

Current Biology

The synergy between protected area effectiveness and economic growth

Highlights

- Protected areas do not limit nighttime increases in neighboring communities
- Half of protected areas show synergy: conservation effectiveness and local development
- Synergy differs between biomes, continents, and countries
- Socioeconomic drivers and protected area size are the best predictors of synergy

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In brief

Protected areas are key to biodiversity conservation but are often treated as obstacles to local development. Li et al. use evidence from 10,143 protected areas to understand if there is compatibility between protected area effectiveness and economic development in neighboring communities and, if so, what factors drive such compatibility.

Article

The synergy between protected area effectiveness and economic growth

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SUMMARY

Protected areas conserve biodiversity and ecosystem functions but might impede local economic growth. Understanding the global patterns and predictors of different relationships between protected area effectiveness and neighboring community economic growth can inform better implementation of the Kunming-Montreal Global Biodiversity Framework. We assessed 10,143 protected areas globally with matched samples to address the non-random location of protected areas. Our results show that protected areas resist human-induced land cover changes and do not limit nighttime increases in neighboring settlements. This result is robust, using different matching techniques, parameter settings, and selection of covariates. We identify four types of relationships between land cover changes and nighttime changes for each protected area: “synergy,” “retreat,” and two tradeoff relationships. About half of the protected areas (47.5%) retain their natural land cover and do so despite an increase of nightlights in the neighboring communities. This synergy relationship is the most common globally but varies between biomes and continents. Synergy is less frequent in the Amazon, Southeast Asia, and some developing areas, where most biodiversity resides and which suffer more from poverty. Smaller protected areas and those with better access to cities, moderate road density, and better baseline economic conditions have a higher probability of reaching synergy. Our results are promising, as the expansion of protected areas and increased species protection will rely more on conserving the human-modified landscape with smaller protected areas. Future interventions should address local development and biodiversity conservation together to achieve more co-benefits.

INTRODUCTION

The Kunming-Montreal Global Biodiversity Framework, finalized in 2022, aims to expand protection to at least 30% for both the land and the sea (Target 3).¹ Knowing where and how to protect areas effectively is essential.² The effectiveness depends on multiple factors, including the engagement and stewardship of local communities who hope to benefit from the establishment of protected areas.³ Uncertainty remains about whether protected areas are compatible with local development, especially economic growth.^{4–7} This uncertainty creates resistance and tension, perhaps thwarting nations’ efforts to expand protected areas.^{8–10}

Globally, it is still being determined whether the effectiveness of protected areas and local economic growth will result in tradeoffs or synergies, but see Andam et al. and Ferraro et al.^{11,12} Protected areas may benefit local communities and alleviate poverty by providing natural resources and ecosystem services to surrounding areas, generating jobs and income in patrolling and ecotourism.¹³ Conversely, they may constrain local livelihoods by restricting access to natural resources or limiting development opportunities. These impacts include restrictions on

infrastructure and agriculture expansion, logging and mining, forced emigration, and others.^{14,15} Protected areas are expanding into more populated areas, perhaps increasing conflicts.^{16,17} We need to understand the prevalence of different relationships between protected area effectiveness and local economic growth, spatial patterns, regional differences, and drivers for such patterns globally.^{6,18}

Places with high biodiversity and poverty overlap. Protected areas are usually in remote locations unsuitable for agriculture or human residence.¹⁹ Ignoring confounding factors that jointly affect where protected areas are and the economic growth of their neighboring communities may lead to the biased conclusion that protected areas restrict development.¹¹ We applied matching to control for the non-random locations of protected areas and address the bias in estimating local development.^{11,20} In this way, we can better measure whether protected areas effectively reduce land cover conversion compared to areas that are not protected and whether neighboring settlements have a similar or quicker economic growth than the control settlements that are not close to a protected area. The communities immediately outside protected areas’ boundaries are influenced more than those further away.²¹ Worries also exist that protected

areas may displace people from inside them to adjacent places and thus increase their poverty.^{11,22} Here, we analyze neighboring communities following definitions from previous studies: settlements with the minimum size of a village (rural cluster) and within 10 km of the boundary of the protected area.^{7,23} This approach allows us to understand the spillover effect of protected areas.

Nighttime light emissions (hereafter: nightlights) captured by remote sensing are widely used as proxies for national gross domestic product (GDP),^{24,25} poverty,^{26–28} and inequality in human development.²⁹ They may reflect essential economic activities often not measured in the national accounts of developing countries.³⁰ They also indicate infrastructure development under the UN Sustainable Development Goals.³¹ Nightlights provide a compelling measure of economic growth, with a high temporal and spatial resolution.^{25,32,33} Although nightlights are imperfect, their use shows advantages over other measures.³⁴ Nightlights offer a consistent, objective, spatially explicit, and globally available empirical measurement over time, which enables the inclusion of data-poor countries. These countries have high biodiversity and poverty.³² Recently, nightlights have proven efficient in evaluating protected areas and representing village-level improvements in developing regions such as Java, Indonesia, rural Vietnam, and Africa.^{35–37} Nightlights provide gridded measurements of economic growth that can be compared across regions, which are critical in areas where reliable, standardized, and repetitive data collection is unavailable.³²

Protected area effectiveness is multifaceted. Existing assessments usually evaluate one or more of the following: design (extent, location, connectivity), management input, threat reduction, and biodiversity outcomes.³⁸ Using direct biodiversity outcomes—such as species counts—to evaluate global protected area effectiveness remains a challenge.³⁹ Such measures are desirable but require repeated, long-term, site-based monitoring. This effort demands substantial funding and capacity support. Such data are only available for well-resourced protected areas. The lack of monitoring in control sites also makes the evaluation less robust.^{39,40} Therefore, we apply a more widely used method, the threat-abatement evaluation. We analyze whether protected areas effectively resist the encroachment of human-induced land cover changes. Land cover changes, such as cropland expansion or deforestation,²⁰ are among the biggest threats to biodiversity, leading to habitat loss, fragmentation, and population declines.^{41–44} Since protected areas are designed to reduce such threats and the data are available globally at a high spatial-temporal resolution, land cover changes have been widely used to evaluate long-term protected area effectiveness.^{45,46} Although land cover change cannot represent all the threats, such as poaching, this proxy can measure how protected areas resist habitat destruction and fragmentation, which are the primary drivers for biodiversity loss. There is a time lag after establishment of a new protected area before it manifests its effects. The desired effects include a fully functional administration, a recovery of ecosystem services, and adapted livelihoods of local communities.⁴⁷ Thus, we examine the effect at least ten years after establishing the protected area instead of the immediate changes in protected area performance and local economic conditions.

Here, we hypothesize that with the effective conservation of natural land cover inside protected areas, the spillover of ecosystem services from within the park can benefit, or at least not obstruct, the economic growth of the local communities immediately outside the park. We call this a synergy between protected area effectiveness and local economic growth. We ask four key questions in this study. First, are protected areas effective in maintaining natural land cover and resisting the encroachment of agriculture, urbanization, and deforestation?⁴⁸ Second, do they influence nightlight changes in neighboring settlements? Third, how are different relationships between protected area effectiveness and local economic growth distributed globally, and what is the most prevalent relationship? And last, what factors predict the synergy outcome?

RESULTS

Effect in resisting natural land cover loss and nightlight change of neighboring communities

We adopted the Mahalanobis distance matching (MDM) technique to compare the natural land cover loss from 2013 to 2020 in protected areas with similar sites at least 20 km away that were not protected. We used the annual land cover data from the European Space Agency (ESA) Climate Change Initiative Land Cover project (Figure 1). With the matched sample, we leveraged the ordinary linear square (OLS) regression model to estimate the causal effect of protected areas on land cover changes while controlling for a rich set of covariates and fixed effects. We did the same to identify the impact of protected areas on nightlight changes in neighboring settlements using the Visible Infrared Imaging Radiometer Suite (VIIRS) nightlight data compared to counterfactuals at least 20 km away.

Instead of obstructing local economic growth, our results demonstrated that protected areas induced a slightly higher nightlight increase than the counterfactuals, although the effect was insignificant. Meanwhile, protected areas significantly lowered natural land cover loss ($p < 0.01$), leading to a difference of 0.53% in the percentage of areas experiencing natural land cover loss between protected areas and the counterfactuals. This pattern was robust, using different OLS regressions with various control variables and fixed effects, which could absorb potential confounding factors (Table 1). We tested the robustness with different sets of matching techniques, matching restrictions, matching parameters (i.e., calipers), and covariates. We then re-ran the fixed effect regression model for each matched sample on changes in nightlights and natural land cover with standard errors clustered at the country level (Table S1). Alternative robust standard errors were also conducted to test the stability of findings (Table S2). The treatment effects on nightlight changes were shown to be positive but statistically insignificant for all 48 models (Tables S1 and S2). In contrast, the treatment effects on loss in natural land cover were significant and negative (Tables S1 and S2). In other words, protected areas are effective in resisting natural land cover loss.

