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Conservation planning for retention, not just protection

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Abstract

Most protected area (PA) planning aims to improve biota representation within the PA system, but this does not necessarily achieve the best outcomes for biota retention across regions when we also consider habitat loss in areas outside the PA system. Here, we assess the implications that different PA expansion strategies can have on the retention of species habitat across an entire region. Using retention of forest habitat for Colombia's 550 forest-dependent bird species as our outcome variable, we found that when a minimum of 30% of each species' habitat was included in the PA system, a pattern of PA expansion targeting areas at highest deforestation risk (risk-prevention) led to the retention, on average, of 7.2% more forest habitat per species by 2050 than did a pattern that targeted areas at lowest risk (risk-avoidance). The risk-prevention approach cost more per km^2 of land conserved, but it was more cost-effective in retaining habitat in the landscape (50%–69% lower cost per km^2 of avoided deforestation). To have the same effectiveness preventing habitat loss in Colombia, the risk-avoidance approach would require more than twice as much protected area, costing three times more in the process. Protected area expansion should focus on the contributions of PAs to outcomes not only within PA systems themselves, but across entire regions.

KEYWORDS
area of habitat, Colombia, conservation prioritisation, deforestation, endemic species, forest-dependent birds

1 | INTRODUCTION

Protected areas (PAs) are established to protect biodiversity within them by restricting activities that could harm it (Dudley, 2008; Gaston et al., 2008; Maxwell et al., 2020). Earth's PA network now covers more than 15% of its terrestrial area and continues to expand (Secretariat of the Convention on Biological Diversity, 2020). This increase in coverage or formal area-based protection is frequently considered a headline measure of progress in biodiversity conservation. For example, Aichi Target 11 aimed for the inclusion of at least 17% of global terrestrial land in PAs by 2020 (Secretariat of the United Nations Convention on Biological Diversity, 2010) and the Kunming-Montreal Global Biodiversity Framework includes a target of 30% of land protected by 2030 (CBD, 2022). Others call for still more area to be protected, with the Half Earth project suggesting a target of 50% of the world protected to effectively halt biodiversity loss (Wilson, 2016) while Allan et al. (2022) argue for 44%. Part of the reason for the disparity in calls for how much of Earth to protect is that the contribution that this protection is intended to make to the overall retention of natural systems is less clear, remembering that habitat is also retained outside PA systems. Another framing of the discussion would be: How much of the world's natural ecosystems are we seeking to retain (and not lose), regardless of protected status (Maron et al., 2018), and how can we maximise the contribution that PAs make to this goal?

Establishing PAs is not an end on itself. Instead, their value arises from their contribution to broader conservation goals for entire landscapes, regions, or jurisdictions. This contribution of any one PA relates only in part to what and how much biota it contains. Of primary importance is the *difference* that the establishment of the PA makes to those biota, relative to a counterfactual scenario (what we define as effectiveness) (Andam et al., 2008; Ferraro, 2009; Pressey et al., 2015, 2021). In some situations, PAs have been shown to have limited capacity to prevent biodiversity loss (Geldmann et al., 2013, 2019; Negret et al., 2020). For example, one-third of PAs globally are under intense human pressure (Jones et al., 2018), half of protected forests have low or medium integrity (Grantham et al., 2020) and 3% of the forest inside PAs was lost in the first decade of the 20th century (Heino et al., 2015). However, poor PA effectiveness arises equally from establishing PAs where there are few immediate threats that such establishment can avert. For example, many PAs are located in areas of low human pressure, far from roads and cities, where slope and elevation are high and agricultural productivity is low (Joppa & Pfaff, 2009; Margules & Pressey, 2000). If a place becomes a PA, but that protected status does not reduce threats because there were few to avert in the first place, then effectiveness is low (Forero-Medina & Joppa, 2010; Geldmann et al., 2019; Joppa et al., 2008; Joppa & Pfaff, 2011), even if there is no biodiversity loss. Therefore, it is possible for large increases in PAs to make minimal difference, or even no difference at all, to the retention of natural areas at a regional scale (Andam et al., 2008; Ferraro, 2009; Ferraro & Pattanayak, 2006; Hernandez et al., 2021; Pressey et al., 2021).

Identifying cost-effective ways to expand PA coverage in order to improve the representation of species and ecosystems within the PA estate continues to be an important endeavour in conservation science (Pressey et al., 2007; Rodrigues et al., 2004; Venter et al., 2014). However, notwithstanding the importance of PA effectiveness, PA planning has often been driven primarily by objectives related to representation of biota solely *within the PA system* (Butchart et al., 2015; Rodrigues et al., 2004; Venter et al., 2014) rather than how increased formal protection of sites contributes to retention of biota *within all retained habitat* within and beyond PAs. Because of biogeographic bias in threats to natural areas and on PA distribution (Joppa & Pfaff, 2009), it has been argued that the most effective PA system should not focus primarily on increasing representation within the PA system itself. Instead, a PA system should be biased to those areas that are more likely to be lost in the absence of the protection so that the PA system makes the greatest contribution to equitable retention of natural areas, and their associated biota, across the region in question (Cowling et al., 1999; Maron et al., 2018; Meir et al., 2004; Pressey et al., 2004, 2015).

