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Global relationships between biodiversity and nature-based tourism in protected areas

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ABSTRACT

The relationships between biodiversity conservation and ecosystem services (ES) are widely debated. However, it is still not clear how biodiversity conservation and ES interact with different strategies in and surrounding protected areas (PAs), the cornerstone for biodiversity conservation. Here, we present results on the interplay between biodiversity conservation and nature-based tourism (a cultural ES), while controlling for environmental and socioeconomic factors in and surrounding terrestrial PAs worldwide. Results indicate that nature-based tourism is more frequent in PAs that are of higher biodiversity, older, larger, more accessible from urban areas and at higher elevation. High population density surrounding PAs and national income levels are also major socioeconomic factors related to nature-based tourism. Furthermore, PAs managed mainly for biodiversity conservation have nearly 35% more visitors than those managed for mixed use. Strict management for biodiversity is also associated with increased biodiversity. These results show the importance of biodiversity in addressing nature-based tourism and suggest this interrelationship could be altered by different management strategies used by PAs.

1. Introduction

For more than a century, designating and managing protected areas (PAs) has been done with a goal of allowing current use of biodiversity, usually through tourism, while preserving resources for future generations (Beissinger et al., 2017). But since the first designation of PAs, there have been conflicts over the appropriate goals in managing such areas (Dietz, 2017a; Joppa and Pfaff, 2010; Liu et al., 2012; Mace, 2014; Tallis and Lubchenco, 2014; Watson et al., 2014). One goal emphasizes the protection of natural systems and biodiversity (nature for itself) (Mace, 2014). The other emphasizes the contribution of ecosystem services (ES) from PAs to human well-being (nature for people) (Mace, 2014). Some PAs are managed with a sharp focus on the sole goal of preserving biodiversity; others are managed with an intent to enhance the provision of multiple types of ES. Of course, preservation of natural systems and biodiversity can contribute to cultural ES, including nature-based tourism (Bayliss et al., 2014; Clements and Cumming, 2017). Additionally, biodiversity may enhance the production of a wide variety of ES beyond just cultural ES (Chung et al., 2015; Smith et al., 2017; Turner et al., 2012) but it is not necessarily the case that managing a PA for biodiversity will optimize overall provision of ES (Karp et al., 2015; Naidoo et al., 2008). Thus, understanding the relationship between ES and biodiversity is a major challenge for sustainability science (Carpenter et al., 2009; Chan et al., 2006; Graves et al., 2017; Ouyang et al., 2016; Turner et al., 2007).

Two further complexities emerge because PAs are not isolated from the rest of the world. First, PAs are often surrounded by a large "buffer zone" that is outside the direct management of the PA but that affects and is affected by what happens in the PA (DeFries, 2017). Further, PAs are telecoupled with non-adjacent systems in several ways that influence the supply of and demand for ES (Bagstad et al., 2013; Liu et al., 2016a). Most visitors to PAs have traveled from distant places to visit them (Liu et al., 2013; Xiao et al., 2017). PAs may provide water purification that have benefits to people hundreds or thousands of kilometers away, and in turn may be affected by upstream degradation of water quality (Watson et al., 2014). Agricultural activities surrounding PAs can negatively influence biodiversity conditions in PAs (Bailey et al., 2016; Palomo et al., 2013). The demand for agricultural products from the surrounding PAs may also be local, regional or global (Liu et al., 2015b). Finally, invasive species, which threaten many PAs, may have their origins across the globe and climate change (Tuanmu et al., 2012), a severe threat to many PAs, has its drivers distributed globally

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as well (Pimm et al., 2014; Zhong et al., 2015).

For many PAs, one of the most important ES is providing an attractive destination for nature-based tourism, which is both regional and global in origin. Such tourism may be influenced in complex ways by how PAs are managed (Graves et al., 2017; Karp et al., 2015). In some PAs, managing primarily for biodiversity might discourage nature-based tourism, while in others such management might be compatible with high demand for visits. Agricultural landscape surrounding PAs may provide additional attractions that could either increase or decrease demand for tourism at a PA (Baudron and Giller, 2014; Fleischer et al., 2018; Jie et al., 2013; Liu et al., 2012).

For individual PAs, we can trace plausible paths by which biodiversity conservation strategies change demand for nature-based tourism via environmental and socioeconomic changes in the PA and surrounding areas. But there is little empirical analysis of the overall effects of PA management on tourism demand and supply. To address this gap in the literature, we used data from PAs worldwide to examine the number of visitors to PAs as a function of the number of species in the PA and the management strategy being used, while controlling for environmental and socioeconomic factors. In addition, we investigated how different conservation strategies influence biodiversity and other factors both inside and outside PAs. Our analysis addresses two questions. First, how does biodiversity and nature-based tourism interact in PAs that may be governed by different conservation strategies? Second, which environmental and socioeconomic factors in and surrounding PAs influence visitation to PAs? Our analysis is based on terrestrial PAs that have visitation information between 2000 and 2014. Our results can contribute to a better understanding of how biodiversity and nature-based tourism interact in PAs and how these interactions may be altered by different conservation strategies used by PAs.

2. Methods

2.1. Data

The dataset was obtained by aggregating data from a number of international institutions, national statistical agencies, online datasets and the grey literature (Table A.1). Our key dependent variable was the average annual visitor numbers for each PA. The final dataset contained 929 PAs in 50 countries with the annual visitor numbers at some point in the period 2000 to 2014 (Fig. 1 and Table A.2). We calculated visitation as the average annual visitor numbers in each PA over the 15-year period.

The two key independent variables are the management strategy being used at the PA and its biodiversity. Management strategy was operationalized as the IUCN management category. The IUCN management category is based on the primary management objectives of PAs, which should apply to more than 75% of the PA area (Dudley, 2008). The IUCN category facilitates global assessments across different countries by providing an international standard for classifying management strategies of PAs. The primary objective of categories II–IV is to protect biodiversity (PAs managed for biodiversity), while categories V–VI are to both protect nature and use natural resources sustainably (PAs managed for mixed use) (Baudron and Giller, 2014; Dudley, 2008; Joppa et al., 2008; Laurance et al., 2012). For example, Categories II–IV focus on minimizing human activities keeping the system in "as a natural state as possible", but Categories V–VI allow sustainable use of natural resources (e.g., hunting and/or forestry) to balance interaction between people and nature (Dudley, 2008). Dividing all PAs into two groups helps to differentiate conservation management practices between those that manage for nature for itself (II–IV) and those that manage for nature and people (V–VI). We divided all 929 PAs into two groups (II–IV and V–VI): 677 PAs in Category II–IV were coded 1 and 252 PAs in Category V–VI were coded 0. We excluded marine PAs and PAs which had not been classified into one of the IUCN management categories. PAs in IUCN category Ia and Ib where visitor access is strictly limited were also excluded. To include active management PAs, we selected PAs that were designated and managed at the national or sub-national level. The designated PAs have a long-term commitment to conservation with legal means (IUCN and UNEP-WCMC, 2017).

Second, biodiversity was operationalized as the number of species of birds, mammals and amphibians within the PA (Jenkins et al., 2013; Pimm et al., 2014). The biodiversity mapping website (http://biodiversitymapping.org) provided a global map of species ranges for birds, mammals and amphibians based on data from IUCN (IUCN, 2014) and BirdLife International NatureServe (BirdLife International NatureServe, 2013). A species range polygon underlies these mapping efforts. We selected mammals, birds and amphibians because these species have most comprehensive data at a global level and because they seem likely to be the species that will influence visitors' preferences (Hausmann et al., 2017a; Siikamäki et al., 2015). The species range maps provide current species native range "determined by using known occurrences of the species" as well as "the knowledge of habitat preferences, suitable habitat, elevation limited, and other expert knowledge of the species and its range (IUCN, 2014)." Although the species range maps are the best available global datasets, we note the maps may overestimate species richness as the range of potential distribution tends to be larger than

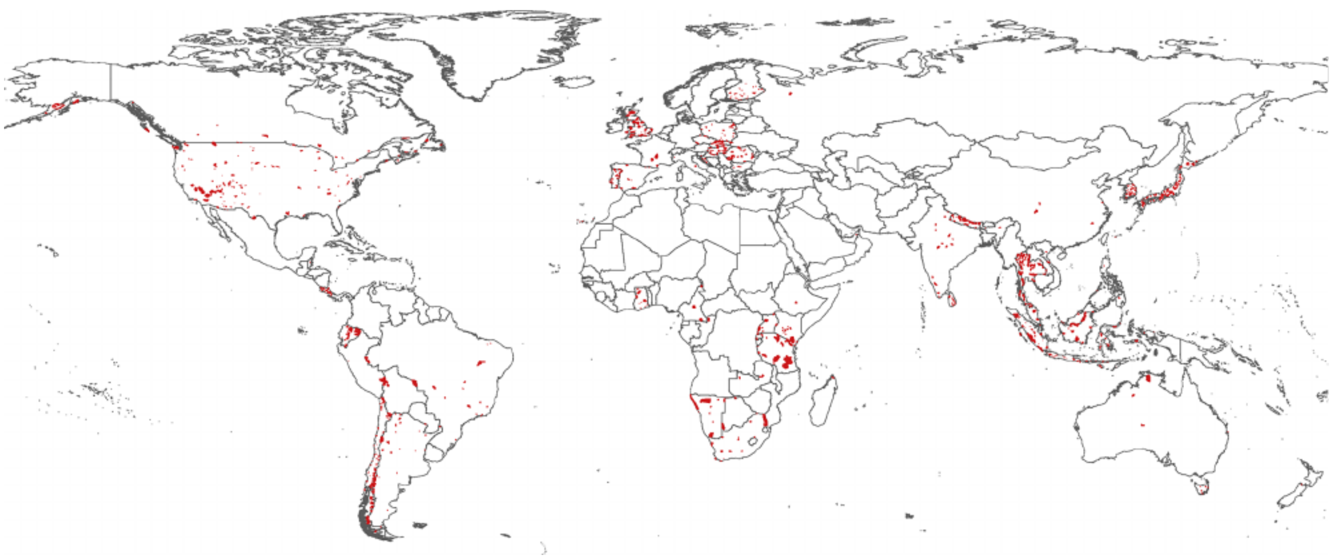

Fig. 1. 929 PA locations in the world.

