics, as well as the social, economic and political context in which PAs are situated, to aid the creation of more efficient and sustainable PA networks. In particular, the dynamics of enacted PADDD events highlight the need to explicitly consider PA robustness as a core component of systematic conservation planning for PA networks.

Keywords: biodiversity conservation, degazettement, downgrade, downsize, land use change, national park, nature reserve, protected area downgrading, downsizing and degazettement, systematic conservation planning

Received 1 July 2015 and accepted 14 August 2015

Introduction

The tropics are facing a biodiversity crisis (Sodhi *et al*., 2008; Wilcove *et al*., 2013). With extinctions at 100–10 000 times the evolutionary background rate, it is believed the world has entered a 6th mass extinction event (Barnosky *et al*., 2011; He & Hubbell, 2011; Ceballos *et al*., 2015). The conservation of tropical regions, with their high levels of biodiversity and endemism (Myers *et al*., 2000; Gibson *et al*., 2011), is of particular importance. Coordinated global action is required to address the increasing pressure on tropical species and ecosystems from population growth (DeFries *et al*., 2010), development (Hosonuma *et al*., 2012; Savilaakso *et al*., 2014) and international trade (Meyfroidt *et al*., 2013). To this end, biodiversity conservation has been officially incorporated into the United Nations Millennium Development Goals in explicit recognition of its global importance (United Nations, 2000).

Correspondence: William S. Symes, tel. +1 656 516 2692, fax +1 656 779 2486, e-mail: wsymes@u.nus.edu

Protected areas (PAs) remain the cornerstone intervention for protecting biodiversity (Gaston *et al*., 2008). The global PA estate now includes more than 150 000 sites, covering approximately 15.4% of the world's terrestrial and inland water area (Juffe-Bignoli *et al*., 2014). This expansion of the global PA network has, thus far, been largely opportunistic, resulting in patchy, biased and inefficient coverage (Soutullo *et al*., 2008; Joppa & Pfaff, 2009; Butchart *et al*., 2012). Moreover, the scientific literature shows equivocal evidence for their efficacy with regard to protecting biodiversity (Rao *et al*., 2010; Laurance *et al*., 2012; O'Kelly *et al*., 2012), reducing habitat loss (Linkie *et al*., 2008; Geldmann *et al*., 2013), reducing deforestation (Gaveau *et al*., 2007; Andam *et al*., 2008) and maintaining connectivity in the face of climate change (Hole *et al*., 2009; Minor & Lookingbill, 2010; Mazaris *et al*., 2013).

Systematic conservation planning aims to improve the efficacy and efficiency of PAs and PA networks using mathematical optimisation algorithms to identify sites for new PAs, according to specific goals or criteria. These PA site selection processes can be tailored to optimise various biotic and economic factors simultaneously. Currently, most conservation planning research focuses on selecting PA networks optimised for biodiversity coverage (Possingham *et al.*, 2000; Venter *et al.*, 2014), cost-effectiveness (McCarthy *et al.*, 2012; Edwards *et al.*, 2014; Kim *et al.*, 2014) and the provision of ecosystem services (e.g. carbon sequestration; Runting *et al.*, 2015).

The literature on both PA network design and efficacy generally assumes PA permanence (i.e. the PA will remain in place indefinitely), and thus, fails to consider the robustness of individual PAs or PA networks as a whole. Recent evidence suggests that PAs are not permanent features, but are instead dynamic and shifting governance constructs that are influenced by diverse social and economic factors at a variety of scales (Mascia & Pailler, 2011; Cumming *et al.*, 2015). The failure of current planning to consider PA dynamism could undermine the conclusions of the increasingly complex optimisation algorithms used in systematic conservation planning. Conversely, this newly recognised PA dynamism may offer an opportunity to address weakness in existing PA networks, by replacing underperforming sites (Fuller *et al.*, 2010).

PA downgrading, downsizing and degazettement (PADDD) exemplifies the dynamic (rather than permanent) nature of PAs (Mascia & Pailler, 2011). Downgrading is the legal process by which PAs have their level of protection reduced through the authorisation of increased human activity within the PA; downsizing is the legal process by which PAs are made smaller through the excision of land or water; and degazettement is the process by which all legal protections are eliminated (Mascia & Pailler, 2011). The proximate causes of PADDD include industrial scale resource extraction and development (e.g. mining, industrial agricultural and infrastructure development) and local land claims and local land pressures (Mascia & Pailler, 2011; Mascia *et al.*, 2014). Shifting attitudes towards PAs may also foster PADDD (De Marques & Peres, 2014). Enacted PADDD events may foster tropical deforestation and carbon emissions, hindering progress towards global goals for biodiversity conservation and reduction in greenhouse gas emissions (Mascia *et al.*, 2014; Forrest *et al.*, 2015).