Strategies of protected area expansion that are more reactive (sensu Brooks et al., 2006)—prioritising places that are at more immediate risk of loss—are likely to incur higher per-hectare costs than proactive strategies—prioritising areas of lower threat but with unique or undisturbed ecosystems. Setting aside areas for conservation limits opportunity to expand some types of economic activities in the future (Adams et al., 2010), and places under more threat tend to be those with greater potential for economic activities and therefore of greater potential economic value (Adams et al., 2010; Margules & Pressey, 2000). As such, even if a reactive strategy is more effective in increasing retention of valued biota, it is not necessarily more cost-effective. Studies at different scales have demonstrated that the spatial distribution of costs can be just as important as that of biodiversity in determining optimal conservation investments (Adams et al., 2010; Guerrero-Pineda et al., 2022; Naidoo et al., 2006; Naidoo & Iwamura, 2007). It is important to highlight that socioeconomic conflicts may arise where PAs are established and that those socioeconomic aspects and other aspects not accounted for in this study must be taken into account when practical conservation decisions are taken (Schleicher et al., 2019). In some circumstances, strict protection might not be appropriate or feasible, and other conservation actions can be more suitable. For example, in Colombia, indigenous and afro-Colombian governance of forest has been shown to reduce forest loss (Negret et al., 2019; Vélez et al., 2020). In these scenarios, investment to facilitate the maintenance or improvement of their governance and support to develop economic activities like ecotourism (Múnera-Roldán & Ocampo-Peñuela, 2022) and agroforestry (Armenteras et al., 2019) can be more suitable actions than to aim for strict protection.

Here, we assess the implications of accounting for the effectiveness of PAs in terms of the retention, rather than just protection, of species' habitat when comparing options for PA expansion. We used Colombian forest birds as a case study. The country has the greatest bird species richness in the world (Ayerbe-Quiñones, 2018), and more than two-thirds of its continental area is covered with forest (World Resources Institute, 2022). We evaluated the impacts of PAs on deforestation rates, given forest loss is acute (Negret et al., 2019) and a major threat to bird habitat (Negret et al., 2021). Our outcome of interest was retention of total forest area in the landscape, and of forest habitat for each of the country's 550 forest-dependent bird species. We simulated the spatial distribution of future deforestation risk across Colombia, using a deforestation model developed in Dinamica EGO (Soares-Filho et al., 2002, 2013). We then developed PA expansion scenarios designed to efficiently achieve representation of different proportions of each species' habitat within the reserve system (20%–60%) under three different approaches: prioritising places where deforestation risk was high; prioritising places where deforestation risk was low; and ignoring deforestation risk. We then used the deforestation model to assess the projected proportion of habitat retained by 2050 for all the forest dependent bird species under the different PA expansion approaches, relative to a business-as-usual scenario (BAU) of no expansion of PAs. Finally, we used data on relative land value to compare the cost-effectiveness of the different approaches, based on their impact on forest and forest bird habitat retention across Colombia, regardless of whether it was inside or outside the PA system. Note that this exercise is intended to be illustrative of the differences in results between approaches to PA expansion, rather than a prescriptive proposal for expansion of PAs in Colombia.

2 | METHODS

2.1 | Distribution data for forest-dependent species

We used the BirdLife International data set depicting distributions of all native birds occurring in Colombia (BirdLife International & Handbook of the Birds of the World, 2021). These distribution maps are generated based on expert knowledge combined with available data for each species (BirdLife International & Handbook of the Birds of the World, 2021; IUCN Red List Technical Working Group, 2019), and even though in some instances they include commission and omission errors (Palacio et al., 2021), they are currently the maps for which the methodology is most transparent, and are the most widely used for scientific analysis. We then filtered the list to include only forest-dependent bird species. We used the Donald et al. (2018) definition of forest-dependent species: those whose listed habitat as defined by the IUCN habitat classification scheme (https://www.iucnredlist.org/resources/habitat-classification-scheme) included only the level 1 classification 'Forest & Woodland'. After filtering out non-forest and multi-habitat species, 550 forest-dependent species remained for analysis (Negret et al., 2021). We acknowledge that our broad classification of potential 'habitat'—forest—does not allow us to account for species-specific specialisations, this is accounted for to a certain extent by restricting habitat amount calculations to within the current range of where species occur. We adhered to BirdLife taxonomy (BirdLife International, 2022).

2.2 | Forest cover change model

We used data on forest extent in 2000, 2010 and 2015 to develop and validate a model of forest cover change in Colombia (Negret et al., 2019). These data were from the Colombian Institute of Hydrology, Meteorology and Environmental Studies—IDEAM (Galindo et al., 2014), who define forest as land with a minimum tree canopy density of 30% and a minimum height of canopy in situ of 5 m at the time of its identification. Tree cover from commercial forest plantations, palm crops and trees planted for agricultural production are excluded. These maps of forest cover had a resolution of 1 km^2 (Negret et al., 2019).