the actual occurrences of the species (Willemen et al., 2015). All species maps have a spatial resolution of 10 km by 10 km, based on 2013 updated data. We only included native and extant species. We overlaid this species range map with the locations of PAs and extracted species number in each PA by using zonal statistics in ArcGIS (ESRI, 2015).

We included as control variables a number of characteristics of the PA that might influence its attractiveness for nature-based tourism: size, mean elevation, mean annual temperature, mean annual precipitation and age (years since formal designation). We also controlled for remoteness which was defined as travel time (in minutes) from the nearest major cities (population > 50,000) and the percentage of total water supply originated in the PA. Higher percentage of water supply in the PA indicates that the PA has more freshwater resources (WRI, 2015). Finally our model included dummy variables for the continent in which the PA was located. Data on size, mean elevation, mean annual temperature, mean annual precipitation and travel time from the nearest urban area for each PA was extracted from the appropriate geographic data bases using PA boundaries to develop zonal statistics in ArcGIS.

In addition to the features of the PA itself, we have characterized buffer zones for each PA. Following previous research (Joppa and Pfaff, 2010; Wittemyer et al., 2008), we specified 10-km buffer zones around each PA. Capturing activity within the buffer zones is important because the PA and its management may influence conditions within the buffer zones and vice versa. For each 10-km buffer zone, we extracted population density, agricultural yield and the percentage of agricultural area. We selected only cases with valid values for all variables excluding those PAs for which data for relevant variables were missing.

We appreciated that specifying a 10-km buffer zone is somewhat arbitrary. To test the sensitivity of our analysis to the size of the buffer zone, we performed a multiple ring buffer analysis in ArcGIS and QGIS (ESRI, 2015; QGIS Development Team, 2014). We designated 10-km distance intervals from the PA boundary (0-km) to 50-km buffer zones. Then, we extracted numerical values from the PA boundary and each of five rings (0–10, 10–20, 20–30, 30–40 and 40–50 km) using the spatial dataset. In each PA boundary and ring, we obtained numerical values of environmental and socioeconomic factors (population density), agricultural factors (agricultural yield and agricultural area) and regulating ES (water supply originated in PAs). In the multiple ring buffer analysis, we did not consider agricultural factors within PA boundaries because many PAs prevent people from engaging in agricultural activities (Palomo et al., 2013). Although some PAs have agricultural activities (Xu et al., 2017), there are efforts to minimize negative agricultural impacts on the environment (Yang et al., 2013).

2.2. Modeling strategy

Our basic model predicts annual visits to each PA as a function of the species richness of the PA and the management strategy being used, with strategies ranging from strict emphasis on biodiversity protection to more mixed use. We also include a variety of control variables in our regressions to minimize the risk that the effects we estimate for biodiversity and management strategy are spurious. We control for features of the PA by including its size, mean elevation, annual mean temperature and precipitation, remoteness and age. We also control for population density within a 10 km buffer zone around the PA and for the affluence (gross domestic product per capita) of the nation in which the PA is located (reliable data on affluence cannot be obtained at a spatial scale corresponding to the 10 km buffer zone). Controls are also included for agriculture in the buffer zone and water supply originated in PAs (agricultural yield, % land area in agriculture and % total water supply originating in PAs). We provide a summary of variables regarding nature-based tourism hypothesis (Table 1). Finally, we include dummy variables for continent.

This model allows us to address our research questions by examining how biodiversity, management strategy and the characteristics of the PA itself and its buffer zone influence the popularity of a site for nature-based tourism.

2.3. Regression model

The multiple regression equation for the nature-based tourism model is in the multiplicative form commonly used in the STIRPAT models (STochastic impacts by Regression on Population, Affluence and Technology) of human drivers of environmental change (Dietz, 2017b):

$$Y = aX_1^{b_1}X_2^{b_2}X_3^{b_3}\cdots X_n^{b_n}E$$

For ease of estimation we used log base e of all except the binary variables, thus:

$$\log(Y) = a + b_1 logX_1 + b_2 logX_2 + b_3 logX_3 + \cdots + b_n logX_n + E$$

where Y stands for the average annual visitor numbers in each PA from 2000 to 2014, X_1 is the number of species, X_2 is IUCN management category, X_3 is the area of each PA, X_4 is mean elevation, X_5 is annual mean temperature, X_6 is annual precipitation, X_7 is PA remoteness from major cities, X_8 is PA age, X_9 is population density, X_{10} is per capita GDP at the national level, X_{11} is agricultural yield, X_{12} is the percentage of agricultural area, X_{13} is % water supply originated in PAs, X_{14}–X_{17} are dummy variables for each continent (Asia and Oceania, Africa, Europe and North America) (Table 2). E is the error term. Note that in this multiplicative form the unstandardized regression coefficients can be interpreted as elasticities. That is, our estimates indicated that a 1% change in an independent variable is associated with a b% change in the dependent variable, net of all other variables in the model. STIRPAT models have frequently been used to examine non-linearities beyond the log–log form and other specifications when there are theoretical arguments to do so. However, since our analysis is an initial exploration of factors related to visitation, we have kept to this rather well known functional form.

To account for model selection uncertainty, we used an information theoretic approach for model averaging. This approach provides robust parameter estimates based on model averaging across the best set of models by information theoretic criteria (e.g., Akaike Information Criterion (AIC)) rather a more traditional approach of selecting the best fitting model (Galipaud et al., 2014; Grueber et al., 2011). We first generated a candidate model set of 131,072 models to determine the model set for averaging. These models were then ranked based on AICc (AIC for small samples) to avoid overfitting (Grueber et al., 2011). Models with a smaller AICc are considered to have a better fit. We used a top 2AICc cutoff criterion which results in a set of three best models. The top 2AICc cutoff criterion indicates that AICc difference between model i and the top-ranked model is less than 2 ($\Delta_i = \text{AICc}_i - \text{AICc}_{top}$) (Burnham and Anderson, 2002). Then, the parameter estimates of the top three models were averaged using Akaike weights (w_i). The Akaike weights (w_i) indicate the relative likelihood of the candidate models with a normalized scale (0-1) and provide a way to interpret Δ_i values as probabilities (Burnham andAnderson,). Models with a bigger Δ_i have a smaller w_i. The percentage of water supply originating in PAs did not appear in the final model as this variable was not included in the top three models developed using the information theoretic approach.

Although some variables were not statistically significant, including all variables allow us to identify indirect relationships on the annual visitations via biodiversity and guards against spurious relationships. To formally test the indirect impacts of other factors on the annual visitations via biodiversity, we performed the regression of visitor numbers on all other variables except biodiversity. To capture the difference in the number of species between PAs primarily managed for biodiversity and PAs managed with more mixed objectives, we also modeled the number of species in PAs as a function of the same independent variables. Since this analysis is secondary to the analysis of tourism, we did not deploy the information theoretical approach to model selection.

Table 1
Summary of variables regarding nature-based tourism hypothesis.

Variables	Relationships with nature-based tourism	Source(s)
Species richness	More species richness contributes to greater nature-based tourism value	Arbieu et al. (2017); Hausmann et al. (2017a); Siikamäki et al. (2015); Smith et al. (2017); Willemen et al. (2015)
Management strategies	PAs managed for biodiversity actively encourage visitors for nature-based tourism	Dudley (2008)
Size of PAs	Larger size of PAs has more visitors	Balmford et al. (2015); Baum et al. (2017)
Elevation	Geographical attributes such as elevation may influence visitors' preferences	Hausmann et al. (2017b); Kumari et al. (2010)
Temperature and precipitation	Climate and weather are important factors for visitors (e.g., low humidity and heat stress)	Scott et al. (2008); Verbos et al. (2017)
PA remoteness	Visitors are reluctant to go remote PAs	Balmford et al. (2015); Neuvonen et al. (2010)
PA age	Visitor numbers increase with PA age	Karanth and DeFries (2011); Neuvonen et al. (2010)
Population	Visitor numbers are higher when there is a higher population density surrounding PAs	Balmford et al. (2015); Ghermandi and Nunes (2013)
GDP per capita	PAs in high-income countries have more visitor numbers	Balmford et al. (2015); Ghermandi and Nunes (2013)
Agricultural factor	Agricultural landscape surrounding PAs may provide additional attractions and/or food-related activities	Baudron and Giller (2014); Fleischer et al. (2018); Hjalager and Johansen (2013); Jie et al. (2013)
Water supply in PAs	Plenty of water resources in PAs provide greater attractions (e.g., lakes, streams, waterfalls)	Cao et al. (2016); Nyaupane and Chhetri (2009); Reinius and Fredman (2007)

Table 2
Descriptive statistics of dependent and independent variables, $N = 929$.