About 12.7% of protected areas showed an absolute loss in natural land cover, which was smaller than this percentage in counterfactuals (18.5%). For these protected areas with a loss in natural land cover, 28.7% displayed a lower loss than similar areas without protection. 90.9% of protected areas

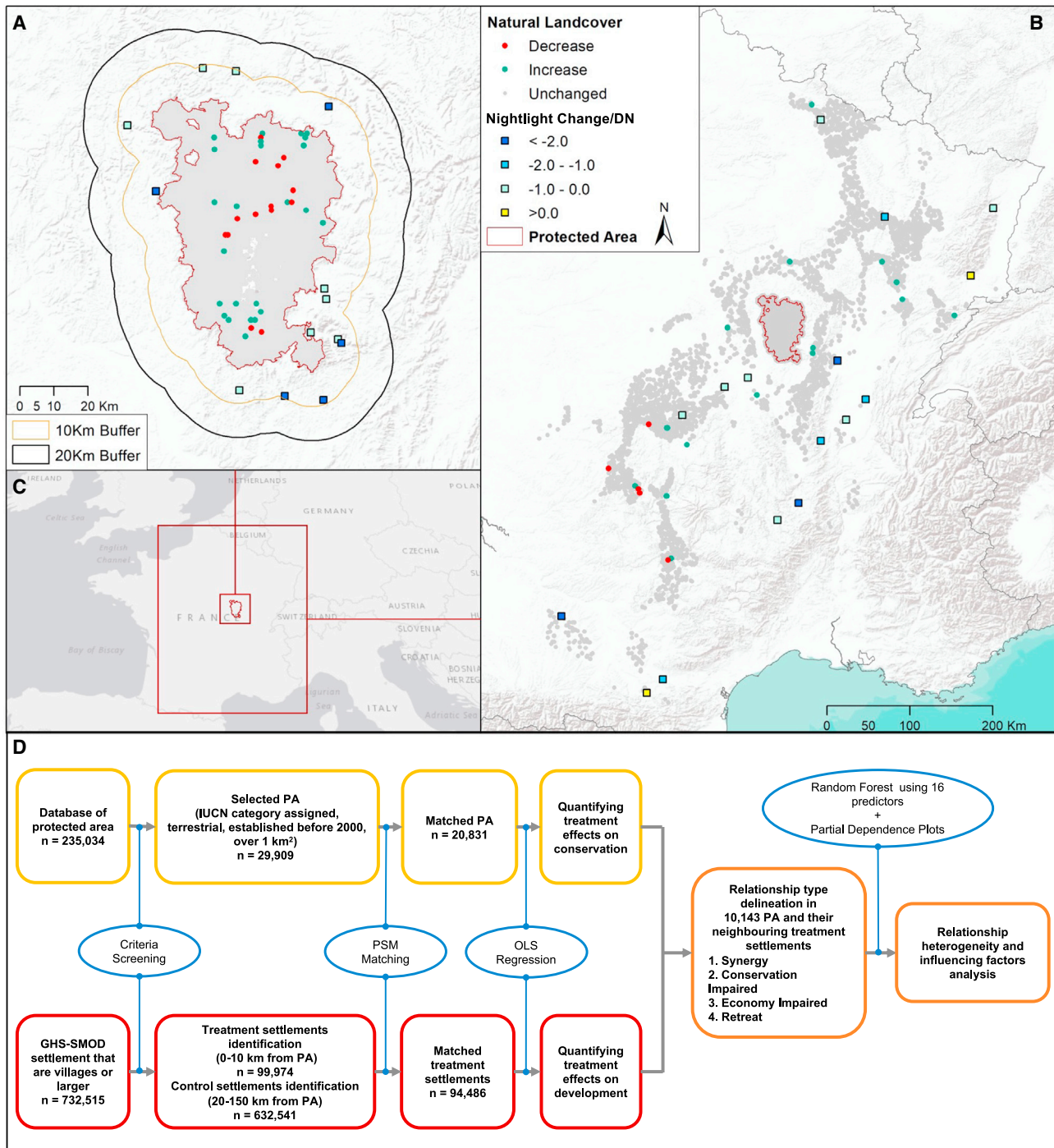


Figure 1. Identification of the relationship between land-use changes and nightlight changes in Morvan Regional Natural Park of France and the flowchart of the study

(A) Shows the nightlight changes in the neighboring settlements within a 10-km buffer and natural land cover change from 2000 to 2013 in the protected area (PA). (B) Shows the control sites for settlements far from protected areas and controlled areas to compare land cover changes from 2000 to 2013. We calculate land cover change by summarizing the percentage of pixels experiencing land cover change in each protected area and its matched samples. To evaluate the effectiveness of this protected area, we compared the difference between the natural land cover change in the protected area and its counterfactual. Similarly, we calculated the difference in nightlight change between neighboring and control settlements. The unit of analysis for nightlight change is the settlement. (C) Shows the location of Morvan Regional Natural Park. (D) Shows the overall flowchart of the study.

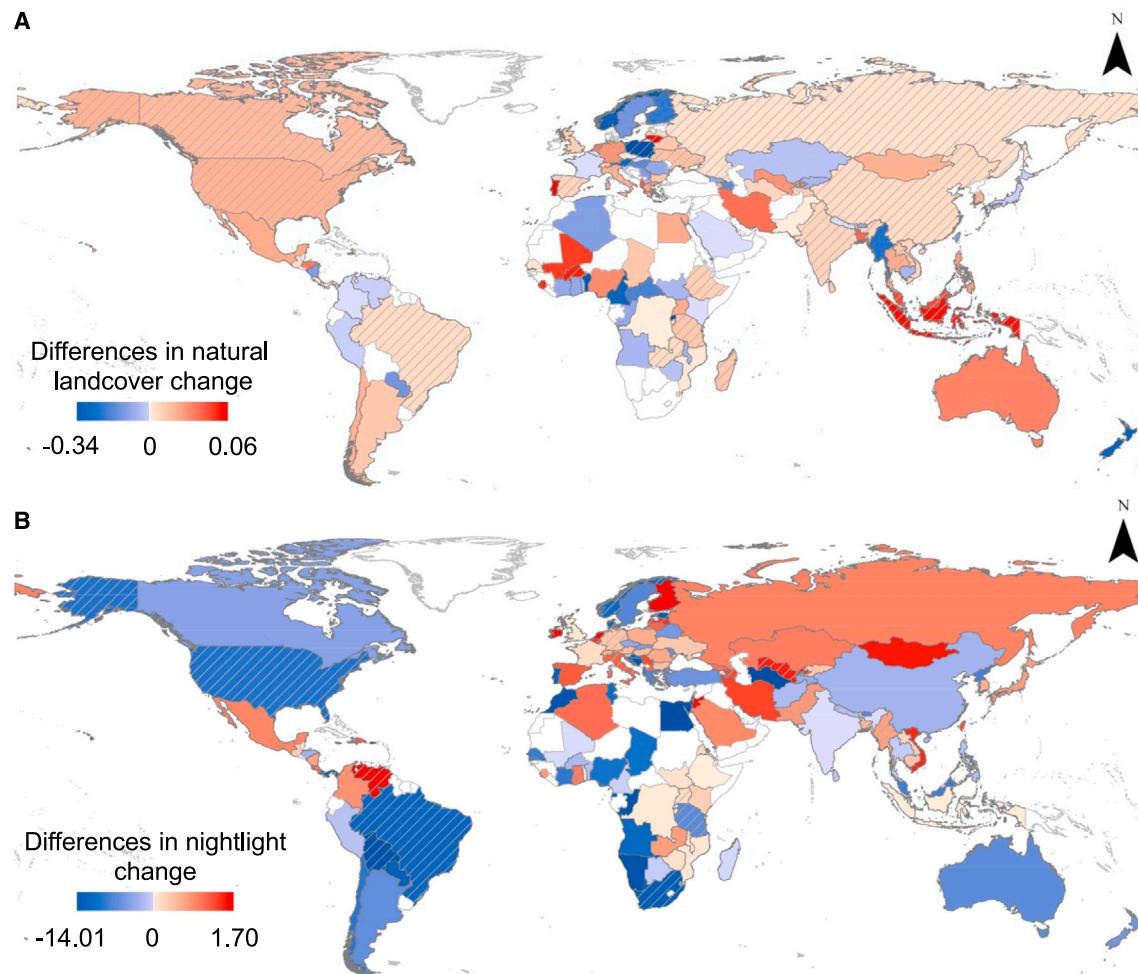


Figure 2. Distribution of the natural land cover change and nightlight change

(A) The effect of protected areas on natural land cover change compared to counterfactuals was summarized by countries. Countries with significant treatment effects are filled with hatches. The positive difference in natural land cover indicates a higher natural land cover increase than the counterfactuals.