The forest cover change model was developed in Dinamica EGO to simulate the spatial distribution of deforestation across Colombia in 2050 using parameters that allocate deforestation on the basis of its empirical association with a set of predictor variables (Soares-Filho et al., 2002, 2013). We used a set of predictor variables that had been shown to be strongly associated with deforestation in the country including: proximity to roads, rivers, mining concessions and oil exploitation wells, distance to previous deforested areas, armed conflict intensity, distance to coca plantations, the presence of PAs, soil erosion, slope and elevation (Negret et al., 2019). Slope, soil erosion, and accessibility are associated with agricultural expansion (Grainger et al., 2003; Laurance et al., 2002). We then assessed the association of the predictor variables with deforestation from 2000 to 2015 using the Weights of Evidence method (Bonham-Carter, 1994; Soares-Filho et al., 2013). The weights of evidence is a Bayesian method, in which the effect of a spatial variable on a transition is calculated independently of a combined solution. The Weights of Evidence represent each variables influence on the spatial probability of a transition (forest to no forest) (Soares-Filho et al., 2009, 2013). We used the weights of evidence coefficients from the spatial determinants of forest change as inputs in a multi-stage process to model the spatial distribution of deforestation probability in the country (Negret et al., 2019; Soares-Filho et al., 2002). The model used the weights of evidence coefficients, the spatial distribution of the biophysical and anthropogenic variables and a predefined deforestation rate to produce a spatial map of deforestation probability. This map of deforestation probability had a resolution of 1 km^2 and values from 0 to 1, where pixels with values of 0 had the lowest deforestation probability while pixels with values of 1 had the highest deforestation probability. The model was calibrated with forest cover data for 2000 and 2010. To validate the accuracy of the model, forest cover change was simulated from 2010 to 2015 and compared with the observed forest change for that time period at different window size resolution, using the reciprocal comparison metric (Soares-Filho et al., 2013). The accuracy of the model in predicting deforestation patterns was 13% at 1 km^2 resolution and increased to 78% at 10 km^2 resolution (Negret et al., 2019). A full description of Weights of Evidence method and the reciprocal comparison metric can be found in Soares-Filho et al. (2013). A full description of the methodology to develop the deforestation model can be found in Negret et al. (2019), and the model inputs and outputs can be found on that article repository (https://doi.pangaea.de/10.1594/PANGAEA.899573).

2.3 | Historical forest cover data

We used maps of historical distribution of forest cover to assess the long-term impact of deforestation on the habitat of forest dependent birds. For this, we used the map of historical cover of forest ecosystems in Colombia created by Etter et al. (2017). This map was created using Landsat images for the country from 1972 to 1977, a combination of different ecosystem maps (Etter, 1998; Etter et al., 2006), and information on the distribution of areas of historical change where deforestation for agricultural land uses have occurred, to define the potential distribution of the extent of forest cover if human intervention and transformation had not occurred (Etter et al., 2006, 2017). The resolution of this forest cover map was 250 m^2 so we generated a 1 km^2 grid covering Colombia to match the resolution of the forest cover maps generated by Negret et al. (2019), and calculated the proportion of historical forest cover for each grid cell. We then, as with the Negret et al. (2019) maps, defined grid cells with >30% forest cover as forest and those with <30% as non-forest based on the threshold used by the Colombian Institute of Hydrology, Meteorology and Environmental Studies—IDEAM

(Galindo et al., 2014; Negret et al., 2019, 2021). Empirical and practical evidence shows that, despite the potential variation between individual species, in forest landscapes that retain less than 30% forest cover, bird species richness is markedly lower than in those with greater cover (Andrén, 1994; Flather & Bevers, 2002; Martensen et al., 2012; Ochoa-Quintero et al., 2015). Any pixel that was classified as non-forest using the historical forest cover layer was treated as non-forest for all subsequent time slices. Forest gain was not included in the analysis since many forest-dependent species do not use secondary forest as primary habitat (Barlow et al., 2007).

2.4 | Protected area expansion scenarios

Our aim was to compare the conservation outcomes, in terms of retention of bird habitat, that result from different approaches to expansion of PAs. To develop PA expansion scenarios for comparison, we used the spatial conservation prioritisation tool Marxan to identify areas where Colombia's PAs could be efficiently expanded to achieve different targets for representation of forest bird species habitat within the PA system. Marxan (Ball et al., 2009) uses a simulated annealing algorithm to identify near-optimal configuration of sites (planning units) within a region of interest where defined conservation targets can be achieved while minimising a determined penalty factor—often referred as cost.

We explored three approaches to PA expansion:

1. *risk-avoidance*: preferentially locating PAs in areas with lower deforestation probability (using deforestation probability as a penalty factor—so that a low probability has a low relative cost);
2. *risk-prevention*: preferentially locating PAs in areas with higher deforestation probability, according to our deforestation model (subtracting one minus the deforestation probability value and using it as a penalty factor [cost in Marxan]—so that a low probability has a high relative cost); and.
3. *risk-neutral*: ignoring deforestation (using a uniform penalty factor).