Category	Variable	Mean	Std. Dev
Nature-based Tourism	Annual visitor numbers in PAs (persons)	367,405	1,793,697
Biodiversity	Total species (species)	326.88	172.540
Protected Area	IUCN category (II–IV = 1)	0.729	0.445
	Size of PAs (km^2)	860.91	2640.659
	Mean elevation (meter)	825.3	880.661
	Annual mean temperature (°C)	14.449	8.063
	Annual precipitation (mm)	1298.898	827.042
	PA remoteness (minutes)	360.8	413.191
	PA age (year)	38.24	23.095
Demographic	Population density[§] (persons/km^2)	140.012	471.987
Economic	GDP per capita[¶] (2005 const. $ per capita)	16,127.7	16,342.57
Agricultural factor	Agricultural yields[§] (tonne/km^2)	553.9	387.914
	Agricultural area[§] (%)	30.051	24.773
Regulating ES	Water supply originated in PAs (%)	13.66	13.827
Region	Asia and Oceania	0.378	0.485
	Africa	0.097	0.296
	Europe	0.231	0.422
	North America	0.127	0.333
	Latin America	0.167	0.373

§ 10-km buffer zone.
¶ Country level data, not PAs level.

According to the correlation matrix for the independent variables, 96% of 76 pairs had the value of r less than 0.5 (Fig. A.1). In addition to the correlation matrix, we examined collinearity using variance inflation factors (VIF) (O'Brien, 2007). All VIFs were less than 5, indicating no serious collinearity problems (Table A.3). All statistical analyses were performed with R software (R Core Team, 2013). The information theoretical model averaging approach was deployed using MuMIn package in R. We used the procedures developed by Frank et al. (2013) to examine the robustness of our results. These procedures calculate what proportion of cases in the data set would have to be replaced with null hypothesis cases in order for the significance of a coefficient to drop below a threshold of interest. We used the conventional $p = 0.05$ as our threshold for statistical significance. If a relatively modest proportion of cases would have to be replaced with null cases for a coefficient to fall below the $p = 0.05$ threshold then the inference is rather fragile; if a high proportion of cases would have to be replaced the inference is robust.

3. Results

3.1. Biodiversity and its conservation strategies have a positive relationship with nature-based tourism

Biodiversity has a positive relationship with the number of annual visitors to PAs (Table 3). Each 1% increase in the number of species is associated with an increase in annual visitors of about 0.87%, indicating that biodiversity is one of the strongest influences on tourism. IUCN management category also has a positive association with the annual visitors meaning that PAs managed strictly for biodiversity conservation attract more visitors than PAs for mixed use. Validation suggests that these results are relatively robust. To invalidate the inference of a positive relationship of the number of species with the annual visitors, 48% of the estimated effect would have to be due to bias (Frank et al., 2013). One can interpret this as 48% (or 446 PAs) of the cases in this study would have to be replaced with null hypothesis cases to invalidate the inference.

Table 3
Summary results of the model averaging predicting annual visitor numbers in PAs.

Category	Variable	Model 1	Model 2	Model 3	Model averaging
Biodiversity	Total species (species)	0.879** (0.231)	0.870** (0.231)	0.868** (0.234)	0.874** (0.232)
Protected Area	IUCN category (II–IV = 1)	0.351* (0.166)	0.347* (0.166)	0.348* (0.166)	0.349* (0.166)
	Size of PA (km^2)	0.309** (0.039)	0.309** (0.039)	0.310** (0.039)	0.309** (0.039)
	Mean elevation (meter)	0.329** (0.058)	0.343** (0.057)	0.331** (0.058)	0.334** (0.058)
	Annual mean temperature (°C)	−0.378* (0.161)	−0.341* (0.160)	−0.383* (0.162)	−0.367* (0.162)
	Annual precipitation (mm)	−0.480** (0.118)	−0.469** (0.118)	−0.483** (0.118)	−0.477** (0.118)
	PA remoteness (minutes)	−0.236* (0.111)	−0.253* (0.111)	−0.240* (0.112)	−0.242* (0.112)
	PA age (year)	0.665** (0.117)	0.668** (0.117)	0.663** (0.117)	0.665** (0.117)
Demographic	Population density[§] (persons/km^2)	0.455** (0.061)	0.469** (0.060)	0.448** (0.066)	0.458** (0.062)
Economic	GDP per capita[¶] (2005 const. $ per capita)	1.262** (0.086)	1.279** (0.086)	1.266** (0.087)	1.268** (0.087)
Agricultural factor	Agricultural yields[§] (tonne/km^2)	0.101 (0.059)	–	0.094 (0.063)	0.099 (0.060)
	Agricultural area[§] (%)	–	–	0.027 (0.091)	0.027 (0.091)
Regulating ES	Water supply originated in PAs (%)	–	–	–	–
Region	Asia and Oceania	1.866** (0.223)	1.837** (0.223)	1.856** (0.226)	1.855** (0.224)
	Africa	0.967* (0.321)	0.867* (0.316)	0.966* (0.321)	0.935* (0.323)
	Europe	0.685* (0.267)	0.687* (0.268)	0.658* (0.282)	0.681* (0.271)
	North America	1.233** (0.304)	1.186** (0.303)	1.221** (0.306)	1.216** (0.305)
Intercept		−9.757** (1.797)	−9.451** (1.790)	−9.695** (1.810)	−9.648** (1.803)
R^2		0.478	0.476	0.478	
k		17	16	18	
AICc		3969.053	3969.936	3971.041	
Δ_i		0.000	0.882	1.988	
w_i		0.129	0.083	0.048	

$^{*}P < 0.05$, $^{**}P < 0.001$.
Values in parentheses are standard errors.
[§] 10-km buffer zone.
[¶] Country level data, not PAs level.
The percentage of water supply originating in PAs did not appear in the final model.

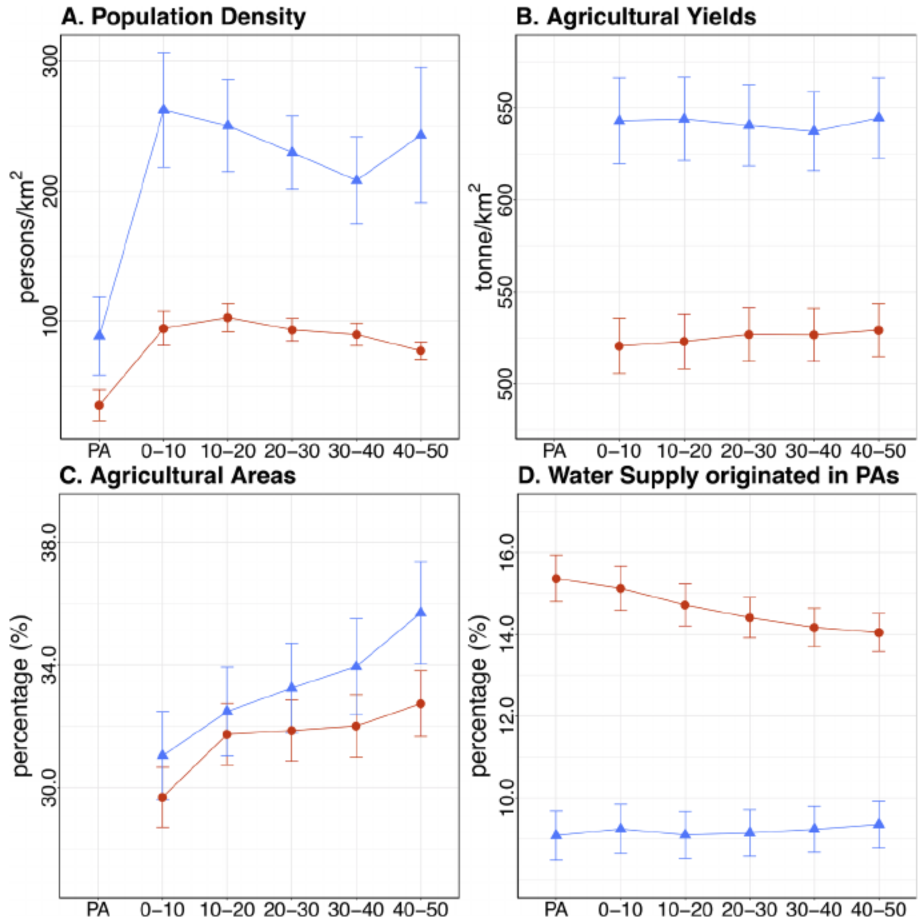

Fig. 2. Buffer zone variables with 10-km distance increments across PAs boundaries. A. Population density, B. Agricultural yields, C. Agricultural areas, D. Water supply from upstream PAs.