(B) Effect of protected areas on nightlight change in neighboring settlements compared to counterfactuals. The positive difference in nightlight change indicates a higher nightlight increase than the counterfactuals.

demonstrated positive effects: no natural land cover loss or less loss than counterfactuals. About 60.3% of the neighboring communities showed a similar or higher nightlight increase compared with the counterfactuals. Among these cases, 68.4% showed a higher increase in nightlights than counterfactuals, and 31.6% showed a similar change.

We conducted a country-level analysis to understand the heterogeneous effect of protected areas across countries. We reran the baseline fixed effect regression model for each country based on the matched sample. This analysis allowed us to evaluate the average effect of protected areas in their land cover changes and nightlight changes in their neighboring communities for each country. About 65.7% of the countries (71 countries) showed higher natural land cover changes in protected areas than in their corresponding counterfactuals, and 23 countries showed a significant effect from protected areas in resisting natural land cover loss (Figure 2A). Although protected areas did not show a significant impact on nightlight changes in the

neighboring settlements globally, there was a notable difference between countries. About 51.5% of the countries showed an average nightlight change similar to or higher than the counterfactuals. Among them, the effects in 18 countries, such as Azerbaijan, Burundi, Costa Rica, the Netherlands, and Venezuela, were significant (Figure 2B). Meanwhile, 11 countries showed a significantly lower nightlight increase in neighboring communities of protected areas than the counterfactuals. Examples of these countries include Tanzania, Brazil, Sri Lanka, South Africa, Nepal, and Bolivia (Figure 2B).

Relationship between the changes in neighboring community nightlights and protected area natural land cover

We defined four relationships according to how protected areas performed in resisting natural land cover loss and how they impacted the nightlight change in neighboring communities compared to counterfactuals (Figure 3). The synergy

Table 1. Regression results of protected area's impact (i.e., the treatment effect) on nightlight change and human-induced land cover change from 2013 to 2020 based on results from MDM approaches

Variables	Nightlight change			Natural land cover loss		
	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Treatment effect	0.007 (0.019)	0.003 (0.017)	0.003 (0.017)	−0.006 ^b (0.001)	−0.006 ^b (0.001)	−0.006 ^b (0.001)
The area size of the settlement	N/A	−0.003 (0.048)	−0.003 (0.048)	N/A	−0.000 (0.000)	−0.000 (0.000)
Access time to cities	N/A	−0.124 ^b (0.022)	−0.125 ^b (0.022)	N/A	−0.001 ^a (0.000)	−0.001 ^a (0.000)
Annual mean precipitation in 2000	N/A	0.084 (0.075)	0.097 (0.079)	N/A	0.003 (0.002)	0.003 (0.002)
Elevation	N/A	0.000 (0.000)	0.000 (0.000)	N/A	0.000 (0.000)	0.000 (0.000)
Slope	N/A	−0.067 ^b (0.019)	−0.068 ^b (0.019)	N/A	0.000 (0.000)	0.000 (0.000)
Road density	N/A	0.021 ^a (0.009)	0.021 ^a (0.009)	N/A	−0.000 (0.000)	−0.000 (0.000)
Constant	0.085 ^b (0.010)	0.084 (0.345)	0.031 (0.358)	0.002 ^b (0.001)	−0.008 (0.009)	−0.008 (0.009)
Observations	187,480	187,480	187,480	161,190	161,190	161,190
R-squared	0.224	0.227	0.230	0.515	0.515	0.515
Country fixed effect	Yes	Yes	Yes	Yes	Yes	Yes
PA fixed effect	N/A	N/A	Yes	N/A	N/A	Yes

Notes: Counterfactuals are constructed following the MDM approach with additional restrictions on matching within the same country, ecoregion, and land cover type. The set of covariates used in the matching include historical nightlights, population density, and net primary productivity, all in 2000, as well as slope, elevation, human footprint, average precipitation, and average temperature. With the matched sample, we then conduct the regression model with fixed effects at the country and protected area (PA) units. Standard errors in parentheses are clustered at the country level.

^a $p < 0.05$

^b $p < 0.01$

relationship has effective protection of natural land cover and a similar or higher nightlight increase in neighboring communities compared to counterfactuals; synergy relationships accounted for 47.7% of the total cases (Figure 3). For these synergy cases, 94.3% showed a higher increase in nightlights than the counterfactuals, with the rest having the same level of nightlight change. Tradeoffs, which included “conservation-impaired” and “economy-impaired” cases, constituted 47.7% of the relationships combined. Only 4.6% of relationships were retreat relationships (Figure 3). Although less prevalent than synergy, economy-impaired cases were the second most common relationship type.

Existing research indicates that it is possible to realize economic growth and conservation goals simultaneously; however, the magnitude of both outcomes may be reduced compared to scenarios where one objective is prioritized over the other.¹² A tradeoff emerges if either outcome is more desired, such as higher economic growth or more natural land cover recovery.¹² Our results do not support this pattern. The average change of nightlights in synergy showed no significant difference from conservation-impaired cases (0.87 versus 1.03 nWcm^{−2}sr^{−2}, nW per centimeter squared per steradian per year, two-sided t test, $t = -1.3072$, $df = 535.55$, $p > 0.05$), which was a type that showed higher economic growth but sacrificed the conservation outcome. Synergy also showed a similar reduction of natural

land cover loss to economy-impaired cases, the latter of which had positive conservation outcomes but restricted the local economic growth (0.96% versus 1.00%, two-sided t test, $t = 0.3052$, $df = 9161.5$, $p > 0.05$).

Heterogeneity in continents, biomes, and countries

Globally, Africa, Europe, and Asia showed a higher percentage of protected areas with the synergy relationship (Figure 4). Synergy was most prevalent in temperate forests, accounting for 49.3% of the cases, followed by grasslands and deserts (Figure 4A). Certain regions showed more than 50% of the cases as synergy, such as tropical forests and savannahs in Africa, temperate forests in Asia and Europe, and temperate forests in South America (Figure S1).

The economy-impaired cases were the second most prevalent pattern globally and showed a higher percentage in grasslands than in other ecosystems. When comparing specific regions, they were the most common relationship in Oceania and North America, both in forest and grassland ecosystems, as well as in grasslands in South America, Amazon, and Southeast Asia (Figure S1).

The other tradeoff relationship—conservation impaired—was less common but showed a higher percentage in Africa, Asia, and South America (Figure 4A). Nonetheless, boreal forests had a much higher percentage of conservation-impaired cases

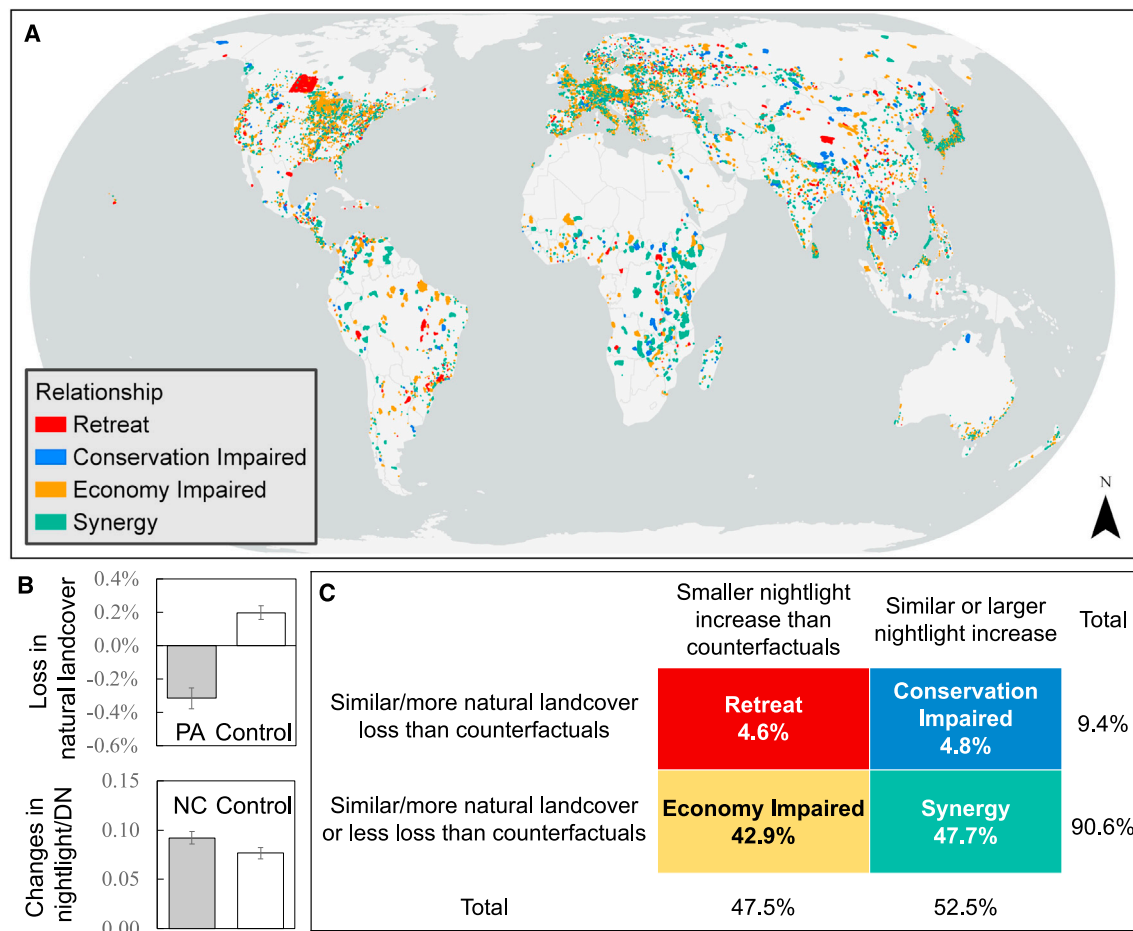


Figure 3. Distribution of the four relationships between protected area effectiveness and neighboring community economic growth

(A) Shows the distribution of four relationships for all the protected areas in this analysis.