For each approach, we re-ran Marxan with a series of forest bird representation targets: inclusion of 20%, 30%, 40%, 50% and 60% of the mapped habitat of each forest-dependent species (as at 2015) within the PA system. We then calculated the average proportion of forest bird habitat protected under each scenario. For the prioritisation analysis we subdivided Colombia into 5 km^2 planning units. We did this as a compromise between the scale of the deforestation layers (1 km^2), and having a better deforestation model accuracy. We ran Marxan 100 times using 10,000,000 iterations. Existing PAs were locked into the solution, while only planning units with forest cover were available for selection by Marxan. The boundary length modifier, which is used to set the desired level of compactness of the protected area network was set to 0 for all the Marxan runs. This was done because our main aim was to evaluate the effect of the use of the deforestation risk in the prioritisation, while comparing overall area outcomes rather that identifying specific locations for selection. Figure 1 shows PA expansion scenarios under the risk-prevention and risk-avoidance approaches for a species PA representation target of 30%.

2.5 | Projections of forest cover retention

To explore the consequences of different PA expansion approaches for forest cover retention to 2050, we fed the most efficient Marxan solution for each scenario (the one that meet the representation target at the lowest penalty factor/cost) into the forest cover change model as alternative PA baselines. We calculated the average annual rate of deforestation between 2000 and 2015 for all of Colombia and separately for only the areas inside PAs. Then, using Dinamica EGO software (Molin et al., 2017; Teixeira et al., 2009), we generated a business-as-usual projection (BAU) of forest cover change in which no PA expansion was included, using the nationwide deforestation rate. We also generated projections of forest cover change for each of the scenarios of PA expansion under the three different expansion approaches. These projections were done using the deforestation rate inside PAs and only for the area that was defined as protected in each scenario. This allowed us to combine the scenarios of forest cover change within PAs with the scenario of forest cover change outside PAs, to develop a series of forest cover change projections for the entire country under each set of assumptions. This meant that the differences in the forest cover projected to 2050 between the BAU scenario, and the different scenarios of PA expansion were attributable only to the PA expansion.

To estimate the amount of habitat retained for each species under the BAU and alternative scenarios, we calculated the extent of suitable habitat for each forest-dependent species at three points in time: historical, 2015, and at the different projected forest cover for 2050 under each approach and representation target. We assumed all forest inside each species' range was potential habitat (recalling that only forest-dependent species were included). This included tropical rainforest, sub-Andean forest, Andean forest, mangrove and subparamo (Negret, 2001). We acknowledge that our broad classification of potential 'habitat'—forest—does not allow us to account for species-specific specialisations within the current range of where species occur. Moreover, we did not generate altitudinal range or forest type refinements for the species analysed as there are large information gaps in some regions of the country, as well as frequent reports of species occurring in previously unreported forest ecosystems or beyond the known elevational range (Gomez-Bernal et al., 2015; Negret et al., 2021). We then determined the projected loss against two baselines (historical and 2015) to calculate the proportion of the estimated habitat extent that the loss represented under each approach and representation target (Figure 2). We did this assessment for the 550 forest dependent species identified and separately for 69 regionally-endemic forest dependent species (defined as having ≥80% of their range in Colombia) (Negret