3.2. Nature-based tourism is influenced by socioeconomic and environmental drivers

We find that agriculture surrounding PAs and water supply in PAs do not have a direct relationship with the annual visitor numbers in PAs at the $p = 0.05$ level. Additionally, indirect associations of agriculture and water supply on visitor numbers via biodiversity are not significant (Table A.4). Population density in 10-km buffer zones around PAs is positively associated with visitor numbers ($P < 0.001$). We acknowledge that our cross-sectional data cannot disentangle causal direction: some people in the buffer zones may also visit the PA (the larger the population, the more visitors) but large numbers of visitors may also encourage local population growth. Per capita GDP has the strongest link to the number of visitors ($P < 0.001$) presumably because in high-income countries there are more people who can afford nature-based tourism and because PAs in high-income nations may be more desirable destinations since there may be larger budgets for tourist infrastructures (e.g., visitor centers), all other things being equal.

The characteristics of PAs also influence the annual visitor numbers in PAs. The age and size of PAs positively affect the visitor numbers ($P < 0.001$). Older PAs have had more time to gain recognition, often represent the most spectacular areas and may have been preserved in more pristine state than more recent PAs. In addition, PAs with larger sizes attract more nature-based tourists, presumably because large PAs have more natural attractions and habitats for species.

While the visitor numbers are positively associated with mean elevation, the visitor numbers are negatively associated with annual mean temperature and annual precipitation. This means that PAs with in a cooler temperature, lower precipitation and higher elevation have more visitors. People may visit PAs with high elevation areas to appreciate novel aesthetic views and natural habitats with high biodiversity because these PAs may avoid development pressures, maintain good natural habitat conditions and often have spectacular scenery. In addition, PA remoteness is negatively associated with the visitor numbers. PAs with good accessibility have more visitors. If PAs are located in the remote areas far from urban areas, people may not be able to afford the cost and/or time to visit the PAs even if the PAs provide good natural attractions.

All regional variables (Asia and Oceania, Africa, Europe and North America) have a significant p-value ($P < 0.05$) when compared with Central and South America, the baseline continent. Net of the controls we have used, PAs in the other four continents have more visitors than those in Central and South America.

There are major variations in management goals in PAs, reflected in the IUCN categorization. We find that this categorization is capturing differences that are important in terms of the amount of biodiversity in a PA, with the PAs primarily managed for biodiversity having 1.05 times more species than the PAs managed with more mixed objectives (Table A.4).

The nature of the buffer zone seems to have some correlation with number of visitors, with each 1% increase in population density associated with a 0.45% increase in visits. Agriculture in the buffer zone has no relationships with visitors to PAs. We tested the sensitivity of our analyses to the size of the buffer zones (Fig. 2). Population and agricultural variables have the same pattern of effects when measured for larger buffer zones as they do in the 10-km buffer zone.

4. Discussion and conclusions

4.1. The role of biodiversity in nature-based tourism

This study examines the relationships of biodiversity and other factors to nature-based tourism and the factors that are associated with biodiversity in PAs. The results demonstrate that biodiversity has a positive relationship with nature-based tourism even when a variety of other factors are controlled: with each 1% increase in biodiversity associates with a 0.87% increase in tourism. Furthermore, management strategies matter: PAs managed primarily for biodiversity protection have nearly 1.35 times the visits of those managed for mixed use. And management for biodiversity is associated with higher biodiversity, given the controls for other factors. Thus, we tentatively suggest that producing both biodiversity and nature-based tourism simultaneously is possible given appropriate conservation strategies. That is, biodiversity is compatible with economic development via tourism if proper strategies are deployed (Oldekop et al., 2016). More visitors can increase opportunities for local economic developments such as hotels, restaurants and employment opportunities for nature guides (Liu et al., 2012). Management plans that consider both biodiversity and local community participation could enhance economic development surrounding PAs and thus provide livelihood benefits to the local residents and reduce economic inequalities (Das and Chatterjee, 2015; Oldekop et al., 2016; Plummer and Fennell, 2009).

Because our data are cross-sectional, we cannot fully disentangle complex causal loops. Nevertheless, we feel our models capture the dominant interrelationships and lay the groundwork for further research. We have used an information theoretic approach to calculate the average of top models among the set of models. These models assume a linear in the logs functional form and specify no interactions of the form that allow effects to differ across subgroups in our data. But we note that results are fairly robust with regard to such specification errors—nearly half the cases would have to be invalidated to change our most important inferences and it seems unlikely that we have missed a predictor variable that has such a powerful influence. Of course, further work is required to overcome a lack of global biodiversity data. Although species richness is a crucial factor of nature-based tourism in PAs (Arbieu et al., 2017; Hausmann et al., 2017a; Siikamäki et al., 2015), the relationship of other aspects of biodiversity (e.g., evenness and abundance) to nature-based tourism in PAs warrants attention (Graves et al., 2017; Siikamäki et al., 2015).

Further research might fruitfully examine more complex causal feedbacks that we have been able to estimate. For example, it may be that higher biodiversity PAs are given more protective management strategies or that there is some feedback from high visitation rates to an emphasis on biodiversity protection policies. We also note that although we have used a well-accepted standard international classification of PA management strategies, we lack data that would allow for detailed comparisons of management strategies (e.g., targeted species, budgets for tourism). In particular, PAs in high-income countries may have better accessibility with larger budgets for tourist infrastructures (e.g., visitor centers, roads within PAs and campgrounds). The causal feedbacks can be complex. For instance, tourist infrastructure can increase the visitor numbers, but construction of tourist facilities, the footprint of the facilities and increased traffic can all be a threat to biodiversity (Daniel et al., 2012).

Several strategies would allow further research to expand on our analyses. There are ongoing efforts for improving global data sets by using social media (Hausmann et al., 2017b; Willemen et al., 2015) and developing global database of protected areas including visitor counts and biodiversity (Dubois et al., 2016; Schägner et al., 2017). These could all allow for more refined analyses. Data over time deployed as a panel would allow for stronger causal inference. And detailed comparative case studies would allow a better understanding of how processes that link tourism, biodiversity and management strategy co-evolve.

4.2. Management implications

ES supply and demand change over temporal and spatial scales (Burkhard et al., 2014; Renard et al., 2015) and so do the interactions between biodiversity and nature-based tourism. Further, these changes are very context specific. It follows that effective plans for biodiversity protection would benefit from local community participation (Kovács et al., 2015; Liu et al., 2007; Pleasant et al., 2014). For example, with the rapid increases of human population and income in many parts of the globe, human demands for food have increased pressure on ecosystems including those in the buffer zone (Tilman and Clark, 2014). The increased human demands have caused unsustainable extraction of natural resources and biodiversity loss in many places (Liu et al., 2016b; Rands et al., 2010). We find PAs managed with mixed uses have higher agricultural yields in the buffer zones than those managed primarily for biodiversity conservation, while the proportion of agricultural areas in the buffer zones does not differ significantly across management strategies (Fig. 2B and C). Population density surrounding PAs managed for mixed uses is also higher than those managed primarily for biodiversity conservation (Fig. 2A). PAs managed primarily for biodiversity conservation have higher biodiversity and more water supply as well as lower anthropogenic pressures than those managed for mixed uses. Since anthropogenic pressures in the buffer zones mainly arise from the population density, land suitability for agriculture (e.g., slope, fertility and climate) and the demand for food production with urban development, these pressures could be reduced by more sustainable agricultural activities (Foley et al., 2011).

Because much of the demand for tourism comes from areas distant from PAs, applying integrated conceptual frameworks such as telecoupling (socioeconomic and environmental interactions over distances) can help develop a more holistic and refined analysis of changes in tourism supply and demand and their impacts on biodiversity over various temporal and spatial scales (Liu et al., 2013; Liu et al., 2016a). From the perspective of the telecoupling framework, nature-based tourism is a telecoupled system with complex interactions among local biodiversity, regional to global origins of nature-based tourism, international networks discussing and advocating management strategies for PAs and global changes in the supply and demand for ES (Liu et al., 2015a,b). Disentangling these influences will require careful analysis of their dynamics over time. Here we have taken a first step by examining, in particular, how biodiversity, management strategy and the characteristics of the buffer zone surrounding a PA influences tourism and in turn how the buffer zone and management influence biodiversity.