(B) Shows the changes in natural land cover between protected areas (PAs) and controlled sites, as well as nightlights between neighboring communities of protected areas (NCs) and controlled settlements from 2013 to 2020. Error bars stand for standard errors.

(C) Breaks down the percentages of protected areas falling within each category. See also [Table S3](#).

(13.65%) compared to other ecosystems, followed by deserts (6.32%) and tropical forests (6.29%) ([Figure 4B](#)). Boreal forests and tropical forests also had the highest proportions of the retreat relationship, with loss in natural land cover in protected areas and less nightlight increase compared with counterfactuals. When examining the specific regions, grasslands in South America ranked among the top for the percentage of retreat (13.56%), similar to boreal forests ([Figure S1](#)).

Some countries performed better in guarding the protected areas against land conversion while improving the nightlights in the neighboring communities ([Table S3](#)). We selected the countries with more than ten protected areas analyzed in this study and ranked the prevalence of different relationships. The countries with the highest retreat percentages were more often developing countries, such as Honduras, Paraguay, Cambodia, and Nigeria ([Figure 4C](#)). The top four countries had more than one-fifth of their protected areas showing retreat. The top ten countries by synergy percentage are distributed across continents with various economic conditions. The top four countries (Belgium, Ethiopia, Pakistan, and Burkina Faso) showed synergy

between conservation and local economic growth in more than 70% of their protected areas ([Figure 4D](#)).

Factors influencing the relationships

Socioeconomic conditions played a more critical role in explaining the relationship than environmental conditions ([Figures 5 and 6](#)). We explored the factors explaining the four relationships between protected area effectiveness and local community development using random forest models while accounting for other contextual variables. The top factors explaining the relationship were the country's Human Development Index (HDI) level, the GDP in the areas surrounding protected areas in 2000, travel time to cities from neighboring settlements, road density in the 0–10 km buffer of the protected area, and the size of the protected area ([Figure 5](#)). The three least predictive factors were population change in the neighboring communities, International Union for Conservation of Nature protected area categories (IUCN category), and the governance type of the protected area.

Our findings indicate that developing regions where synergy is most needed did not consistently show this relationship. Places

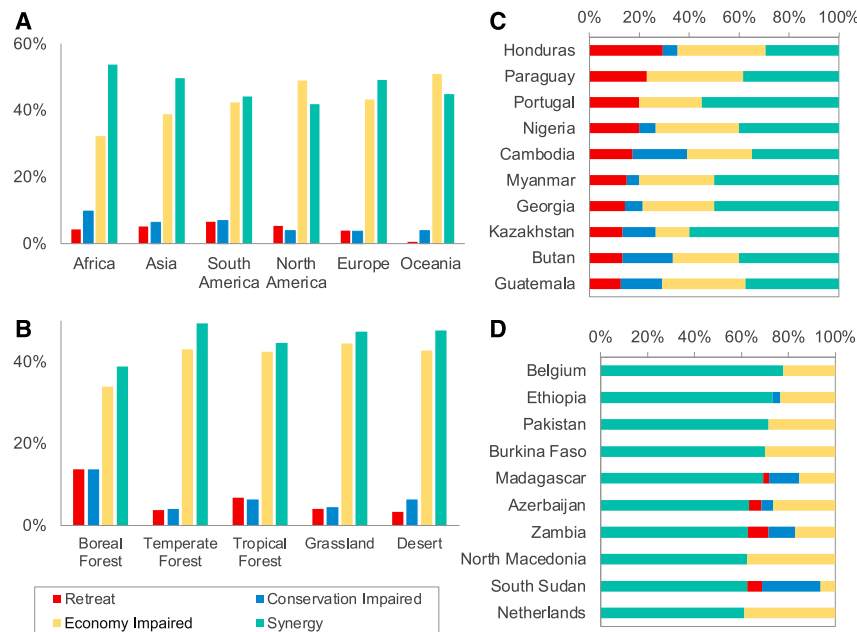


Figure 4. Distribution of the relationships in different regions

(A–D) (A) Continents, (B) biomes, (C) top ten countries with the highest percentages of the retreat relationship, (D) top ten countries with the highest percentages of the synergy relationship. We only considered countries with ten or more protected areas that qualified for analysis to rank here. See also [Figure S1](#) and [Table S3](#).

with low GDP tended to have a lower proportion of synergy than areas with higher GDP ([Figure 5](#)). The chances of reaching synergy increased with the HDI but dropped again when the level was about 0.85 ([Figure 5](#)). For simplicity, we called countries with an HDI ≥ 0.85 “developed” and “developing” otherwise. With the increase in GDP, the proportion of synergy outcomes increased consistently in developed countries ([Figure 6](#)). However, in developing countries, the proportion of synergy cases dropped in highly developed regions. Although retreat cases fell with increasing local GDP in both types of countries, developing countries tended to have more retreat relationships than developed countries in most cases ([Figure 6](#)).

Accessibility to cities of these settlements and the road density around protected areas ranked among the best predictors for the relationship between protected area effectiveness and local development ([Figure 5](#)). Intermediate levels of access to cities and moderate road density resulted in the highest probability of synergy ([Figure 5](#)). Places with few roads or limited access to cities, as well as areas near densely populated cities or with a high density of roads, were much less likely to have synergy ([Figure 5](#)). Notably, the proportions of retreat cases increased with the travel time to cities in both developing and developed countries ([Figure 6F](#)). Areas with no roads showed a smaller proportion of retreat compared to regions with a low density of roads, the latter of which had a higher retreat probability than areas with more roads (density $> 250\text{m}/\text{km}^2$) ([Figure 6E](#)). This indicates a higher chance of retreat in areas when roads first entered.

Conservation planning favors larger protected areas because they provide enough space for large home-ranged species, such as top predators; safeguard large-scale ecosystem processes; and ensure landscape connectivity.^{49,50} A large protected area does not guarantee synergy. With the increase in the size of the protected area, the probability of synergy dropped rapidly ([Figure 5](#)). This trend was the same in both developed and developing countries. In contrast, the

proportion of retreat cases increased with the size of the protected area ([Figure 6B](#)). The pattern was much more evident in developed countries. Meanwhile, extremely large protected areas ($>1,000\text{ km}^2$) in developing countries performed better than those in developed countries and also better than the smaller protected areas in the same region ([Figure 6A](#)). These large protected areas showed a higher proportion of synergy and a much lower retreat rate.

Some consider the permission to use

natural resources inside a protected area essential for their success, especially for areas with Indigenous communities.⁷ Our results showed that less strict protected areas performed similarly to or even better than the strictest ones (IUCN I and II) in achieving synergy ([Figure 5](#)). These regions included tropical forests in Africa and South America (e.g. Amazon), grasslands in Asia, and savannahs in Africa ([Figures S2–S4](#)). Exceptions were tropical forests in Asia and grasslands in South America ([Figures S4 and S5](#)).

DISCUSSION

About half of the protected areas globally retain their natural land cover despite increasing nightlights in the neighboring communities. Contrary to a pervasive perception, synergy is prevalent: protected areas are not restricting economic growth compared to areas with similar environmental and socioeconomic conditions. Although this pattern applies to the global scale, conservation should pay special attention to specific regions and countries where such restrictions on development manifest ([Figure 2](#)).

Nonetheless, the tradeoff relationships (conservation impaired and economy impaired) are almost as common. Moreover, the lower percentage of synergy in some developing regions is of concern; such compatibility is most needed here. These regions harbor exceptionally rich biodiversity along with the last remaining large habitats.⁵¹ They shoulder the cost of protecting the global public good of biodiversity.