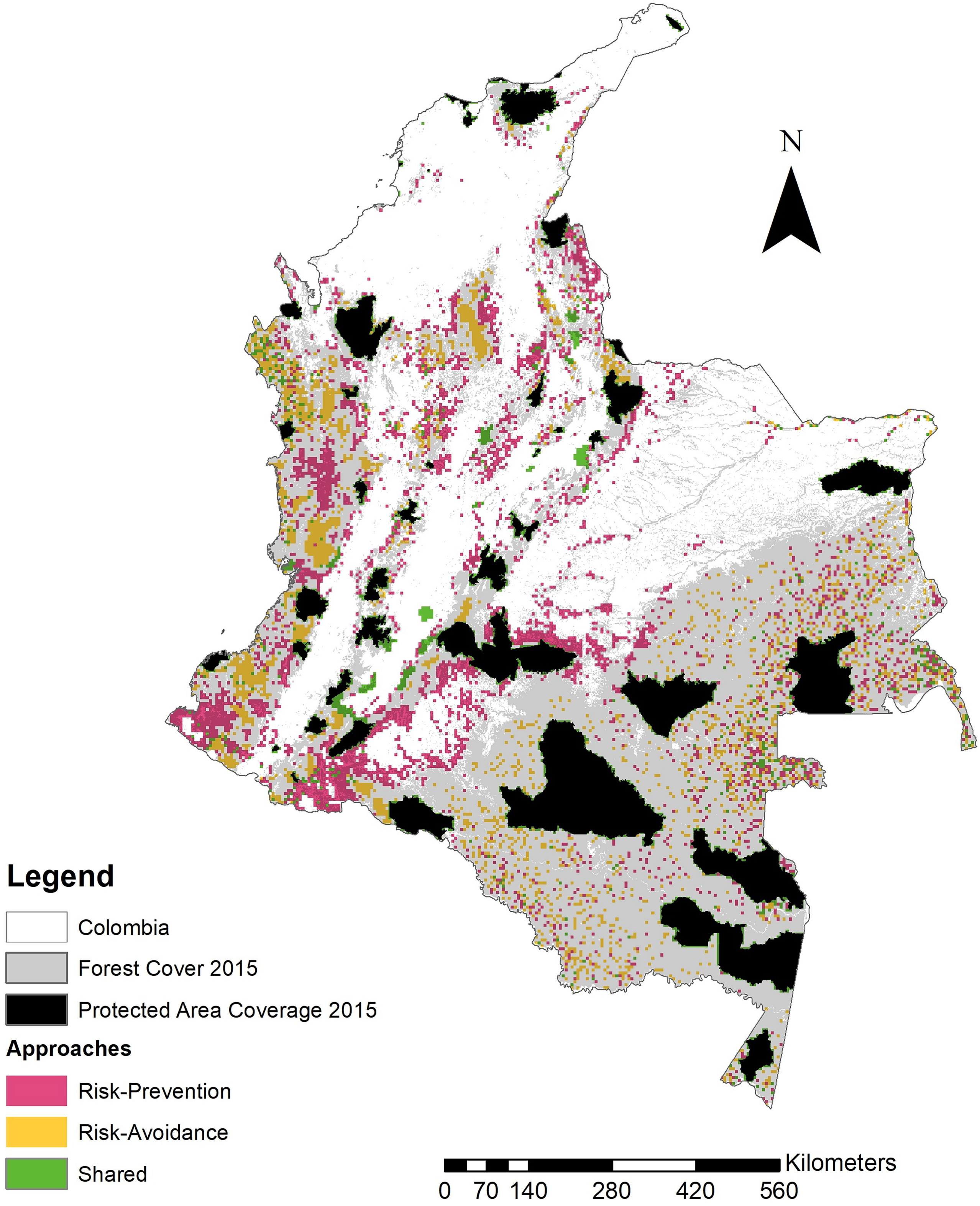

FIGURE 1 Maps of two PA expansion scenarios to protect at least 30% of the habitat of 550 forest dependent species in Colombia. Yellow represents a scenario where the expansion is done favouring the selection of areas of low deforestation, red represents an scenario favouring the selection of areas of high deforestation and green shows the areas shared by the two scenarios. Black represents the PA network in Colombia by 2015. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

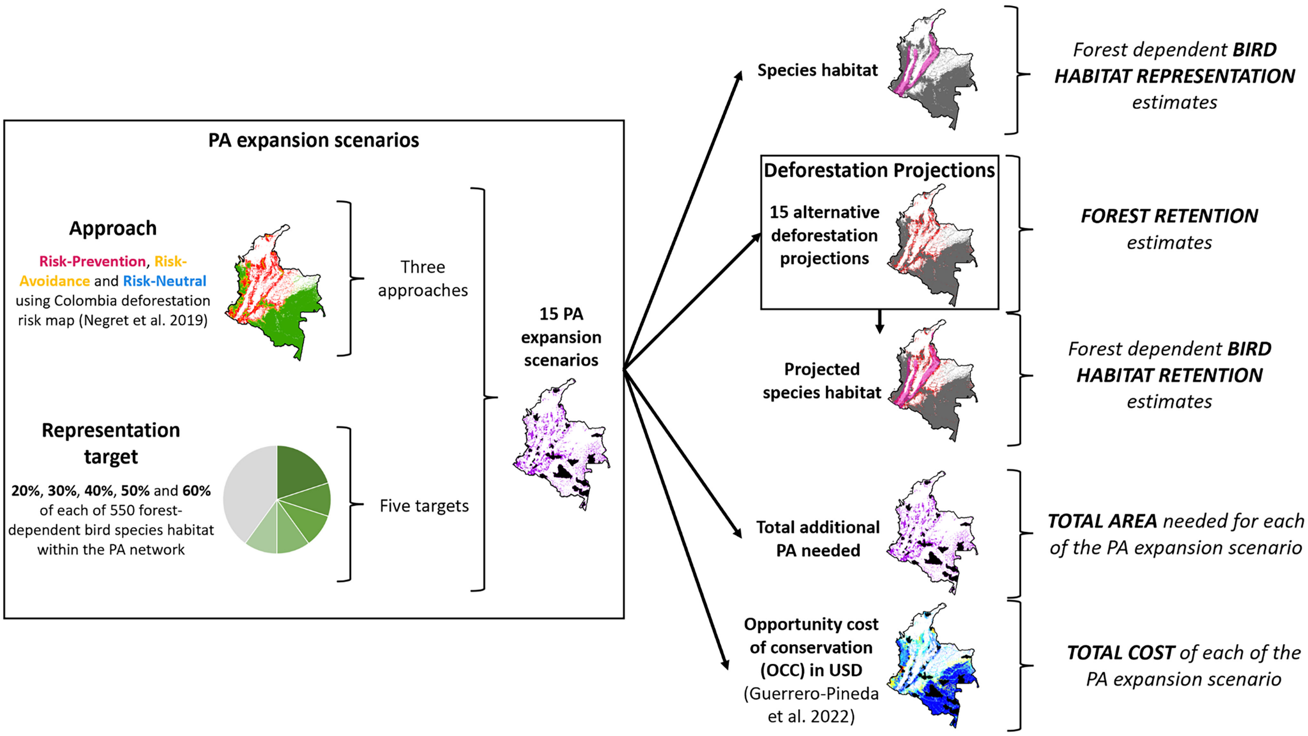

FIGURE 2 Methodological framework of the input data used and the process to generate the protected area expansion scenarios, the deforestation projections for the year 2050, the forest dependent habitat retention estimates for 2050 and the estimation of the total area needed and the cost of each of the scenarios. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

et al., 2021). For these species long-term survival is heavily dependent on their persistence in Colombia.