Although enacted PADDD events are numerous and widespread, the factors that influence the spatial occurrence of PADDD events remain unknown – as are the implications for systematic conservation planning of PA networks. To address this knowledge gap, we quantify the influence of global economic, demographic and geographic factors on the spatial occurrence of enacted PADDD events in the tropics and subtropics. In particular, we examine the influence of local population density, spatially explicit GDP, potential agricultural rent, altitude and PA size on the probability of an enacted PADDD event. Our results provide insights for incorporating PA robustness into systematic conservation planning processes and associated optimisation algorithms for the design of PAs and PA networks.

Materials and methods

Data collection

We collected data from a variety of sources and wherever possible we used figures from 2005. Our data sources and justification of explanatory variables are as follows:

PADDD data set. We used PADDDtracker.org Data Release Version 1.0 (January 2014), which contains verified and validated data regarding enacted PADDD events between 1900 and 2010 from Africa, Asia, Latin America and the Caribbean (World Wildlife Fund, 2014; available via www.PADDDtracker.org). The data were originally collected through extensive review of the available scientific and grey literature (Mascia *et al.*, 2014; World Wildlife Fund, 2014).

Tropical and subtropical PAs. We downloaded polygons and points (for those with an unknown boundary) for all the world's PAs from the World Database on Protected Areas (WDPA) (IUCN & UNEP-WCMC, 2014). We then processed these data to remove errors which could bias results (full methods are available in the Supplementary Methods S1).

Size of PA. As the size of a PA is directly related to the opportunity costs associated with its existence, we hypothesised size would have an influence on PADDD. We calculated the size of each PA in ArcGIS 10.2.1 from the polygons provided by the WDPA. For PAs where the boundary was not known, the points were buffered according to the size provided in the WDPA, and then, the size of the buffer zones was recalculated using ArcGIS to ensure measurement consistency. For PAs that had undergone PADDD, we calculated the size from the polygon corresponding to the WDPA ID listed in the PADDD database. We used only the size after the PADDD events, so our analysis represents a conservative estimate of the effect of PA size.

Spatially explicit gross domestic product. We used the Geographically based Economic data (G-Econ project). These data are a gridded data set at 1 degree resolution, containing information on gross cell product (Nordhaus *et al.*, 2006). The influence of economic development in previous studies (Mascia & Pailler, 2011; Mascia *et al.*, 2014) and the complex nature of the relationships between PAs and poverty (Naughton-Treves *et al.*, 2006; Barrett *et al.*, 2011) suggest the spatial distribution of gross domestic product (GDP) might be a good predictor of PADDD.

Population data. These again were taken from the G-Econ project (Nordhaus *et al.*, 2006). Given the rapidly increasing population in the tropics and the implications for achieving conservation objectives (Wilcove *et al.*, 2013), deforestation (DeFries *et al.*, 2010) and food security (Phalan *et al.*, 2011), we hypothesised it to have an influence of PADDD.

Agricultural rent. Agricultural expansion, both subsistence and commercial, drives habitat loss in the tropics (Koh & Wilcove, 2008; Koh & Ghazoul, 2010; Phalan *et al.*, 2011). We hypothesised agricultural opportunity cost associated with PAs may influence the occurrence of enacted PADDD events. We developed a map to represent the total potential value of agriculture in the PA from the top 10 crops in tropical regions by value and the top 10 by area, a total of 18 crops (wheat, sugarcane, soya beans, sorghum, rice, pulses, oil palm, millet, maize, groundnuts, cowpeas, cotton, coffee, coconut, cocoa, cassava and banana). We calculated the potential rent by multiplying the potential yield for the rain fed crop at intermediate fertiliser input [taken from the Global Agro-ecological Zones database (FAO & IIASA, 2014)] by the national producer prices (FAO, 2014). Where the producer price for a country was not available, we used a regional average. We used the crop with the highest potential rent as the potential agricultural value.

Altitude. Given the disproportionately high coverage of mountains in global PA networks (Rodríguez-Rodríguez *et al.*, 2011), altitude seems to influence PA designation. We hypothesised therefore that the opposite might be true and altitude could be influential on PADDD. Altitude data at 1 km resolution were taken from the NASA Shuttle Radar Topographical Mission Digital Elevation Map version 4 (Jarvis *et al.* 2008).

Accessibility. We hypothesised that accessibility might be influential on PADDD occurrence because of the well-established connection between infrastructure development and environmental degradation (Dobson *et al.*, 2010; Laurance *et al.*, 2014). We used the estimated travel time (in minutes) from the centre of the PA to the nearest population centre of 50 000 people or more (Nelson, 2008).