Areas with low baseline economic conditions in developing countries are more likely to experience retreat. This result further supports the idea that poverty traps exist in developing regions. Without addressing the poverty alleviation of local communities effectively, establishing protected areas may lead to a loss in both biodiversity and development. On the other hand, if managed well, the neighboring communities in less-developed regions could benefit more in health, welfare, and income from the spillover of natural resources and ecosystem services from protected

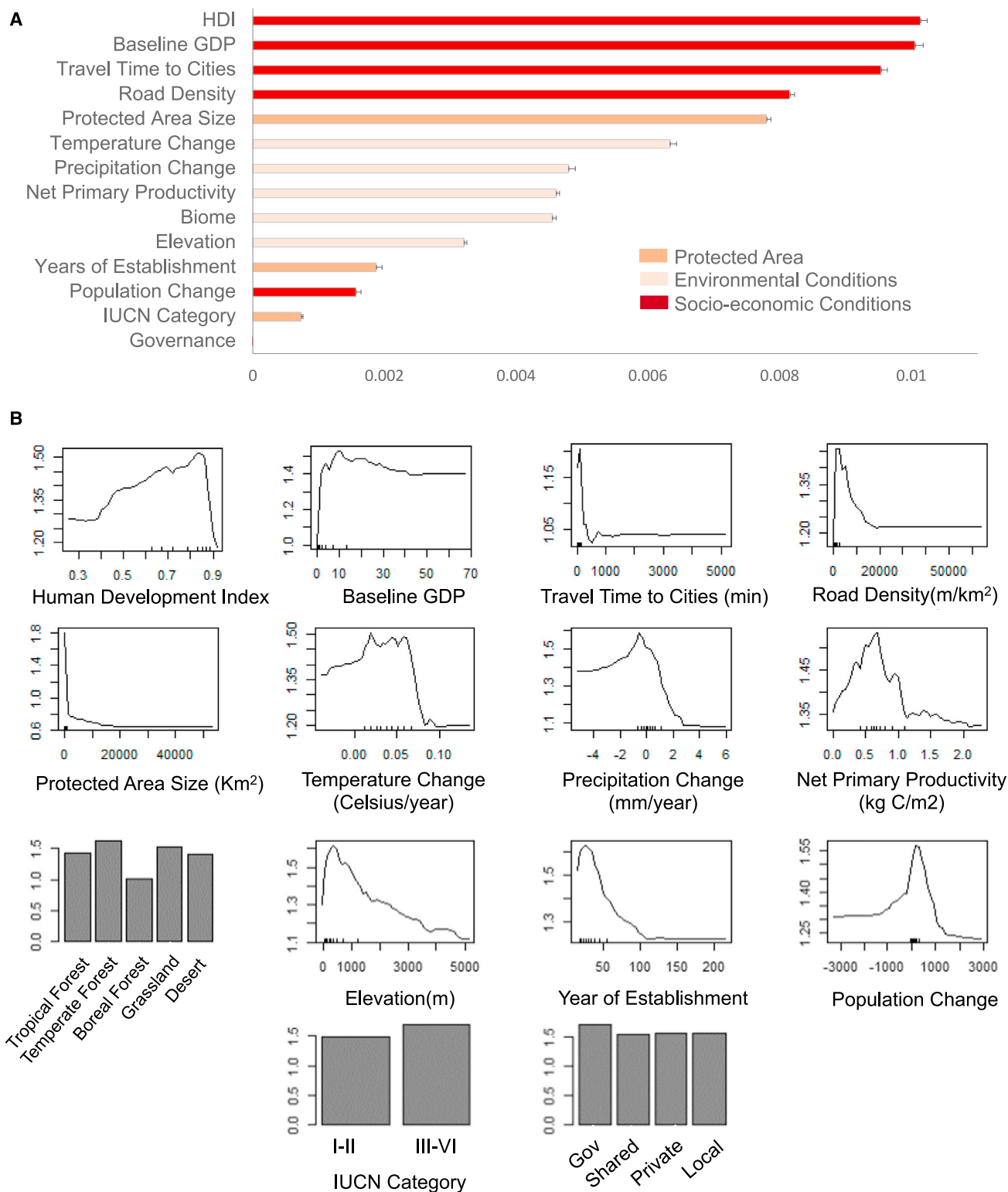


Figure 5. Top factors explaining the relationship between protected area effectiveness and local community development

(A) Random forest variable importance indices (mean decrease accuracy) for the relationship between protected area effectiveness and local community development. The error bar stands for the standard error from 100 runs.

(B) Partial dependence plot for each variable in the random forest model, ranked by the mean decrease accuracy. The plot depicts the marginal effect of a variable on the “synergy” class probability. Gov, shared, private, and local stand for governance by government, shared governance, private governance, and governance by Indigenous people and local communities. See also [Figures S2–S5](#).

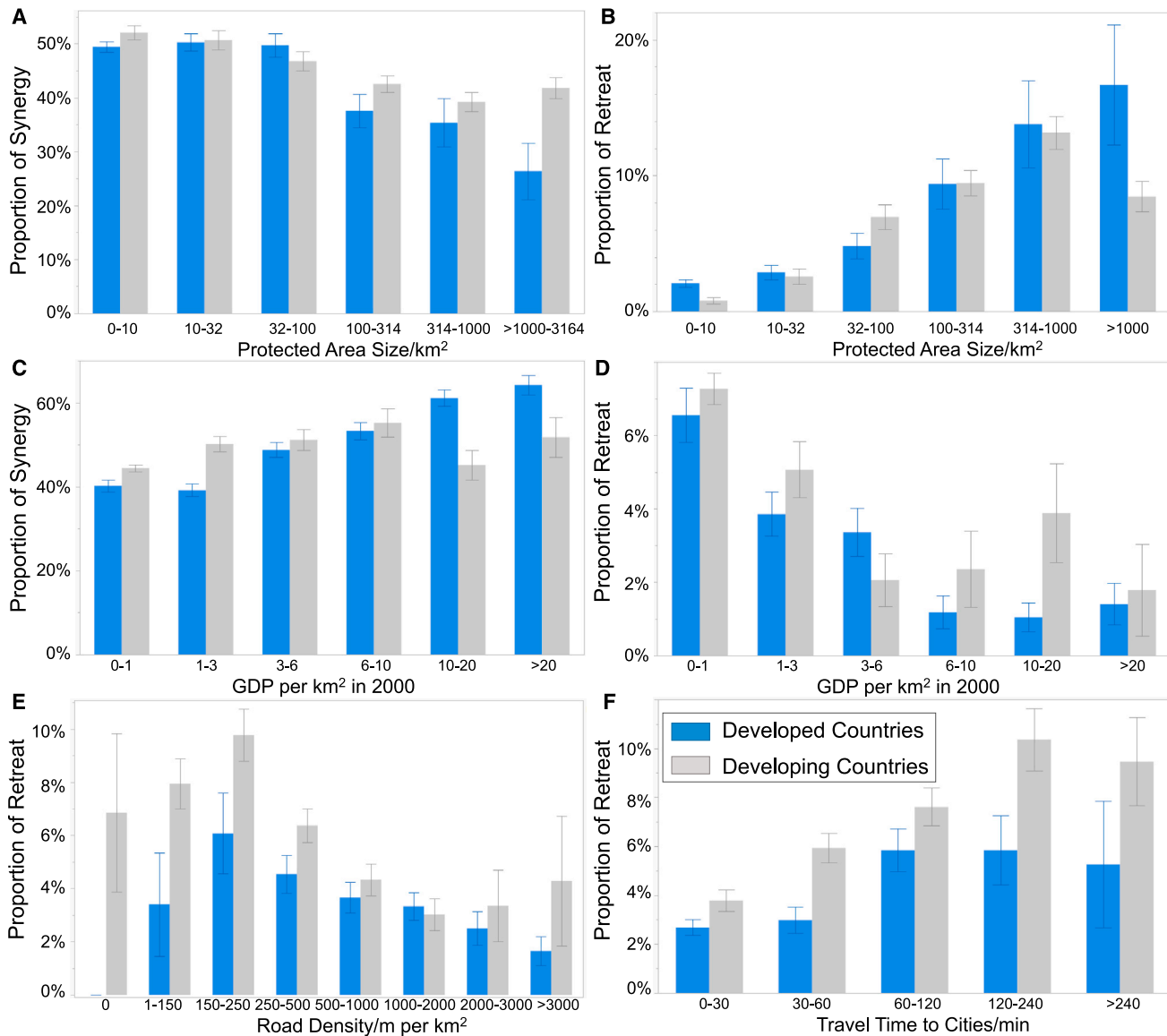


Figure 6. The difference between developed and developing countries lies in key factors

(A–F) The proportions of synergy and retreat cases with protected area size (A and B), baseline gridded GDP (1 km²) (C and D), proportion of retreat cases for road density in the 10 km buffer of the protected areas (E), and travel time to cities from the neighboring settlements (F). The cases were divided into developed (high human development level, HDI ≥ 0.85) and developing countries (low development level, otherwise). Error bars represent standard errors.

areas, such as provisioning of food, clean water, and changes in infrastructure, as well as tourism opportunities from protected areas.^{13,52} Examples include the Corcovado National Park⁵³ and other parks in Costa Rica¹³ and other countries.