2.6 | Spillover effects

Spillover effects are caused when protection in one area impacts the nontarget neighbouring areas, with potentially negative (leakage) or positive (blockage) implications for biodiversity (Fuller et al., 2019). While the direction of spillover effects in Colombia is uncertain (Clerici et al., 2020; Fuller et al., 2019), we performed a sensitivity analysis that models deforestation projections for 2050 under different levels of hypothetical proportional average leakage for the proposed PAs under the different approaches. We first incrementally attributed a percentage of 25%, 50%, 75% and 100% leakage from the proposed PAs under each approach and species target, and assessed the changes to the overall results in terms of forest retention by 2050. We also explored a more extreme case—attributing a percentage of 25%, 50%, 75% and 100% leakage to the proposed PAs under the risk-prevention approach only, for each species target, while maintaining a hypothetical 0% leakage for the risk-avoidance approach. Potential blockage, where the unprotected surroundings of PAs experience less land-use change than would have otherwise occurred due to a positive spillover effect (leakage) (De Assis Barros et al., 2022; Fuller et al., 2019), was not modeled as this would only increase the effect that we reported in the main analysis.

2.7 | Relative cost of the three approaches

As the final step, we explored likely differences in the costs associated with the three different approaches to PA expansion, to compare their cost-effectiveness in achieving the retention of forest habitat in the entire landscape, as opposed to just the retention of forest inside protected areas. We did this by calculating both the cost by km^2 of forest protected, as well as the cost per km^2 of additional forest retained, under the different approaches. To approximate spatial variation in the likely cost of land acquisition for conservation, we used the opportunity cost of conservation values (OCC) developed by (Guerrero-Pineda et al., 2022) for the Colombian territory. The OCC is a broad proxy for the expected cost of potential conservation interventions across Colombia. It was used only to explore cost in relative terms among different PA expansion scenarios, not to estimate an absolute cost of implementing an scenario. Their approach models the expected net present value of potential net rents resulting from agricultural uses of a forested parcel, while accounting for the probability of conversion to agriculture (including coca crops) or cattle ranching. With the assumptions that each agricultural use, k, has annual expected return per unit area R_k, and each parcel i has probability of conversion P_{ik} from forest to agricultural use k, the expected value for a given discount rate δ is

$$\text{OCC} = \sum_{i=1}^{I} \sum_{k=1}^{K} P_{i,k} \frac{R_k}{\delta}.$$

Thus, OCC represents the sum of the probability-weighted expected agricultural returns, summed across parcels (Guerrero-Pineda et al., 2022). The probability of conversion (P_{ik}) was estimated based on the product of an alternative deforestation risk model (P_{def}) and a second model that predicts the probability of conversion to a particular type of agricultural activity (P_{ag_k}) (Guerrero-Pineda et al., 2022). Both models are then used to compute the total probability of conversion to each type of agricultural activity k in a parcel i ($P_{ik} = P_{def_i} \times P_{ag_{i,k}}$). For more detail on the OCC modelling procedure, refer to (Guerrero-Pineda et al., 2022). The discount rate accounts for the risk-adjusted future opportunity cost of purchasing the land. We used three discount rates of 5%, 10% and 20% to account for the uncertainty related to this parameter (Campos et al., 2015; Guerrero-Pineda et al., 2022). We calculated the OCC value per km^2 to match the resolution of the forest cover maps. In order to not omit the pixels that were classified as no forest by (Guerrero-Pineda et al., 2022) we used the average OCC value of the pixels within a 20km buffer.

3 | RESULTS

3.1 | Forest cover retention

Under the BAU scenario, with no PA expansion, 13% of the forest cover extent that existed in 2015 was projected to be lost by 2050 (Figure 3a). The spatial distribution of land selected for protection differed substantially among the three PA expansion approaches (Figure 1). This led to notable differences in the forest retention outcomes achieved (Figure 3), despite the same representation targets being achieved (Table 1), and no substantial differences among approaches in the area of forest habitat protected for a given representation target (Table 1; Figure S1a).