Data analysis

We limited our analyses to only those countries in which there was an enacted PADDD event, in tropical and subtropical regions between 40° North and 40° South, removing 43 events which fell outside this region (Fig. 1). We also removed all enacted PADDD events for which the location was unknown (157 events). In total, 200 of the original 543 enacted PADDD events were removed, leaving 343 PADDD events in 207 PAs, across 44 countries in the final data set for analysis (see Table 1 for a regional breakdown and Table S1). As the PADDD data set only included PAs managed at a national level, we removed all private reserves and international PA designations from the PA data set. We examined and verified spatially the PAs and marine reserves were removed, leaving a total of 10 253 PAs which have not undergone PADDD in the analysis data set. In our analysis data set, 44 PAs had undergone downgrading, 139 downsizing and 24 degazettements; 3 had undergone both downgrading and downsizing (compared with 63 downgradings, 330 downsizings and 150 degazettements in the original unprocessed data set); and 59 PAs (29%) had undergone multiple events. We extracted the data from our layers in ArcGIS (10.2.1) by calculating the centroids of the polygons from the WDPA and using the function to extract multivalues to points. For the map of potential agricultural rent, we implemented bilinear interpolation to get a better measure of the rent across the whole area of each PA.

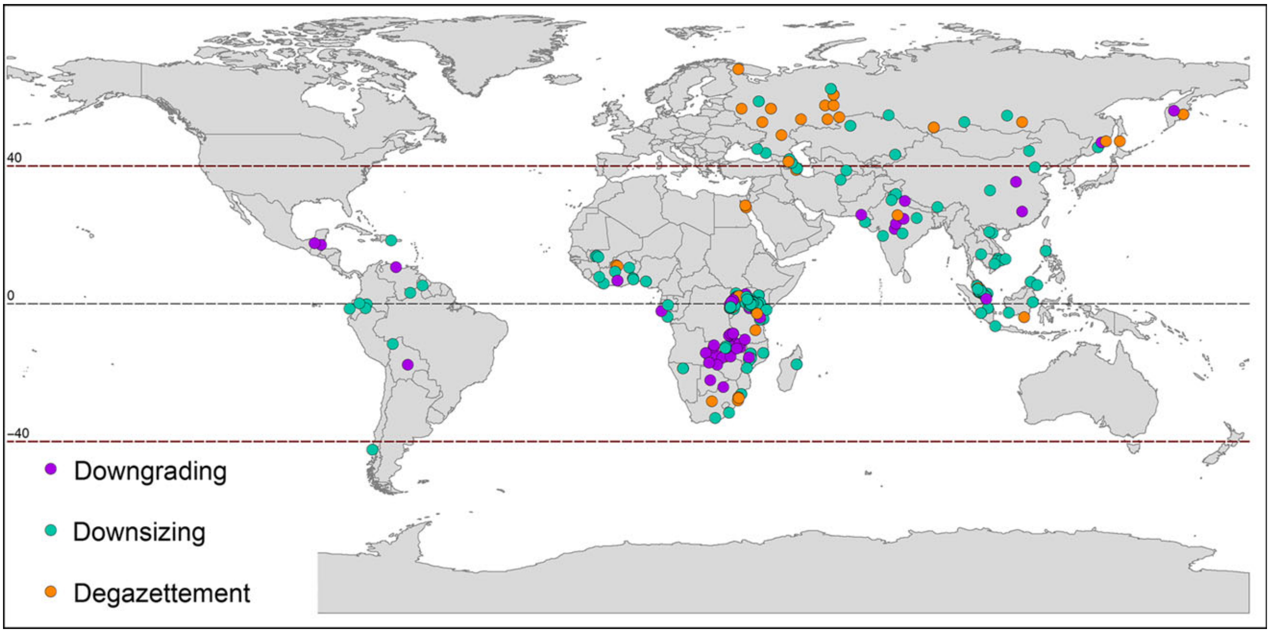

Fig. 1 Global distribution of PADDD events in our data set. The gridlines at 40 degrees north and 40 degrees south represent the area of our analysis, and the black line represents the equator.

Table 1 Summary of the total number of PADDD events by region in both the original and the analysis data sets. Note the original PADDD data set includes all records globally, even those with an unknown location, whereas the analysis data set only includes the records after the data have been processed as outlined in the methods. The data set was downloaded from www.PADDD-tracker.org (World Wildlife Fund, 2014)

	Downgrading		Downsizing		Degazettement	
Region	Analysis	Original	Analysis	Original	Analysis	Original
Africa	39	45	190	206	20	64
Asia	9	14	68	110	5	82
Latin America and the Caribbean	4	4	8	14	0	4
Total	52	63	266	330	25	150

We used the centroids rather than polygons to avoid introducing spurious precision (and error) using boundaries which are known to be inaccurate (as a result of PADDD).