Acknowledgements

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Appendix A

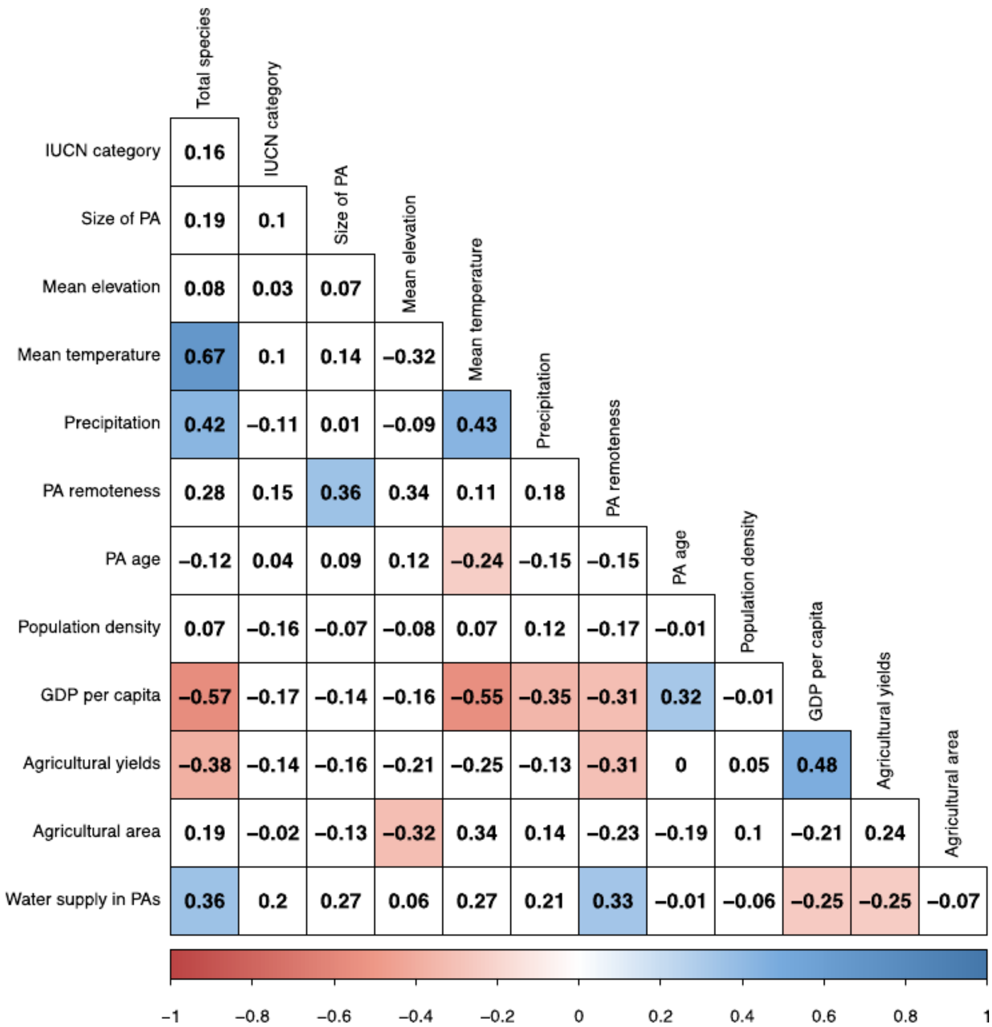

Fig. A1. The Pearson's correlation matrix for the independent variables. Blue indicates positive correlation for a given pair, and red indicates negative correlation. Colored correlation coefficients are significant at the $p = 0.05$ level. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table A.1
The descriptions of dependent and independent variables.

	Variable	Dataset	Unit of Measure	Time Period	Spatial Extent	References	Link
Nature-based Tourism	PAs visitor numbers	Annual visitation data for PAs	person	2000–2014	Global	Balmford et al. (2015), National Statistics, Gray literatures	http://journals.plos.org/plosbiology/article?id=https://doi.org//10.1371/journal.pbio.1002074
Demographic	Population	LandScan	person (30arc second ~ 1 km^2)	2002–2012	Global, raster	Bright et al. (2013)	http://web.ornl.gov/sci/landscan
Biodiversity	The number of species	Birds, Mammals, Amphibians	species	2000s	Global, raster	Pimm et al. (2014)	http://biodiversitymapping.org
Agricultural factor	Agricultural Yields	Yields for 175 crops	tonne/km^2 (5arc minute ~ 10 km^2)	2000	Global, raster	Monfreda et al. (2008)	http://www.earthstat.org/data-download
	Agricultural area	Cultivated and managed vegetation area	proportion (0–100, 30arc second ~ 1 km^2)	the early 2000s	Global, raster	Tuanmu and Jetz (2014)	http://www.earthenv.org/landcover.html
Regulating ES	Upstream Protected Land	% total water supply originated in protected land	% of total water supply originated in PAs	2000s	Global, watershed	WRI (2015)	http://www.wri.org/resources/data-sets/aqueduct-global-maps-21-data
Economic	Income level	GDP per capita	2005 USD const.	2000–2014	Country level	United Nations Statistics Division (2015)	http://data.un.org
Protected Area	PAs management status	IUCN PAs management category	Category, II–VI	2014	Global	IUCN and UNEP-WCMC (2017)	http://www.protectedplanet.net
	PAs age	Subtraction of PAs establishment year from 2014	year	2014	Global	IUCN and UNEP-WCMC (2017)	http://www.protectedplanet.net
	Size of PAs	PAs areas	square kilometers	2014	Global	IUCN and UNEP-WCMC (2017)	http://www.protectedplanet.net
	Elevation	Global Multi-resolution Terrain Elevation (GMTED 2010)	Elevation (30arc second ~ 1 km^2)	2010	Global, raster	EROS Data Center (2015)	http://earthexplorer.usgs.gov https://lta.cr.usgs.gov/GMTED2010
	Temperature	Annual mean temperature	°C (30 arc second ~ 1 km^2)	1950–2000	Global, raster	Hijmans et al. (2005)	http://www.worldclim.org
	Precipitation	Annual mean precipitation	millimeter (30 arc second ~ 1 km^2)	1950–2000	Global, raster	Hijmans et al. (2005)	http://www.worldclim.org
	PAs remoteness from major cities (> 50,000)	Travel time to major cities: A global map of Accessibility	Time (minutes) (30 arc second ~ 1 km^2)	2000	Global, raster	Nelson (2008)	http://forobs.jrc.ec.europa.eu/products/gam/download.php

Table A.2
List of PAs (N = 929).