As expected, the approach that prioritised areas of high deforestation risk for PA expansion (risk-prevention) outperformed approaches that ignored deforestation (risk-neutral) or avoided it (risk-avoidance) in terms of forest retention across the country. For example, when the PA network was expanded to 25.3% of the country's forest under the risk-prevention approach (the area selected under the 20% representation target), it was projected to avoid 20,388km^2 of BAU forest loss by 2050. Under this scenario 89.8% of present-day forest would be retained. In order for the risk-avoidance approach to achieve a similar retention of forest, an expansion of the PA network to 59.3% of the country's forest would be needed (the area selected under the 60% representation target). This would avoid 21,400km^2 of BAU forest loss by 2050 and retain 90% of the country's forests (Figure 3a) but require more than twice area protected than if the risk-prevention approach was used. The scenarios using the risk-neutral approach when the PA expansion is done ignoring deforestation risk slightly outperformed the risk-avoidance one in overall retention of forest habitat but remained far inferior to the risk-prevention approach (Table 1; Figure 3a).

3.2 | Spillover effects

The results from the sensitivity analysis incrementally attributing a percentage of 25%, 50%, 75% and 100% leakage to the proposed PAs under each approach and species target showed that our substantive conclusions would be unchanged, except in the implausible scenario of 100% leakage (when all approaches perform equally; Figure S2). For the second sensitivity analysis attributing a percentage of 25%, 50%, 75% and 100% leakage to the proposed PAs under the risk-prevention approach only, for each species target, while maintaining a hypothetical 0% leakage for the risk-avoidance approach showed that leakage in the risk-prevention approach would have to be 75% higher than for the risk-Avoidance approach for our substantive conclusions to be changed (Figure 4).

3.3 | Cost comparison among scenarios

The total and per km^2 cost of expanding the PA system was greater when prioritising protection of areas of higher deforestation risk (risk-prevention) than other approaches with the same representation targets (Table 1; Figure S1d). However, the risk-prevention approach was the most cost-effective in achieving the retention of forest and forest bird habitat within Colombia (Table 1; Figure 3d,e), independent of the discount rate used (Figure S3). For example, using the risk-prevention approach to achieve a forest retention outcome of 89.8% was estimated to cost \$11.8 billion USD, when using a 10% discount rate. On the other hand, using the risk-avoidance approach to retain a similar amount of forest (90%) incurred estimated costs of \$36.1 billion USD—more than three times more expensive (Figure 3b). The scenarios using the risk-neutral approach, in which the PA expansion ignored deforestation risk, were slightly more cost-effective than the risk-avoidance approach, but their performance, in terms of habitat retention was very similar (Table 1; Figure 3). While the total cost of each approach varied depending on the discount rate used, the proportional differences between approaches were maintained (Figure S3).

3.4 | Species habitat retention

Under the BAU scenario, forest-dependent bird species in Colombia were expected to lose an average of 23.5% of their 2015 habitat extent by 2050 (Figure 3b,e). Expanding the PA network to 25.3% of the country's forest, using the approach that prioritised areas of high deforestation (risk-prevention), would decrease the average loss of habitat for forest dependent species to 16.8%, and was the most cost-effective approach. On the other hand, when the PA expansion targeted areas of low deforestation risk (risk-avoidance), an expansion of the PA network to 59.3% of the country's forest would be required to reduce the average loss of habitat to a similar level (16.3%). However, this would imply an estimated