Due to data paucity, we only created two groups of models: one analysing downsize events only and one analysing all PADDD events together. For all the models, PADDD was converted to a binary variable, 1 represented a PA that had undergone PADDD, and 0 was a PA that had not. To avoid potential pseudoreplication, we included PAs where multiple PADDD events had occurred only once in the data set. We analysed the data using the statistical software R version 3.0.1 (R Core Team, 2014). As the dependent variable was binary, we created a generalised linear model using a binomial error structure containing only the main effects of the explanatory variables. From this, we calculated the variance inflation factor to check for multicollinearity in the variables. The variables that presented a score greater than four were removed from the analysis (in this case none). To test for spatial autocorrelation, we calculated the semivariance that was plotted in a variogram. We also tested a negative binomial error structure; however, despite the large number of zeros in the data set, there was little overdispersion present and a binomial error structure was used.

To account for variables distributed at the national level for which spatially explicit data were not available, such as governance, corruption, national priorities or civil unrest, we created generalised linear mixed-effects models (GLMM) with a random intercept for country. The explanatory variables that we coded as fixed effects were population, accessibility, potential agricultural rent, size of PA, spatially explicit GDP and altitude. We also considered the first-order interactions between these variables. We scaled all the variables (by subtracting the mean and dividing by the standard deviation for each variable) to make the estimated coefficients of the different explanatory variables directly comparable. All the GLMMs were created using the package LME4 (Bates *et al.*, 2014). To fit the models, we used the Laplace approximation instead of penalised quasilikelihood, as the latter can be inaccurate when applied to models with a binary explanatory variable (Bolker *et al.*, 2009).

We used an information theoretic approach for model selection (Johnson & Omland, 2004). We created a list of 76 candidate models to test the hypotheses outlined above through an iterative process, whereby model complexity was slowly increased by testing the combinations of main effects and then including two-way interactions (Table S3). As we suspected nonlinear relationships, quadratic terms for the main effects were introduced into the models. We used the Akaike information criterion (AIC) to select models (Johnson & Omland, 2004). Lastly, we calculated the weighted average parameter estimates of all the models that had a difference in AIC score of < 4 with respect to the model with the lowest AIC score [the MUMIN package for model comparison and averaging (Barton, 2013)].

Robustness analysis

Recent country-specific work on PADDD, most notably from Brazil (Bernard *et al.*, 2014; De Marques & Peres, 2014), has indicated that some PADDD events were missing from our data set. Therefore, to explore sources of bias from under-reporting of PADDD, we constructed zero-inflated negative binomial models (ZINB) using the package PSCL (Zeileis *et al.*, 2008) and zero altered negative binomial models (ZANB) using the package glmmADMB (Fournier *et al.*, 2012). ZANB and ZINB models require count data, so in these cases we used the number of enacted PADDD events at each PA as the explanatory variable (as opposed to the binary PADDD vs. no PADDD). This gave us the added advantage of being able to investigate whether the increased information in the count data altered the patterns of influence. Both ZINB and ZANB models are two part models where the chance of getting a non-zero result is modelled with a binomial distribution, and then, count data are modelled separately. The main difference between them is in a ZINB model zeroes are included in the count model and in the ZANB they are not. It is also much easier to incorporate random effects into a ZANB model; hence, we calculated both.

Further to this, we conducted several separate analyses of reduced data sets to evaluate the robustness of our results. First, we used a data set containing only the countries for which the original creators of the data set were confident all PADDD events were included. The three countries included were Russia (not included in the original analysis data set), Uganda and Kenya. GLMMs and an information theoretic approach (with the same candidate model list as above) was used to analyse these countries together, and generalised linear models were used to analyse each country separately. Finally to explore the sensitivity of our models to issues related to temporal changes in the distribution of several explanatory variables, we split the data between PADDD events occurring pre- and post-2000. The split at 2000 was chosen as it was the latest possible date which allowed enough data on both sides of the split for correct model convergence. In total, we performed 6 different analyses on the data (full data set, confident countries only, pre-2000 events, post-2000 events, ZINB and ZANB). We also conducted traditional stepwise model simplification to explore the sensitivity of our results to model selection approach. We used a maximal model containing all first-order and second-order interactions and subsequently removed one explanatory variable at a time, using likelihood ratio tests, to find the minimum adequate model.

Finally, we also tested model performance by plotting the receiver-operating characteristic (ROC) curve and calculating the area under the curve (AUC) score, using the leave-one-out cross-validation method with the model with the lowest AIC score.