Africa (N = 90)	
Cameroon	Mbam et Djerem (II), Nki (II), Waza (II)
Republic of the Congo	Nouabale-Ndoki (II)
Ethiopia	Bale Mountains (II)
Ghana	Bomfobiri (IV), Bui (II), Digya (II), Gbele (VI), Kakum (II), Kalakpa (VI), Mole (II), Owabi (IV), Shai Hills (VI)
Kenya	Aberdare (II), Amboseli (II), Arabuko Sokoke (II), Hell's Gate (II), Lake Bogoria (II), Lake Nakuru (II), Longonot (II), Meru (II), Mount Kenya (II), Nairobi (II), Samburu (II), Shimba Hills (II), Tsavo East (II), Tsavo West (II)
Madagascar	Analamerana (IV), Montagne d'Ambre (II)
Namibia	Ai-Ais Hot Springs (II), Cape Cross Seal Reserve (IV), Daan Viljoen Game Park (II), Etosha (II), Gross Barmen Hot Springs (III), Hardap Recreation Resort (V), Khaudum (II), Mangetti (II), Mudumu (II), Nkasa Rupara (II), Popa Game Park (III), Skeleton Coast Park (II), Von Bach Recreation Resort (V), Waterberg Plateau Park (II)
Rwanda	Akagera (II), Nyungwe (IV), Volcans (II)
Tanzania	Arusha (II), Gombe (II), Katavi (II), Kilimanjaro (II), Kitulo (II), Lake Manyara (II), Mahale (II), Mikumi (II), Mkomazi (IV), Ruaha (II), Rubondo (II), Selous (IV), Serengeti (II), Tarangire (II), Udzungwa Mountains (II)
Uganda	Bwindi Impenetrable (II), Katonga (III), Kidepo Valley (II), Lake Mburo (II), Mgahinga Gorilla (II), Mount Elgon (II), Murchison Falls (II), Queen Elizabeth (II), Rwenzori Mountains (II), Semuliki (II)
South Africa	Agulhas National Park (II), Augrabies Falls National Park (II), Bontebok National Park (II), Golden Gate Highlands National Park (II), Kalahari Gemsbok National Park (II), Karoo National Park (II), Kruger National Park (II), Mapungupwe National Park (II), Marakele National Park (II), Mokala National Park (II), Mountain Zebra National Park (II), Namaqua National Park (II), Richtersveld National Park (II), Table Mountain National Park (II), Tankwa-Karoo National Park (II), Vaalbos National Park (II)
Zambia	Kasanka (II), Lavushi Manda (II)
Asia and Oceania (N = 351)	
UAE	Dubai Desert Conservation Reserve (II)
Australia	Ben Lomond (II), Douglas-Apsley (II), Hartz Mountains (II), Hastings Caves (III), Kakadu National Park (II), Mole Creek Karst (II), Moreton Island (II), Mount Field (II), Purnululu (II), Uluru-Kata Tjuta National Park (II)
China	Dafengmilu (Jiangsu) (V), Huanglongsi (V), Jiuzhaigou (V), Wolong (V), Wuyishan (V)
Indonesia	Alas Purwo (II), Baning (V), Bantimurung Bulusaraung (II), Batang Gadis (II), Batu Angus (V), Batu Putih (V), Berbak (II), Betung Kerihun (II), Bogani Nani Wartabone (II), Bromo Tengger Semeru (II), Bukit Baka - Bukit Raya (II), Bukit Barisan Selatan (II), Bukit Dua Belas (II), Bukit Kaba (V), Bukit Serelo (V), Bukit Tiga Puluh (II), Bunder (VI), Camplong (V), Cani Sirenreng (V), Carita (VI), Cimanggu (V), D. Sicikeh-cikeh (V), Danau Matano (V), Danau Sentarum (II), Grojogan Sewu (V), Gunung Baung (V), Gunung Ciremai (II), Gunung Gede - Pangrango (II), Gunung Guntur (V), Gunung Halimun - Salak (II), Gunung Kelam (V), Gunung Leuser (II), Gunung Meja (V), Gunung Merapi (II), Gunung Merbabu (II), Gunung Palung (II), Gunung Pancar (V), Gunung Rinjani (II), Gunung Tampomas (V), Holiday Resort (V), Jember (V), Kawah Ijen (V), Kawah Kamojang (V), Kayan Mentarang (II), Kelimutu (II), Kerandangan (V), Kerinci Seblat (II), Klamono (V), Kutai (II), Laiwangi Wanggameti (II), Lejja (V), Lore Lindu (II), Madapangga (V), Malino (V), Mangolo (V), Manupeu Tanadaru (II), Manusela (II), Meru Betiri (II), Minas (Sultan Sarif Hasyim) (VI), Muka Kuning (V), Nanggala III (V), Papandayan (V), Pulau Kembang (V), Punti Kayu (V), Rawa Aopa Watumohai (II), Rimbo Panti (V), Ruteng (V), Sebangau (II), Seblat (V), Semongkat (V), Siberut (II), Sidrap (V), Sorong (V), Sultan Adam (VI), Suranadi (V), Tahura Ir. H. Juanda (VI), Talaga Bodas (V), Telaga Patengan (V), Telogo Warno Pengilon (V), Tesso Nilo (II), Tretes (V), Way Kambas (II)
India	Bandhavgarh (II), Bandipur (II), Bhadra (IV), Corbett (II), Jaldapara (IV), Kalakad (IV), Kanha (II), Kaziranga (II), Ken Gharial (IV), Melghat (IV), Mudumalai (IV), Panna (II), Pench (II), Periyar (IV), Rajiv Gandhi (Nagarhole) (II), Ranthambhore (II), Sariska (IV), Satpura (II), Valley Of Flowers (II)
Japan	Aichikogen (V), Akan (II), Akiyoshidai (V), Aso kuju (V), Bandai asahi (II), Biwako (V), Chichibu tama kai (V), Chubusangaku (II), Daisetsuzan (II), Echigosanzan-Tadami (II), Hakusan (II), Hayachine (II), Hiba-Dogo-Taishaku (V), Hida-Kisogawa (V), Hyonosen-Ushiroyama-Nagisan (V), Ibi-Sekigahara-Yoro (V), Iriomote (IV), Ishizuchi (V), Kitakyushu (V), Kongo-Ikoma-Kisen (V), Koya-Ryujin (V), Kurikoma (II), Kushiroshitsugen (II), Kyushuchuosanchi (V), Meiji Memorial Forest Minoo (V), Meiji Memorial Forest Takao (V), Minami alps (II), Muroo-Akame-Aoyama (V), Myogi-Arafune-Sakukogen (V), Nikko (V), Nishichugokusanchi (V), Onuma (V), Shikotsu toya (II), Shiretoko (IV), Sobo-Katamuki (V), Suzuka (V), Tanzawa-Oyama (V), Tenryu-Okumikawa (V), Towada hachimantai (II), Tsurugisan (V), Yaba-Hita-Hikosan (V), Yamato-Aogaki (V), Yatsugatake-Chushinkogen (V), Zao (V)
South Korea	Biseulsan County Park (V), Bogyeongsa County Park (V), Bongmyeongsan County Park (V), Bukhansan (V), Bullyeonggyegok County Park (V), Cheongnyangsan Provincial Park (V), Cheongwansan Provincial Park (V), Cheonmasan County Park (V), Chiaksan (II), Chilgapsan Provincial Park (V), Daedunsan Provincial Park (V), Daeiri County Park (V), Deogyusan (V), Duryunsan Provincial Park (V), Gajisan Provincial Park (V), Gangcheonsan County Park (V), Gayasan (II), Geumosan Provincial Park (V), Gibaeksan County Park (V), Gobok Provincial Park (V), Gwangyang Baegunsan (IV), Gyoungpo Provincial Park (V), Hwangmaesan County Park (V), Hwawangsan County Park (V), Ipgok County Park (V), Jangansan County Park (V), Jirisan (II), Juwangsan (II), Maisan Provincial Park (V), Moaksan Provincial Park (V), Mungyeongsaejae Provincial Park (V), Myeongjisan County Park (V), Naejangsan (II), Naksan Provincial Park (V), Namhansanseong Provincial Park (V), Odaesan (II), Sangnim Woods in Hamyang (IV), Seonunsan Provincial Park (V), Seoraksan (II), Sobaeksan (II), Songnisan (II), Taebaeksan Provincial Park (V), Unmunsan County Park (V), Upo Wetland (IV), Valley of Bulyeongsa Temple in Uljin (V), Wolchulsan (II), Woraksan (II)
Sri Lanka	Bundala (II), Gal Oya (II), Galway's Land (IV), Horton Plains (II), Kaudulla (II), Lahugala (II), Lunugamwehera (II), Maduru Oya (II), Minneriya (II), Uda Walawe (II), Wasgamuwa (II), Wilpattu (II), Yala East (Kumana) (II)
Malaysia	Batang Ai (II), Endau Rompin (Johor) (II), Gunong Gading (II), Kubah (II), Lambir Hills (II), Loagan Bunut (II), Niah (II), Taman Negara (II), Tanjong Datu (II), Tawau Hill Park (II)
Nepal	Annapurna (VI), Api - Nampa (VI), Bardia (II), Chitwan (II), Dhorpatan (VI), Gauri-Shankar (VI), Kanchanjunga (VI), Khaptad (II), Koshi Tappu (IV), Krishnasar (VI), Langtang (II), Makalu-Barun (II), Manaslu (VI), Parsa (IV), Rara (II), Shey-Phoksundo (II), Shivapuri-Nagarjun (II), Suklaphanta (IV)
New Zealand	Abel Tasman (II)
Philippines	Mount Kitanglad Range (II), Mt. Pulag National Park (II), Puerto Princesa Subterranean River (III)
Thailand	Bang Lang (II), Budo-Sungai Padi (II), Chae Son (II), Chalearm Rattanakosin (II), Doi Inthanon (II), Doi Khuntan (II), Doi Luang (II), Doi Phaklong (II), Doi Phukha (II), Doi Suthep-Pui (II), Erawan (II), Huai Nam Dang (II), Kaeng Krung (II), Kaeng Tana (II), Kaengkrachan Forest Complex (II), Khao Chamao-Khao Wong (II), Khao Khitchakut (II), Khao Laem (II), Khao Luang (II), Khao Nam Khang (II), Khao Nan (II), Khao Phanom Bencha (II), Khao Phravihan (II), Khao Pu - Khao Ya (II), Khao Sib Ha Chan (II), Khao Sok (II), Khao Yai (II), Khlong Lamngu (II), Khlong Lan (II), Khlong Wang Chao (II), Khuen Si Nakarin (II), Khun Chae (II), Khun Pra Vor (II), Klong Phanom (II), Kuiburi (II), Lansaang (II), Mae Charim (II), Mae Moei (II), Mae Phang (II), Mae Ping (II), Mae Puem (II), Mae Wa (II), Mae Wang (II), Mae Wong (II), Mae Yom (II), Mukdahan (II), Nam Nao (II), Nam Phong (II), Namtok Chat Trakan (II), Namtok Huai Yang (II), Namtok Klong Kaew (II), Namtok Mae Surin (II), Namtok Ngao (II), Namtok Phleiw (II), Namtok Sai Khao (II), Namtok Si khid (II), Namtok Yong (II), Ob Luang (II), Pa Hin Ngam (II), Pang Sida (II), Pha Tam (II), Phu Chong - Na Yoi (II), Phu Hin Rong Kla (II), Phu Kao - Phu Phan Kham (II), Phu Kradueng (II), Phu Lan Ka (II), Phu Langka (II), Phu Pa - Yol (Huai Huat) (II), Phu Pha Lek (II), Phu Pha Man (II), Phu Phan (II), Phu Rua (II), Phu Sa Dokbua (II), Phu Soi Dao (II), Phu Toei (II), Phu Wiang (II), Phu Zang (II), Ramkamhaeng (II), Sai Thong (II), Sai Yok (II), Salawin (II), Si Nan (II), Si Phangnga (II), Sri Lanna (II), Sri Satchanalai (II), Ta Phraya (II), Taad Moak (II), Taad Ton (II), Tai Romyen (II), Taksin Maharat (II), Thaleban (II), Tham Pla - Pha Seu (II), Thap Lan (II), Thong Pha Phum (II), Thung Salaeng Luang (II), Wiang Kosai (II)