Roads and accessibility may threaten protected areas, especially by accelerating deforestation or other land cover changes and natural resource extraction.⁵⁴ Nonetheless, better access to cities and markets increased the chance of synergy and reduced the chance of retreat, especially for developing countries. This is similar to previous findings (Figure 6).⁵⁵ Studies in the Brazilian Amazon and Costa Rica show that protected areas closer to roads or cities avoid more forest clearing than the distant protected areas.^{56,57} Most retreat cases occurred where road

density was extremely low. When roads first enter areas, they may harm conservation while not benefiting the local communities. Nonetheless, when road density increased and access to markets was easier, the chances for synergy increased, and retreat cases dropped. This pattern implies that whether roads threaten the environment is context dependent. Remote areas do not necessarily mean lower deforestation.

The lack of access to essential facilities and services for local communities can lead to increased destruction of natural land cover. In rural areas near Gunung Palung National Park of Borneo, one of the drivers behind illegal logging of local communities was a need to pay for healthcare.⁵⁸ Such care was only available in larger towns far from the park. Many view tourism as the most

direct mechanism to benefit local development. Various factors determine its success, including accessibility. A study in the Peruvian Amazon showed that with long travel times due to poor accessibility, even protected areas with ecotourism potential attracted very few tourists. This lack of easy access led to almost no positive socioeconomic effects for these national parks.⁵⁹ Our study also shows consistent results, as many cases were classified as retreat or economy-impaired relationships. An opposite case is the synergy outcome of Wuyishan National Nature Reserve in Fujian, China. Easy accessibility through flights, high-speed rail, and the highway, together with the beautiful scenic views and local tea culture, helped this county attract more than 16 million visitors in 2019. Instead of advocating for no infrastructure expansion in these areas, we want to emphasize equity in developing communities around protected areas. Sustainable linear infrastructure, which aims to reduce the environmental impact while improving local livelihoods, should be implemented in these areas to facilitate the development of responsible and sustainable livelihood, including ecotourism.⁶⁰

Large protected areas do not guarantee synergy. They may suffer from insufficient funding per unit area, resulting in a lack of staffing, patrols, and monitoring, making them more vulnerable to encroachment.⁶¹ In our analysis, about 51.2% of protected areas with an area larger than 1,000 km² showed an absolute loss of natural land cover. However, this proportion decreased dramatically in smaller protected areas and reached 6.0% for those under 100 km². This pattern that larger protected areas are less effective at resisting anthropogenic encroachment was consistent across different biomes and regions. Improving the synergy outcomes in these areas requires considerable investment in funding, staffing, and management input and innovations in conservation finance.⁶² With most of the past expansions built on protecting large wilderness areas that are usually arid and cold, many regions run out of space to establish more large protected areas.¹⁶ To reach Target 3 in the Kunming-Montreal Global Biodiversity Framework, which aims to expand protected areas from under 17% now to 30% in 2030, will rely more on smaller protected areas in more populated regions. Promisingly, our results indicate that these scenarios have a high probability of achieving conservation-development compatibility if they address the other factors well.

Protected area effectiveness has multiple aspects, including habitat protection, target species recovery, equitable governance, and others.^{16,57,59} We evaluated how protected areas resist human-induced land cover changes. This approach cannot represent the changes caused by poaching or overharvesting, which are not visible from remote sensing and may cause an overestimate of effectiveness in some cases. Nevertheless, how protected areas resist threats, especially this most significant driver for biodiversity loss, is essential to understanding their effectiveness. The predominance of synergy also indicates that the development of neighboring communities does not necessarily induce natural land cover loss inside the protected area.⁶³ Nonetheless, the development could be built on destroying habitat outside the protected areas (e.g., cropland expansion, deforestation, mining, etc.) and accelerate the isolation of protected areas and landscape fragmentation.⁶³ Future conservation planning should also integrate landscape connectivity by promoting sustainable natural resource

use in the buffer zones or corridors between the protected areas.

The type of governance of the protected areas was not a top predictor for our global analysis. The few types of governance in our data may drive this pattern. Local, private, and shared governance only accounted for 0.02%, 2.8%, and 4.5% of our samples, respectively. Previous studies have shown that where local communities and Indigenous people play an equitable role in the management and stewardship of the protected areas, better conservation and socioeconomic outcomes can be produced.³ As the expansion and effectiveness of protected areas will rely more on protecting more populated or human-modified landscapes, the contribution and engagement of Indigenous peoples and local communities (IPLCs) will be imperative for the synergy outcome.⁶⁴ This process requires empowering local communities through stewardship, recognizing their local institutions, involving them from the start, understanding their needs and values, and promoting inclusive and equitable governance.³ Cultural and historical influences, funding and staff support, and social and institutional stability contribute to long-term synergy.^{65–68} Future studies should investigate such mechanisms for synergy and how they work in different contexts.¹³ The interconnection between biodiversity conservation and sustainable development shown by our analysis indicates the need to involve these goals in reciprocal agenda setting, including implementing the Kunming-Montreal Global Biodiversity Framework. This process needs the engagement of stakeholders from the regional to the local level to address the drivers for such compatibility. We urge a closer look at these cases when devising local-scale management and policy interventions.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2024.05.044>.

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AUTHOR CONTRIBUTIONS

Conceptualization, B.V.L. and S.L.P.; methodology, B.V.L., S.W., and J.C.; investigation, B.V.L., S.W., J.C., and S.L.P.; visualization, B.V.L. and S.W.; writing – original draft, B.V.L. and S.W.; writing – review & editing, B.V.L., S.W., J.C., and S.L.P.

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The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Original code	This paper	https://doi.org/10.5281/zenodo.11181051
Software and algorithms		
R studio ver 2023.06.1 + 524	R Core Team	https://cran.r-project.org/
QGIS ver 3.26.2	QGIS project	https://qgis.org/
ArcGIS ver 10.7	Esri	https://www.arcgis.com/
Stata ver 18	StataCorp LLC	https://www.stata.com/
Other		
Protected area coverage	World Database of Protected Areas	https://www.protectedplanet.net/
Protected area coverage of China	Li et al. ⁶⁹	https://doi.org/10.1111/cobi.12618
Land cover	ESA Climate Change Initiative Ecosystem Cover Project ⁷⁰	http://maps.elie.ucl.ac.be/CCI/viewer/download.php
Visible Infrared Imaging Radiometer Suite nightlight	Chen et al. ⁷¹	https://doi.org/10.5194/essd-13-889-2021
LandScan™ global population data	Oak Ridge National Laboratory ⁷²	https://landscan.ornl.gov/
Human footprint data	Wildlife Conservation Society, Center for International Earth Science Information Network, and Columbia University ⁷³	https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic
Harmonized World Soil Database	Food and Agriculture Organization of the United Nations ⁷⁴	https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/
Gross domestic product	Chen et al. ⁷⁵	https://doi.org/10.1038/s41597-022-01322-5
Net primary productivity	NASA ⁷⁶	https://lpdaac.usgs.gov/products/mod17a3hgv006/
Annual precipitation	WorldClim ⁷⁷	https://worldclim.org/data/monthlywth.html
Annual temperature	WorldClim ⁷⁷	https://worldclim.org/data/monthlywth.html
Global human settlement	European Union's space programme ⁷⁸	https://human-settlement.emergency.copernicus.eu/download.php?ds=smod
Human development index	UNDP ⁷⁹	http://hdr.undp.org/en/content/human-development-index-hdi
Access time to cities	Weiss et al. ⁸⁰	https://doi.org/10.1038/nature25181
Road density	Meijer et al. ⁸¹	https://doi.org/10.1088/1748-9326/aabd42

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Binbin V. Li (Binbin.li@dukekunshan.edu.cn).

Materials availability

This study did not generate new materials.

Data and code availability

This paper analyzes existing, publicly available data. These accession numbers for the datasets are listed in the key resources table. The original code has been deposited at 10.5281/zenodo.11181051 and is publicly available as of the date of publication. DOIs are listed in the key resources table as well. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Protected area data

We created a global protected area dataset based on the world protected area polygon data from the World Database of Protected Areas (WDPA 2020 July version) (available at <https://www.protectedplanet.net/>), which covered 232 countries or regions. Since the WDPA had an incomplete list of protected areas in some countries, especially China, we substituted the part of China with the more complete data from Li et al.⁶⁹ We supplemented it with information from 2014 to 2017 from the Ministry of Ecology and Environment website (<http://www.mee.gov.cn/gkml/>). The combined protected area dataset contained location, area size, year of establishment, and IUCN-protected area categories.