Results

In all analyses, larger PA size was found to be associated with a higher probability of PADDD. In the analysis of the full data set, we found size of PA to have the strongest positive relationship with the probability of PADDD with coefficients of 1.93 (standard error (SE) = 0.34) for all events and 2.70 (SE = 0.53) for downsizing (see Fig. 2 and Tables S4 and S5). In all but one of our analyses (ZINB), the interaction between size and local population density was associated with a higher probability of PADDD. This interaction was even stronger than the effect of size in the full data set analysis with coefficients of 2.37 (SE = 0.72) and 3.80 (SE = 0.99) for all events and downsizing, respectively. Our results show increasing local population densities to be enhancing the influence of PA size on the probability of PADDD. Our results also indicate a difference between all PADDD and downsize, indicating size of PA and its local population density interaction is more influential on the probability of downsizing as opposed to downgrading or degazettement.

We also found altitude to have a small but significant and positive influence on PADDD occurrence across all

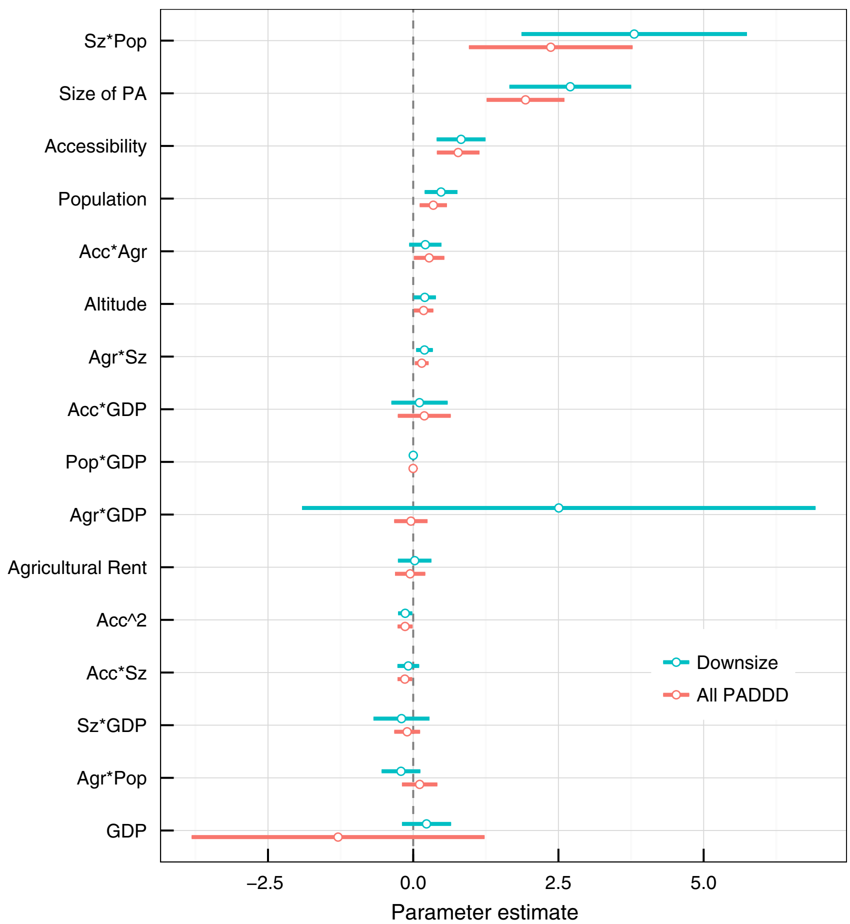

Fig. 2 Plot of effect sizes with confidence intervals for both average models for the analysis of the entire data set, listed in order of effect size from highest to lowest. The abbreviations are as follows: Acc = Accessibility, Alt = Altitude, Agr = Agricultural rent, GDP = Spatial GDP, Pop = Population density, Sz = Size of PA.

but one of the analyses (post-2000 events), suggesting PA in upland areas have an increased probability of PADDD. However, the size of this effect was much smaller than the effect of PA size and the PA size–population interaction, with coefficients in the full data set analysis of 0.18 (SE = 0.09) and 0.2 (SE = 0.1) for all PADDD and downsizing, respectively.

We found a wide variation in the probability of PADDD on a country-by-country basis (Fig. 3), indicating that in our data set some countries were much more or less likely to contain a PADDD than others. Spatially explicit GDP consistently showed no significant influence on the occurrence of PADDD in our analysis.