(*continued on next page*)

Table A.2 (*continued*)

Vietnam	Cuc Phuong (II), Phong Nha-Ke Bang (II)
Europe (*N* = 215)	
Bulgaria	Centralen Balkan (II), Vitosha (V)
Czech Republic	Česke Švycarsko (II), Krkonošsky narodni park (V), Šumava (II)
Spain	Aiguestortes i Estany de Sant Maurici (II), Cabaneros (II), Donana (II), El Teide (II), Garajonay (II), La Caldera de Taburiente (II), Ordesa y Monte Perdido (II), Parque Nacional de Timanfaya (II), Picos de Europa (II), Sierra Nevada (II), Tablas de Daimiel (II)
Finland	Helvetinjarven kansallispuisto (II), Hiidenportin kansallispuisto (II), Isojarven kansallispuisto (II), Kauhanevan-Pohjankankaan kansallispuisto (II), Kolin kansallispuisto (II), Koloveden kansallispuisto (II), Kurjenrahkan kansallispuisto (II), Lauhanvuoren kansallispuisto (II), Leivonmaen kansallispuisto (II), Liesjarven kansallispuisto (II), Linnansaaren kansallispuisto (II), Nuuksion kansallispuisto (II), Paijanteen kansallispuisto (II), Patvinsuon kansallispuisto (II), Petkeljarven kansallispuisto (II), Puurijarven ja Isonsuon kansallispuisto (II), Pyha-Hakin kansallispuisto (II), Repoveden kansallispuisto (II), Rokuan kansallispuisto (II), Salamajarven kansallispuisto (II), Seitsemisen kansallispuisto (II), Sipoonkorven kansallispuisto (II), Tiilikkajarven kansallispuisto (II), Torronsuon kansallispuisto (II), Valkmusan kansallispuisto (II)
France	Causses du Quercy (V), La Narbonnaise en Mediterranee (V), Volcans d'Auvergne (V)
UK	Arundel Park (IV), Attenborough Gravel Pits (IV), Aylesbeare Common (IV), Berney Marshes & Breydon Water (IV), Blean Woods (IV), Brampton Wood (IV), Brandon Marsh (IV), Brecon Beacons (V), Broads (V), Cairngorms (V), Castle Eden Dene (IV), Clifton Country Park (IV), Clumber Park (V), Coombe Valley Woods (IV), Danbury and Lingwood Commons (V), Dartmoor (V), Dungeness (IV), Elmley (IV), Epping Forest (IV), Exe Estuary (IV), Exmoor (V), Fairburn Ings (IV), Fowlmere (IV), Frampton Pools (IV), Gamlingay Wood (IV), Garston Wood (IV), Geltsdale (IV), Gibside (V), Ham Wall (IV), Havergate Island & Boyton Marshes (IV), Haweswater (IV), Hodbarrow (IV), Ken-Dee Marshes (IV), Lake District (V), Leighton Moss (IV), Loch Lomond and The Trossachs (V), Lochwinnoch (IV), Marshside (IV), Mere Sands Wood (IV), Mid Yare Valley (IV), Minsmere (IV), Nagshead (IV), Nene Washes (IV), New Forest (V), North Warren (IV), North York Moors (V), Northumberland (V), Northward Hill (IV), Oare Marshes (IV), Ogden Water (IV), Orford Ness (V), Otmoor (IV), Ouse Washes (IV), Parndon Woods & Common (IV), Peak District (V), Pembrokeshire Coast (V), Poole's Cavern and Grin Low Wood (IV), Pulborough Brooks (IV), Queenswood (IV), Radipole Lake (IV), Rye Meads (IV), Sherwood Forest (IV), Snettisham Carstone Quarry (IV), Snowdonia (V), South Downs (V), The Lodge (IV), Titchfield Haven (IV), Titchmarsh (IV), Tudeley Woods (IV), West Sedgemoor (IV), Wolves Wood Reserves (IV), Wood Of Cree (IV), Yorkshire Dales (V)
Croatia	Krka (II), Paklenica (II), Plitvicka jezera (II), Risnjak (II), Sjeverni Velebit (II)
Hungary	Aggteleki (II), Balaton-felvideki (V), Bukki (II), Duna-Drava (V), Duna-Ipoly (V), Ferto-Hansagi (II), Hortobagyi (II), Kiskunsagi (II), Koros-Maros (V), Orsegi (V)
Italy	Parco nazionale dei Monti Sibillini (II), Parco regionale La Mandria (V)
Poland	Babiogorski Park Narodowy (II), Białowieski Park Narodowy (II), Biebrzański Park Narodowy (II), Bieszczadzki Park Narodowy (II), Drawieński Park Narodowy (II), Gorczański Park Narodowy (II), Kampinoski Park Narodowy (II), Karkonoski Park Narodowy (II), Łomżyński Park Krajobrazowy Doliny Narwi (V), Magurski Park Narodowy (II), Narwiański Park Narodowy (II), Ojcowski Park Narodowy (V), Park Narodowy “Bory Tucholskie” (II), Park Narodowy “Ujście Warty” (II), Park Narodowy Gor Stołowych (II), Pieniński Park Narodowy (II), Poleski Park Narodowy (II), Roztoczański Park Narodowy (II), Świętokrzyski Park Narodowy (II), Tatrzański Park Narodowy (II), Wielkopolski Park Narodowy (II), Wigierski Park Narodowy (V)
Portugal	Alvao (V), Arriba Fossil da Costa da Caparica (V), Douro Internacional (V), Estuario do Sado (IV), Estuario do Tejo (IV), Montesinho (V), Paul de Arzila (IV), Paul do Boquilobo (IV), Peneda-Geres (II), Ria Formosa (V), Sapal de Castro Marim e Vila Real de Santo Antonio (IV), Serra da Estrela (V), Serra da Malcata (IV), Serra de Sao Mamede (V), Serra do Acor (V), Serras de Aire e Candeeiros (V), Sintra-Cascais (V), Tejo Internacional (V), Vale do Guadiana (V)
Romania	Balta Mica a Brailei (V), Bucegi (V), Buila - Vanturarita (II), Calimani (II), Ceahlau (II), Cheile Bicazului - Hasmas (II), Cheile Nerei - Beusnita (II), Comana (V), Cozia (II), Defileul Jiului (II), Domogled - Valea Cernei (II), Geoparcul Dinozaurilor Tara Hategului (V), Geoparcul Platoul Mehedinti (V), Gradistea Muncelului - Cioclovina (V), Lunca Joasa a Prutului Inferior (V), Lunca Muresului (V), Muntii Apuseni (V), Muntii Macinului (II), Muntii Maramuresului (V), Piatra Craiului (II), Portile de Fier (V), Putna - Vrancea (V), Retezat (II), Rodna (II), Semenic - Cheile Carasului (II), Vanatori Neamt (V)
Russia	Kenozersky (II)
Slovakia	Biele Karpaty (V), Cerova vrchovina (V), Horna Orava (V), Kysuce (V), Mala Fatra (II), Muranska planina (II), Pieninsky (II), Polana (V), Poloniny (V), Slovensky raj (II), Stiavnicke vrchy (V), Strazovske vrchy (V), Tatransky (II)
Central and South America (*N* = 155)	
Argentina	Baritu (II), Bosques Petrificados (III), Calilegua (II), Campo de los Alisos (II), Chaco (II), El Leoncito (II), El Palmar (II), El Rey (II), Iguazu (II), Lago Puelo (II), Laguna Blanca (II), Laguna de los Pozuelos (III), Lanin (II), Lihue Calel (II), Los Alerces (II), Los Cardones (II), Los Glaciares (II), Mburucuya (II), Nahuel Huapi (II), Perito Moreno (II), Pre-Delta (II), Quebrada del Condorito (II), Rio Pilcomayo (II), San Guillermo (II), Sierra de las Quijadas (II), Talampaya (II)
Belize	Bermudian Landing Community Baboon Sanctuary (IV)
Bolivia	Eduardo Avaroa (IV), Madidi (II), Noel Kempff Mercado (II)
Brazil	Area De Protecao Ambiental Da Chapada Dos Guimaraes (V), Floresta Nacional De Brasilia (VI), Parque Nacional Da Chapada Dos Veadeiros (II), Parque Nacional Da Serra Da Canastra (II), Parque Nacional Da Serra Da Capivara (II), Parque Nacional Da Serra Da Cipo (II), Parque Nacional Da Serra Do Divisor (II), Parque Nacional Da Serra Dos Orgaos (II), Parque Nacional Da Tijuca (II), Parque Nacional Das Emas (II), Parque Nacional De Aparados Da Serra (II), Parque Nacional De Caparao (II), Parque Nacional De Sete Cidades (II), Parque Nacional De Ubajara (II), Parque Nacional Do Itatiaia (II), Parque Nacional Serra Das Confusoes (II)
Chile	Alerce Andino (II), Alerce Costero (III), Alto Biobio (IV), Altos de Lircay (IV), Altos de Pemehue (IV), Bellotos El Melado (IV), Bosque Fray Jorge (II), Cerro Castillo (IV), Cerro Nielol (III), Chiloe (II), Conguillio (II), Contulmo (III), Coyhaique (IV), Cueva Del Milodon (III), Dos Lagunas (III), El Morado (III), El Yali (IV), Federico Albert (IV), Futaleufu (IV), Hornopiren (II), Huemules de Niblinto (IV), Huerquehue (II), La Campana (II), Lago Cochrane (IV), Lago Jeinemeni (IV), Lago Las Torres (IV), Lago Penuelas (IV), Laguna del Laja (II), Laguna El Peral (IV), Laguna Parrillar (IV), Laguna Torca (IV), Lahuen Nadi (III), Las Chinchillas (IV), Las Vicunas (IV), Lauca (II), Llanos del Challe (II), Llanquihue (IV), Los Flamencos (IV), Los Queules (IV), Los Ruiles (IV), Magallanes (IV), Malalcahuello (IV), Malleco (IV), Mocho - Choshuenco (IV), Nahuelbuta (II), Nalcas (IV), Nevado Tres Cruces (II), Nuble (IV), Pali Aike (II), Pampa del Tamarugal (IV), Pan De Azucar (II), Pichasca (III), Puyehue (II), Queulat (II), Radal Siete Tazas (IV), Ralco (IV), Rio Clarillo (IV), Rio Los Cipreses (IV), Rio Simpsom (IV), Robleria Cobre Loncha (IV), Salar De Surire (III), Tolhuaca (II), Torres del Paine (II), Vicente Perez Rosales (II), Villarrica (II), Volcan Isluga (II), Yerba Loca (IV)
Costa Rica	Arenal (II), Bahia Junquillal (estatal) (IV), Barbilla (II), Barra del Colorado (mixto) (IV), Barra Honda (II), Braulio Carrillo (II), Cano Negro (mixto) (IV), Carara (II), Chirripo (II), Golfito (mixto) (IV), Grecia (VI), Guanacaste (II), Iguanita (estatal) (IV), Internacional La Amistad (II), Juan Castro Blanco (II), Las Tablas (VI), Los Santos (VI), Mata Redonda (estatal) (IV), Palo Verde (II), Rincon de la Vieja (II), Rio Macho (VI), Taboga (VI), Volcan Irazu (II), Volcan Poas (II), Volcan Tenorio (II)
Equador	Cajas (II), Cayambe Coca (VI), Chimborazo (IV), Cotacachi Cayapas (VI), Cotopaxi (II), Cuyabeno (VI), El Boliche (V), Limoncocha (VI), Llanganates (II), Parque Lago (V), Podocarpus (II), Sangay (II), Sumaco Napo-Galeras (II), Yacuri (II), Yasuni (II)
Peru	Bahuaja Sonene (II), Calipuy (III)
North America (*N* = 118)	
Canada	Bruce Peninsula National Park of Canada (II), Cape Breton Highlands National Park of Canada (II), Elk Island National Park of Canada (II), Fathom Five National Marine Park of Canada (VI), Fundy National Park of Canada (II), Georgian Bay Islands National Park of Canada (II), Grasslands (III), Gros Morne National Park of Canada (II), Gwaii Haanas National Park Reserve and Haida Heritage site (II), Kejimkujik National Park and National Historic site of Canada (II), Mount Revelstoke National Park of Canada (II), Parc National du Canada de la Mauricie (II), Point Pelee National Park of Canada (II), Prince Edward Island National Park of Canada (II), Pukaskwa National Park of Canada (II), Reserve de Parc National du Canada de l'Archipel-de-Mingan