Indicator data

We obtained the 300 m land cover data from the ESA Climate Change Initiative Ecosystem Cover Project (<http://maps.elie.ucl.ac.be/CCI/viewer/download.php>).⁷⁰ This dataset has been widely used to evaluate land cover changes in biodiversity hotspots and the performances of protected areas.^{71,82} This dataset covers the global extent with 300m spatial resolution each year from 1992 to 2020. The constancy over time is a crucial characteristic of this dataset, as the annual land cover maps are not created separately but based on a distinct baseline map made using the complete MEIdium Resolution Imaging Spectrometer (MERIS) archives spanning from 2003 to 2012. Land cover changes are detected using a series of satellite data; any observed changes are subsequently re-mapped at 300 m.⁷⁰ We obtained the global Visible Infrared Imaging Radiometer Suite (VIIRS) nightlight data with 15 arcsec resolution (approximately 500 m near the Equator) from 2013 to 2015 and 2020 to 2022 at <https://doi.org/10.7910/DVN/JRM2XE>.⁸³ The dataset was annually summarised from the monthly VIIRS nightlight data after calibration. Dark background masks and nightlight intensity thresholds were also applied to remove unstable or abnormal pixels.⁸³

Covariate data

The population density data were from the LandScan global population data with a 1 km resolution from the Oak Ridge National Laboratory (available at <https://landscan.ornl.gov/landscan-datasets>). The data mainly rely on sub-national census counts but are also validated by slope, roads, land cover, urban areas, village locations, and high-resolution remote sensing data.⁷² The human footprint data provided a map showing the anthropogenic impacts on the environment with a 1 km resolution (available at <https://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic>).⁷³ It is created from nine global data layers that cover human population pressure (population density), human land use and infrastructure (built-up areas, nightlights, land use, and land cover), and human access (coastlines, roads, railroads, navigable rivers).⁷³ The soil type data were from the Harmonized World Soil Database with a 1 km resolution and are available at <https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/>.⁷⁴ The dataset combined existing regional and national updates of soil information worldwide, such as Soil and Terrain Databases, Ecological Site Descriptions, Soil Map of China, World Inventory of Soil Emission Potentials and FAO-UNESCO Soil Map of the World. The GDP information was extracted from the global 1 km *1 km gridded revised real gross domestic product from Chen et al.⁷⁵ The yearly Moderate Resolution Imaging Spectroradiometer (MODIS) NPP dataset (MOD13A3HGF v006) with 1 km resolution and global coverage was used as the source of NPP and downloaded from the NASA Land Processes Distributed Active Archive Center (available at <https://lpdaac.usgs.gov/products/mod17a3hgf006/>).⁷⁶ The annual precipitation and temperature data were obtained from the WorldClim 2.1-downscaled Climatic Research Unit gridded Time Series dataset (available at <https://worldclim.org/data/monthlywth.html>) and resampled to 1 km resolution.⁷⁷ The global human settlement grid data were downloaded from <https://human-settlement.emergency.copernicus.eu/download.php?ds=smod>.⁷⁸ We obtained the Human Development Index data from <http://hdr.undp.org/en/content/human-development-index-hdi> to test the effects of external support.⁷⁹ The data of access-time-to-cities and road density were obtained from Weiss et al.⁸⁰ and Meijer et al.,⁸¹ respectively.

METHOD DETAILS

Selection of protected areas

As the recovery of ecosystem services can be slow and local communities may take time to adjust their livelihood with the establishment of the protected areas, we here specifically examine the long-term effects of how protected area performs in resisting landcover changes and their impact on local economic growth. So, we selected protected areas established before 2000 and examined their performances from 2013 to 2020. We only kept protected terrestrial areas larger than 1 km² and with designated IUCN protected area management categories. The 1 km² cut-off was to exclude protected areas that were too small so that the surrounding changes could easily influence them. We only kept protected areas with management category information because we wanted to test the effect of the IUCN category on relationship types. The WDPA and Li et al.⁶⁹ database contained 235,034 protected areas and covered an area of ~56,179,476 km². After excluding protected areas without assigned IUCN-categories ($n = 68,735$, ~29.24%), non-terrestrial ($n = 59,705$, ~25.40%), established after 2000 ($n = 35,780$, ~15.22%) and less than 1 km² ($n = 40,905$, ~17.40%), a total of 29,909 protected areas remained for further analysis.

Indicators for protected area condition

We used whether a protected area could maintain its natural land cover—that is, resist human-induced land cover change in the protected areas—as a proxy for performance. Here, the human-induced land cover change refers to converting natural land cover to agriculture and urban areas or additional deforestation that converts forest to other land cover types.² Although livestock grazing causes degradation in open habitats and is a significant threat many protected areas face, it is difficult to detect its impacts through remote-sensed land cover changes.^{84,85} Therefore, our assessment of protected area conditions can be over-optimistic, especially for open ecosystems. The differences between the two periods represent the land cover change between 2013 and 2020.

Indicators for neighbouring communities' development

Nightlights have been widely used as an indicator of economic status.^{25,86} Nightlights are a robust proxy for GDP,^{24,25} poverty,^{26–28} inequality²⁹ in human development, and informal economic activities, especially in developing countries.²⁵ Compared to the Defense Meteorological Satellite Program Operational Linescan System (DMSP-OLS) nightlight data, the VIIRS dataset has less oversaturation in highly developed areas, fewer miss-detections in underdeveloped areas, more recent data coverage, and on-board calibration capability.⁸⁷ Since the intensity of nightlights fluctuates between years and to exclude the influences of natural light sources such as wildfires,²⁵ we used the three-year average (i.e., 2013 to 2015 and 2020 to 2022) to represent the nightlight in 2013 and 2020, respectively.

QUANTIFICATION AND STATISTICAL ANALYSIS

Matching for protected area effectiveness assessment

Before assessing their effectiveness, we used the matching technique to account for the non-random location and socioeconomic context of protected areas.⁴⁵ The unit of analysis was 1km*1km pixels generated inside and outside the protected areas, following Geldmann et al.²⁰ The variables used in matching were found to be able to both theoretically and empirically bias the location of PA, including 1) elevation, 2) slope, 3) population density in 2000, 4) land cover in 2000, 5) access time to cities, 6) road density, 7) country, 8) ecoregion, and 9) soil type.^{6,20,45} The rationale for including them in the matching is listed in [Table S4](#). We applied MDM without replacement using “nearest neighbour” for elevation, slope, access time to cities, road density, and initial population density.⁸⁸ We used exact matching for the country, initial land cover type, and ecoregion. This meant that protected pixels were only compared to unprotected pixels within the same country, ecoregion, with the closest match for terrain and initial pressure. A total of 20,831 protected areas were matched with counterfactuals to evaluate the effectiveness of protected areas in resisting human-induced land-cover changes ([Figure 1](#)). We calculated the landcover change as the percentage of pixels in a protected area or of the counterfactual pixels experiencing human-induced land cover change between 2013 and 2020. Protected areas were used as the unit of analysis for the following steps.

Matching for nightlight changes

Whether the conditions in neighbouring communities changed for the better or worse is a relative question. We are interested in knowing whether the adjacency of a protected area will restrict development compared to sites not adjacent to protected areas. Thus, we applied the matching method to compare the differences between nightlight changes from 2013 to 2020 in the settlements within a 10 km buffer of protected areas²¹ (i.e., treatment areas) and control sites similar to the treatment areas but not adjacent to protected areas.^{6,13} To perform the matching analysis, we first identified human settlements defined as villages, suburban or peri-urban areas, towns, and cities using the Global Human Settlement Grid data. The data delineate different settlement types worldwide at 1 km² resolution via a logic of cell clusters' population size, population, and built-up area densities.⁷⁸ As there could be a disappearance and emergence of human settlements, we included all the areas defined as human settlements by either 2000 or 2013 to form our human settlement dataset. We calculated the nightlight changes in these settlements between 2013 and 2020. We excluded protected areas without human settlements within the 10km buffer from this analysis. We extracted the average value of the matching variables and response variables to each settlement, which was used as the unit of analysis for local development in this study.

Our matching was based on a suite of variables that could influence the location of protected areas and development, including 1) development level in 2000 (proxied by nightlight value); 2) population density in 2000; 3) human footprint (1995–2004); 4) land cover in 2000; 5) annual mean precipitation in 2000; 6) annual mean temperature in 2000; 7) elevation; 8) slope; 9) net primary productivity in 2000; and 10) country^{6,20,45} ([Table S4](#)). We leveraged the matching to construct a comparison group with settlements further away (>20 km) from the protected area to serve as the counterfactuals. We matched the closest control unit for each treated unit according to the propensity score matching. We allowed matching with replacement to avoid introducing extra bias in the selection of control units, ensuring that each treated unit was matched with the closest comparison unit. More importantly, we put in additional matching restrictions that require the matched control and treated units to be from the same country, ecoregion, and land cover type.