Robustness analysis results

Our main analysis of the full data set also showed a significant positive influence of local population density on the probability of PADDD with coefficients of 0.35 (SE = 0.12) and 0.48 (SE = 0.14) for all PADDD and downsizing, respectively. However, the ZINB and ZANB models showed that there was significant zero inflation associated with decreasing local population densities and PA size (Tables S6 and S7), suggesting an increasing chance of not detecting an enacted PADDD event in areas of lower population density and smaller PAs. Despite this, the influence of PA size was robust to zero inflation and remained significant and positive across all analyses and the size–population interaction was significant and positive in all but the ZINB. In the ZINB models, the effect of local population densities on the probability of PADDD was not significant, although it remained significant in the ZANB analysis. Our analysis of PADDD in the confident countries also supported this result, as population had no significant influence on the probability of PADDD.

The influence of accessibility was also inconsistent across the different analyses, we showed a significant nonlinear (negative quadratic) trend across the whole data set, and pre-2000 events, but not in the post-2000, confident countries or ZANB analysis. While accessibility was associated with zero inflation in our ZANB

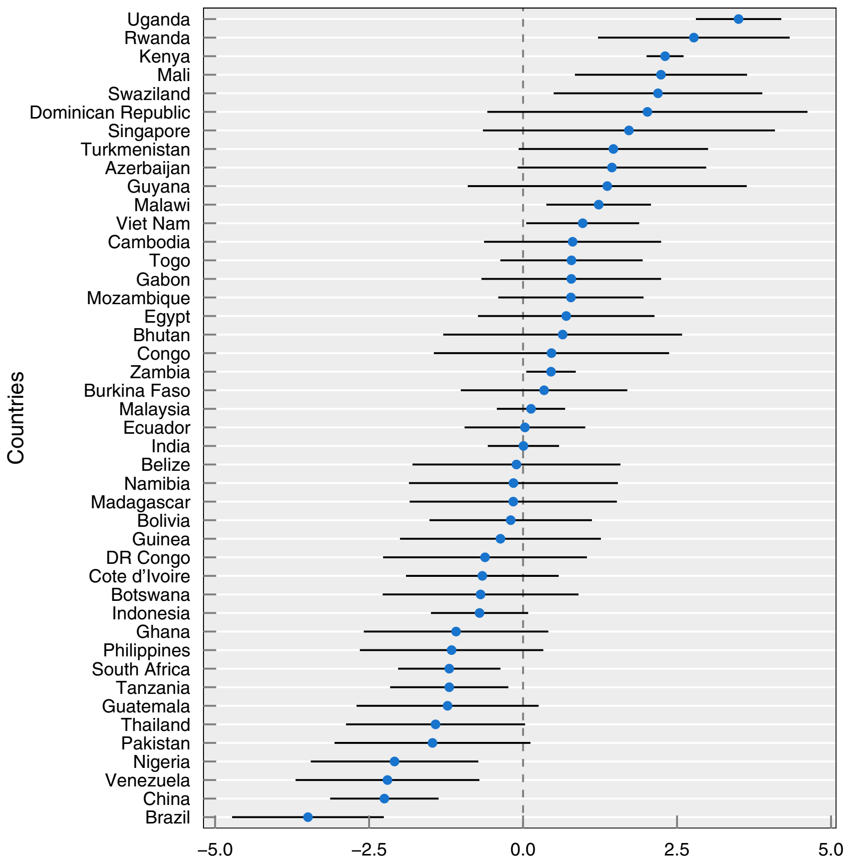

Fig. 3 Plot of values for the best linear unbiased predictors and 95% prediction intervals for the random effects used in the generalised linear mixed effects model for all PADDD events. The *y*-axis shows the country name, and the *x*-axis shows the random intercepts used by the model. A positive value indicates that a PA in that particular country has a higher probability of undergoing a PADDD event than the global mean (the mean across all countries), and the negative value indicates a lower probability than the global mean.

analysis, it was not in the ZINB model. This indicated that zero inflation due to accessibility may be coming from a different source than the zero inflation due to population or PA size (e.g. structural zeros rather than sampling zeros) as the ZANB model makes no distinctions regarding the type of zeros present.

Our analysis of the pre-2000 events and post-2000 events showed the effect of PA size and interaction of PA size and local population to be consistently significant and positive across the temporal range of the enacted PADDD data set (Fig. S1). There are some differences in the patterns of influence pre- and post-2000. For example, accessibility and altitude were significant and positive in the pre-2000 data set but not post-2000. Similarly, the interaction of accessibility and agricultural rent had a significant positive influence on PADDD post-2000 but not pre-2000. When we used traditional stepwise deletion, the minimum adequate model was identical to the model with the lowest AIC score from the information theoretic approach (Tables S8 and S9), indicating our results are robust to differing model selection approaches.