(*continued on next page*)

Table A.2 (*continued*)

	(II), Riding Mountain National Park of Canada (II), Terra Nova National Park of Canada (II), Thousand Islands National Park of Canada (II), Waterton Lakes National Park of Canada (II)
USA	Acadia (IV), Agate Fossil Beds (V), Alibates Flint Quarries (V), Allegheny Portage Railroad (II), Aniakchak (V), Apostle Islands (V), Arches (II), Badlands (II), Bandelier (V), Big Bend (II), Big Thicket (V), Black Canyon of the Gunnison (II), Bluestone (V), Bryce Canyon (II), Canyonlands (II), Capitol Reef (II), Carlsbad Caverns (II), Casa Grande Ruins (V), Catoctin Mountain (II), Cedar Breaks (III), Chiricahua (V), City of Rocks (V), Colorado (III), Congaree (II), Coronado (III), Cowpens (III), Crater Lake (II), Craters of the Moon (III), Cumberland Gap (III), Cuyahoga Valley (II), Death Valley (II), Dinosaur (III), El Malpais (III), El Morro (V), Fort Bowie (III), Fort Pulaski (V), Fort Union Trading Post (III), Fort Washington (V), Gila Cliff Dwellings (V), Glacier (II), Grand Canyon (II), Grand Portage (V), Grand Teton (II), Great Basin (II), Great Sand Dunes (II), Great Smoky Mountains (II), Guadalupe Mountains (II), Hovenweep (V), Indiana Dunes (V), Jean Lafitte National Historical Park and Preserve, Barataria (V), Jewel Cave (V), John Day Fossil Beds (III), Johnstown Flood (III), Joshua Tree (II), Katmai (II), Kenai Fjords (II), Kings Canyon / Sequoia (II), Klondike Gold Rush (V), Lake Chelan (V), Lake Mead (V), Lava Beds (III), Little Bighorn Battlefield (V), Mammoth Cave (II), Mesa Verde (II), Missouri (V), Mojave (V), Montezuma Castle (V), Mount Rainier (II), Mount Rushmore (V), Natural Bridges (III), Niobrara (V), North Cascades (II), Olympic (II), Oregon Caves (V), Organ Pipe Cactus (III), Ozark (V), Pecos (V), Pictured Rocks (V), Pipe Spring (V), Rio Grande (V), Ross Lake (V), Saguaro (II), Santa Monica Mountains (V), Scotts Bluff (V), Shenandoah (II), Sleeping Bear Dunes (V), Theodore Roosevelt (II), Theodore Roosevelt Island (II), Timpanogos Cave (V), Tonto (V), Tumacacori (V), Tuzigoot (V), Voyageurs (II), Washington Monument (V), White Sands (V), Wupatki (III), Yosemite (II), Zion (II)

(in parentheses) IUCN management categories.

Table A.3
Variance Inflation Factor (VIF) for variables used in linear regression.

Category	Variable	VIF
Biodiversity	Total species (species)	3.244
Protected Area	IUCN category (I–IV = 1)	1.244
	Size of PA (km^2)	1.734
	Mean elevation (meter)	1.763
	Annual mean temperature (°C)	2.507
	Annual precipitation (mm)	1.908
	PA remoteness (minutes)	3.625
	PA age (year)	1.262
Demographic	Population density[§] (persons/km^2)	3.373
Economic	GDP per capita[¶] (2005 const. $ per capita)	3.690
Agricultural factor	Agricultural yields[§] (tonne/km^2)	1.440
	Agricultural area[§] (%)	2.635
Regulating ES	Water supply originated in PAs (%)	1.344
Region	Africa	2.699
	Europe	2.035
	North America	3.193
	Latin America	2.351

§ 10-km buffer zone.
¶ Country level data, not PAs level.

Table A.4
Unstandardized coefficients from multiple regression model predicting annual visitor numbers except biodiversity and total species in PAs.

Category	Variable	Annual visitors	Total species
Biodiversity	Total species (species)	–	–
Protected Area	IUCN category (II–IV = 1)	0.392* (0.168)	0.052* (0.023)
	Size of PA (km^2)	0.316** (0.040)	0.008 (0.006)
	Mean elevation (meter)	0.362** (0.058)	0.035** (0.008)
	Annual mean temperature (°C)	−0.132 (0.148)	0.289** (0.020)
	Annual precipitation (mm)	−0.329* (0.111)	0.178** (0.015)
	PA remoteness (minutes)	−0.225* (0.113)	0.018 (0.016)
	PA age (year)	0.651** (0.118)	−0.013 (0.016)
Demographic	Population density[§] (persons/km^2)	0.447** (0.066)	−0.0002 (0.009)
Economic	GDP per capita[¶] (2005 const. $ per capita)	1.176** (0.085)	−0.104** (0.012)
Agricultural factor	Agricultural yields[§] (tonne/km^2)	0.076 (0.063)	−0.020* (0.009)
	Agricultural area[§] (%)	0.077 (0.091)	0.058** (0.013)
Regulating ES	Water supply originated in PAs (%)	0.059 (0.081)	0.060** (0.011)
Region	Asia and Oceania	1.894** (0.227)	0.044 (0.031)
	Africa	1.232** (0.315)	0.306** (0.044)
	Europe	0.756* (0.283)	0.113* (0.039)
	North America	1.529** (0.297)	0.357** (0.041)
Intercept		−6.251**	3.978**
R^2		0.470	0.692
F-statistic		50.61	127.9
DF		912	912

*$P < 0.05$, **$P < 0.001$.
Values in parentheses are standard errors.
§ 10-km buffer zone.
¶ Country level data, not PAs level.

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