Robustness check for matching

We carefully assessed the credibility of the matching procedure using balancing tests. Specifically, before assessing the effects of protected areas on land cover change, we leveraged the Quantile-Quantile Plot (Q-Q plot) to compare the distribution of covariates between the treatment and matched control groups ([Figure S6](#)). There was no significant difference between the two groups for all

covariates used in matching and even those not used (i.e., nightlights, precipitation, and temperature). These results suggest that our matching strategy performs well in extracting controlled units similar to the protected units within the same country.

In the robustness check, we adopted another popular matching technique, i.e., Propensity Score Matching (PSM). We have also conducted a rich set of alternative matching models to test the robustness, including two matching techniques (i.e., MDM and PSM), three alternative matching restrictions (i.e., matching within eco-region, landcover type, soil type), three alternative sets of covariates, and two alternative calipers for PSM (i.e., 0.01 and 0.02 for caliper). Three sets of covariates include historical nightlight, population density, and net primary productivity, all in 2000. Besides, set 1 includes slope, elevation, human footprint, average precipitation, and average temperature; Set 2 includes slope, elevation, and human footprint; and Set 3 includes slope, elevation, and road density. For each of the two matching techniques, we vary by alternative matching restrictions and sets of covariates used in the matching. For MDM, we consider one-to-one nearest-neighbor matching. For PSM, we also account for alternative calipers for selecting control groups.

After completing the matching process, we then move on to the regression stage. In total, we ran 48 combinations to test the robustness and sensitivity of the findings. We re-run the fixed effect regression model for each matched sample on changes in nightlights and natural land cover while accounting for the granular PA fixed effect and country fixed effect (Tables S1 and S2). In general, the treatment effects on changes in nightlights are positive but statistically insignificant. In contrast, the treatment effects on changes in natural land cover are negative and statistically significant. All the results show consistent average effects of protected areas on land cover and nightlight changes (Tables S1 and S2), demonstrating the robustness of our matching results.

OLS regression

With the matched sample, we leveraged the OLS regression model to estimate further the protected area's treatment effect on human-induced land cover and nightlight changes. The regression model is proposed as follows:

$$Y_{ijc} = \alpha_1 PA_{ijc} + X_{ijc} + \gamma_i + \delta_j + \theta_c + \varepsilon_{ijc},$$

where subscript i indicates PA (protected area), j stands for ecoregion, and c captures country. The outcome variables, denoted by Y_{ijc} , include changes in human-induced land cover or nightlights (2013 to 2020). The main explanatory variable of interest is PA_{ijc} , a binary indicator equalling one if the unit i in ecoregion j at country c is the protected area unit and zero otherwise. X_{ijc} absorbs a rich set of protected area-level covariates, including area size of settlement, access time to cities, annual mean precipitation, elevation, slope, human footprint, and road density. This set of covariates controls for potential factoring, leading to changes in outcome variables. Besides, we include many fixed effects at the ecoregion or country levels, denoted by δ_j and θ_c , respectively. These two fixed effects control for unobservable confounding factors at the ecoregion or country level. Finally, we replace these two fixed effects with more granular protected area fixed effects captured by γ_i , controlling for unobservable factors at the protected area unit. We also addressed the area of protected areas by applying the area as analytic weights and probability weights with additional analysis and reporting them in the supplementary materials (Table S5). Standard errors are clustered at the country level, allowing for serial correlation for error terms across countries. The coefficient of interest, α_1 , captures the treatment effect of the protected area. It compares outcome variables of interest (nightlight changes and human-induced land cover changes) between the protected area unit and similar counterfactual units while controlling for other possible confounders.

Relationship type definition

We depicted four relationships between protected areas and their neighbouring communities based on the changes in protected areas (land conversion) and nightlights. We estimated the effectiveness of each protected area by calculating the difference between the percentage of human-induced land cover change between 2013 and 2020 for all pixels within each protected area and matching control pixels. Specifically, if there was a lower rate of human-induced land cover change than the control sites between the beginning and end of the study period, we deemed a protected area effective at resisting land conversion and guarding natural habitat.^{20,45} This method values the contribution of protected areas in high land-use pressure regions.

For the neighbouring communities, similar or significantly higher nightlight increases than those in the matched settlements, we treated as no restriction of a protected area on development. After excluding protected areas without neighbouring community information, the final dataset to analyse the relationship contained 10,143 protected areas, which covered an area of approximately 3,891,986 km². We further compared the proportions of each relationship across different continents, biomes, and countries. In this analysis, we compared countries with more than ten protected areas to avoid the bias caused by small sample sizes.

Predictors for relationship types

After screening for correlation to avoid collinearity and selecting variables with a variance inflation factor less than 10, we included 14 predictors in the random forest model to test their effects on relationship-type occurrences (Synergy, Conservation Impaired, Development Impaired, and Retreat) (Table S4).⁸⁹ These predictors covered three major aspects: characteristics of protected areas, environmental conditions and socioeconomic conditions.

For the characteristics of protected areas, we selected the protection level (IUCN category), protection time (years of establishment), governance type (governance by the government, shared governance, private governance and governance by indigenous peoples and local communities) and area size (km²) as predictors. We classified the IUCN category I and II protected areas as strict protected areas and the other categories as less strict ones.

We included the net primary productivity (NPP), elevation, climatic conditions, and biome as predictors that can influence the ecosystem condition of protected areas and the way of living for people in neighbouring communities.⁹⁰ The changes in climatic factors could strongly influence some land cover changes and socioeconomic activities such as agricultural expansion and the suitability of human settlement.⁹¹ Thus, we calculated the changing rates in temperature and precipitation from 2000–2020 for each protected area using the Theil-Sen estimator and included them in the model. We included the biome in which the protected area is located following the classification system of Dinerstein et al.⁹⁰ NPP measures the amount of carbon fixed by vegetation after their respiratory requirements have been met in an ecosystem and is an indicator of ecosystem productivity.⁹² Since land productivity is a major driver of human settlement and development,⁹³ we calculated the average NPP in the neighbouring communities to assess its effects.

To reflect the socioeconomic drivers of the relationship between protected areas and neighbouring communities, we used the baseline economic development status (GDP) in 0–10km buffer, population density,⁷² population growth rate from 2000–2020, the connectivity to markets (travel time to nearby cities, mins) from the settlements, average road density in 0–10 km buffer of protected areas, and the country's development level (Human Development Index (HDI)) as predictors. The Human Development Index is a comprehensive indicator of life expectancy, education, and gross national income per capita. It is commonly used to represent the overall development level of a country.^{20,94} In addition, economic activities usually depend on market connectivity,⁸⁰ which can be indicated by the travel time to nearby cities from neighbouring communities. Since cities are economic development centres, the shorter it takes to reach a city, the stronger its market connectivity,⁸⁰ we calculated the average travel time to nearby cities for neighbouring communities. At the same time, roads around protected areas could pose greater pressure on natural resource use, thus causing land cover and land use changes, as well as other conflicts such as road kills.^{95,96} So, we added road density in the 0–10 km buffer of protected areas to reflect the pressure.⁸¹ This factor showed a low correlation coefficient with access time to cities from the settlements in the 0–10 km buffer, which was about -0.18 .

Random forest

We applied the random forest model in protected areas and their corresponding neighbouring communities to explore the possible effects of different predictors on relationship types. A random forest classifier grows unpruned classification trees and uses the majority of classification results from every individual tree to generate the final result.⁹⁷ It is especially effective and reliable in dealing with noisy data and containing different data types and sources; hence, it is widely used in ecological and geographic studies.^{98,99} Random forests can account for higher-order interactions and nonlinear relationships. This is suitable for our analysis because such interactions and relationships could exist between the predictors and the relationship types.¹⁰⁰ We excluded highly correlated variables (Figure S7). We then selected the model based on the overall accuracy of the model and the final model. To determine the most influential factors, we used the Mean Decrease Accuracy to determine the variable importance.⁹⁸ The Mean Decrease Accuracy index estimates the loss in prediction performance when the variable is omitted. This difference in accuracy was calculated by averaging this index across all trees in the forest, and it is more robust than other measures, such as the Gini indices.¹⁰¹ Each forest was created by generating 10,000 classification trees from a bootstrap sample of the data. To ensure the robustness of the random forest result, we ran the random forests 100 times with random seeds. We averaged the Mean Decrease Accuracy of these variables to understand the variable importance.

Since there were regional differences due to variations in economic development and ecosystems, we analysed different regions separately to understand possible drivers for each area. We focused on 14 major regions and calculated the percentage of each relationship (Figure S1). To understand if the factors explaining the relationship were the same across different developing regions, we derived the variable importance rank from random forests built for each of them. We used the R "randomForest" package¹⁰² to perform the above analyses.