In our confident country analysis, in the three countries included (Russia, Uganda and Kenya), potential agricultural rent and the interaction between this and spatial GDP showed significant positive influences on the probability of PADDD (0.41, SE = 0.18 and 0.89, SE = 0.38, respectively, see Fig. S2). Finally, the AUC scores obtained through cross-validation of the best models, 0.86 for all events and 0.88 for downsizing events only, indicate our analysis was not sensitive to the presence of outliers in the data (Figs S3 and S4).

Discussion

Our results show PADDD probability increases with PA size and through a synergistic interaction with local population density. These insights form part of a growing literature showing the importance of PADDD to national, regional and global conservation goals (Mascia & Pailler, 2011; Bernard *et al*., 2014; De Marques & Peres, 2014; Mascia *et al*., 2014; Forrest *et al*., 2015). Without incorporating PADDD and PA robustness into systematic conservation planning frameworks, conservation practitioners and planners risk creating PA networks with inherent structural vulnerabilities to economic and demographic pressures. Given recent attempts to assess the efficacy of PAs worldwide (e.g. Geldmann *et al*., 2013; Laurance *et al*., 2012) and calls to replace underperforming PAs (Fuller *et al*., 2010), the need for systematic planning processes that not only optimise biodiversity but also consider the potential fate of the PAs within the network is becoming increasingly apparent.

Understanding the underlying processes behind how and why PADDD occurs is essential to better integrate PA robustness in future conservation planning. The influence of PA size in our study is likely due to larger PAs having more potentially exploitable land and geographic features, such as mineral deposits. Hence, larger PAs have higher opportunity costs with regard to other land uses. Similarly, the larger the PA, the more costly it is to circumvent through infrastructure development, potentially disrupting the economic activities of large regions.

The original PADDD data set ascribes proximate causes to some of the events, and while the majority of the 342 events, we analysed were not given causes (187 events), 43% of the events that were given one can be considered economic in origin (67 from 155). These causes include forestry, industrial agriculture, industrialisation, mining and oil and gas exploration. A further 5 PADDD events were considered a result of infrastructure development and 29 presented multiple causes, and while these are difficult to disaggregate, almost all of these events involve some kind of economic action (Mascia *et al*., 2014). Therefore, approximately 65% of PADDD events with known causes were caused by economic factors and/or infrastructure development, supporting the hypothesis that PADDD events are more likely in larger PAs due to the higher opportunity cost of large PAs in relation to these activities.

We are not, however, suggesting the higher probability of PADDD in larger PAs renders such sites undesirable for conservation when compared to smaller sites. There are many species and ecosystems that require large undisturbed regions for survival (see Tscharntke *et al*., 2002; Tjørve, 2010), so to ignore such sites in future conservation plans would be unwise. Instead, our analysis shows larger PAs to be less robust in the face of economic, demographic and legislative pressure. Importantly, this potential vulnerability should be explicitly recognised by conservation planners and practitioners, to ensure appropriate safeguards are in place.

That PAs are coming under pressure from local populations is well established (Green *et al*., 2012; Laurance *et al*., 2012) and the synergistic influence of population and PA size directly supports this. While under-reporting in areas of low population density has made the direct influence of population density on PADDD more difficult to identify in our analysis, the indirect influence, through the synergistic interaction with PA size, is very well supported. Furthermore, when the results from the count model of the ZANB model are also considered, the link becomes stronger, with population density being a direct driver of further PADDD events in PAs where one event has already taken place. This is important information to consider when devising management plans for PAs and PA networks and highlights the difficulties with managing PAs in highly populated areas. Such PAs become increasingly vulnerable to PADDD with increasing PA size, especially if the legal frameworks and systems that lead to PADDD are already in place.

Our analysis also builds on recent studies regarding road building (Laurance *et al*., 2014), to help better elucidate how the global expansion of roads will affect PA networks. While the direct relationship between accessibility and PADDD was not clear across all the analyses (there was indication of a negative quadratic relationship in the full, pre-2000 and ZINB analyses), improved road networks are likely to facilitate the movement of people and increase development opportunities in more remote areas. Our analysis suggests these factors will then act synergistically with PA size to increase the chance of PADDD at formerly low probability sites. These effects are exacerbated by infrastructure development taking place directly in a PA [e.g. hydropower dams in Brazil (Bernard *et al*., 2014)] and the associated access improvements of these developments making industrial resource extraction more profitable, both of which are more likely in larger PAs.

The positive effect of altitude on PADDD ostensibly runs counter to the positive influences of population, which is normally associated with lowland areas. As our analysis treats the entire PA as a single entity and we calculated altitude from the centroid (using interpolation), then if the lowland areas within upland PAs are disproportionately affected by PADDD, this could lead to the positive association in the model. Potentially, the increasing difficulty of trying to justify the protection of lowland areas in PAs with a primary function of protecting upland areas, or maybe the increased suitability of upland areas for agriculture in arid countries such as Kenya, may also be influential. However, more information and further research is required to fully understand this counter-intuitive result.

Our study, however, has temporal limitations. Most of our variables were taken from 2005 (accessibility is from 2000), but the PADDD data set spans the years 1900–2010. We therefore had to assume that the distribution of demographic and economic factors across the entire duration of the data set was similar to the situation in 2005. However, 49% (94 from 192) of PADDD with a known date have occurred since 1990. The fact that the results of our validation analysis where the data were split at 2000 showed similar patterns to the full analysis indicated that this assumption was reasonable.

The results of the ZINB and ZANB (SI Tables S6 and S7) suggest that PADDD is under reported in areas of low population and in smaller PAs; however, they also show the influence of PA size and the PA size–population interaction to be robust to this under reporting. The secondary validations, using only countries where we have high confidence all PADDD events are included, concurs with the zero inflated models reinforcing the conclusion that population on its own is not driving PADDD events. The validation analysis includes data from Russia which were not included in the original analysis and also showed similar patterns of influence on PADDD, further strengthening our conclusions.

National level nuances in PADDD are clearly apparent from the random effects estimates for each country (Fig. 3). These indicate several interwoven country level factors may be influencing PADDD at a national level. For example, rule of law, environmental governance, land tenure or policy likely interact in complex ways to alter the frequency and location of PADDD events. Furthermore, international and trans-national drivers of PADDD, such as conflicts, trade agreements and tele-coupled systems (Bruckner *et al*., 2015), likely alter the patters of occurrence between countries and regions in ways we are not able to clearly capture in this analysis. Our findings show the importance of understanding PADDD dynamics in the national context and how essential it is to understand the process and nuances of PADDD to design effective conservation programmes nationally.

With increasing pressures on PA networks, evaluating their performance has become vital (Naughton-Treves *et al*., 2005; Gaston *et al*., 2008; Laurance *et al*., 2012), especially with a view to optimising scant resources available to conservation (Fuller *et al*., 2010; McCarthy *et al*., 2012). Our results show PA size can work synergistically with external factors, such as population to increasing the probability of PADDD and consequently, reducing the likely permanence of some PAs within a larger network. This information is useful to conservation planners for two reasons: firstly, it will allow them to assess current PAs for potential vulnerability to economic and demographic factors, and secondly, it provides a relatively simple method for assessing the robustness of any new additions to PA networks.

PADDD is a phenomenon that is both current and increasing in certain parts of the world (De Marques & Peres, 2014). As such, it is essential we develop our understanding of what is driving PADDD, use this knowledge to underpin our targeting of conservation resources and improve the planning of national PA networks. We hope this study will provide impetus for further investigation of PADDD (and PA dynamism more generally), which will help better underpin conservation planning, resource allocation and the creation of more sustainable long-term conservation interventions.

Acknowledgements

W.S.S. and L.R.C. are thankful for research funding from a Tier 2 grant from the Ministry of Education of Singapore, WBS R154000574112. M.B.M. was supported by a grant from the Gordon and Betty Moore Foundation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Methods S1. Supplementary methods for GIS data.
Table S1. A summary of all enacted PADDD events (as downloaded from www.PADDDtracker.org data release V1.0), the last column denotes whether the event was included in our analysis after the data was processed using the protocol outlined in the methods.
Table S2. Summary table of World Bank country income categories for the 45 countries included in the analysis.
Table S3. Model selection table showing all the models tested during the analysis.
Table S4. Shows the weighted average model of all models within delta 4 AIC of the best model (for a list of component models see appendix B), for the analysis of all PADDD events together.
Table S5. Shows the weighted average model of all models within delta 4 AIC of the best model (for a list of component models see appendix B), for the analysis of all only downsize events.
Table S6. Results of the zero inflated model, the first table is the count model coefficients and the second is the zero-inflated model coefficients for the 2 part model.
Table S7. Results of the hurdle models for the best supported (lowest AIC score) model in our analysis for all PADDD combined.
Table S8. Results for the minimum adequate model using stepwise parameter deletion and likelihood ratio tests for all PADDD events.
Table S9. Results for the minimum adequate model using stepwise parameter deletion and likelihood ratio tests for downsize events only.
Figure S1. Results of the validation analysis with the data split between PADDD events pre and post 2000.
Figure S2. Comparisons of the model estimates for the full data set and only the countries with high confidence of complete PADDD coverage: Kenya, Russia and Uganda.
Figure S3. Plot of the true positive rate against false positive rate for the best model for all PADDD events (AUC score 0.90).
Figure S4. Plot of the true positive rate against false positive rate for the best model for downsize events (AUC score 0.96).