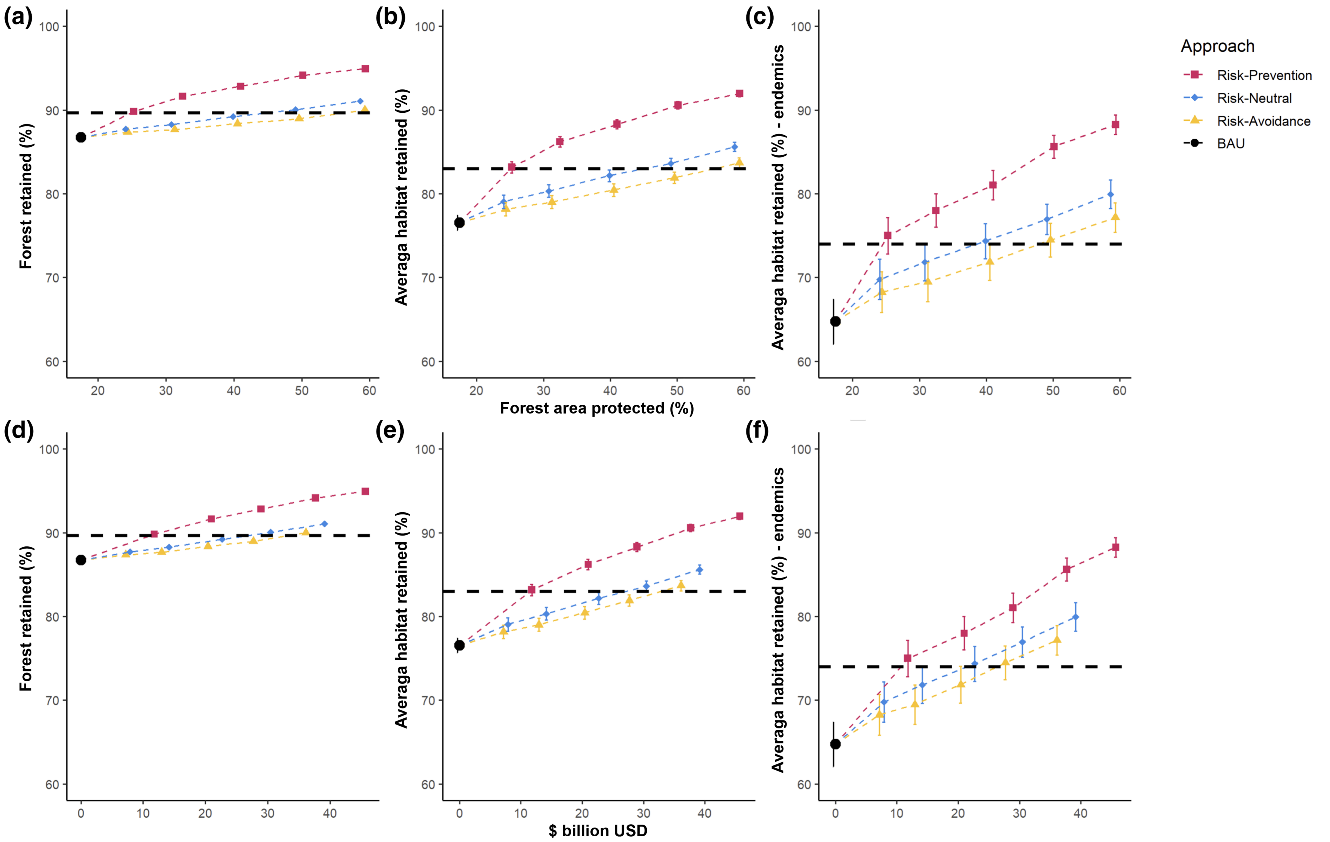

FIGURE 3 Amount and cost of forest area protected and the (a, d) proportion of forest retained in Colombia by 2050 under a BAU scenario of no PA expansion (black circles) and three different approaches of PA expansion. Favouring the selection of areas of low deforestation (yellow triangles), favouring the selection of areas of high deforestation (red squares) and not taking into account deforestation pressure (blue diamonds). The yellow, blue and red figures represent the amount and cost of PA needed under each scenario to meet the prioritisation representation targets (20%, 30%, 40%, 50% and 60% of each species habitat protected). The black circle represents the amount and cost of PA in Colombia by 2015. (b, e) Average proportion of 550 forest dependent species habitat retained in Colombia by 2050 under the three different approaches of PA expansion. (c, f) Average proportion of 69 endemic forest dependent species projected habitat retained in Colombia by 2050 under the three different approaches of PA expansion. Vertical bars show the standard error. The horizontal dashed lines indicate thresholds of forest retention or average habitat retention for the reader to compare differences in the performance of approaches. The opportunity cost of conservation calculations for these figures were done using a 10% discount rate.

cost three times higher, compared to the risk-prevention approach (Figure 3e). When the PA expansion ignored deforestation risk (risk-neutral), it slightly outperformed the approach of avoiding areas of high deforestation risk (risk-avoidance) in terms of retention of bird habitat (Figure 3b,e).

When assessing the expected habitat retention by 2050 against the historical habitat available for each species the differences in performance among approaches had the same pattern as for the loss compared to the 2015 habitat extent, but the differences were more pronounced. Under BAU forest dependent species were projected to lose, on average, 37.7% of their historical habitat by 2050 (Figure S1b). While expanding the PA network in areas of high deforestation (risk-prevention) to 25.3% of the country's forest would decrease this average loss to 33.3%, when the PA expansion was done targeting areas of low deforestation (risk-avoidance), expansion of the PA network to 59.3% of the country's forest for a price three times higher would be needed to reduce the average loss of habitat to a similar level (33.2%; Figure S1b,e).

3.5 | Regionally endemic species habitat retention

When focussing only on habitat retention for regionally endemic species, the relative performance of the three approaches was similar to that of all species. However, the difference in outcomes among approaches decreased, especially in relation to cost. Under BAU, regionally endemic forest-dependent species were projected to lose on average 35.3% of their current and 52.3% of their historical habitat by 2050 (Figure 3c–f; Figure S1c–f). Expanding the PA network in areas of high deforestation (risk-prevention) to 25.3% of the country's forest would decrease these values to 25.0% and 46.4%, respectively. On the other hand, when the PA expansion targeted areas of low deforestation (risk-avoidance), an expansion of the PA network to 49.6% of the country's forest would be required to reduce the average current and historical loss of habitat to a similar extent (Figure 3c,f; Figure S1c,f). This implies twice the amount of area needed and a cost more than two times greater, to achieve a similar outcome.

TABLE 1 Amount of protected forest needed, in km^2 and in percentage of the total forest cover in Colombia in 2015, and the total and per km^2 cost of protecting and retaining the habitat of 550 forest dependent species under three different PA expansion approaches. Favouring the selection of areas of low deforestation (risk-avoidance), favouring the selection of areas of high deforestation (risk-prevention), and not taking into account deforestation pressure (risk-neutral). The representation targets show the minimal amount of habitat covered by PAs for each of the 550 forest dependent species (20%, 30%, 40%, 50% and 60%) under each PA expansion scenario. The opportunity cost of conservation calculations for this table were done using a 10% discount rate.

Scenario	Representation target	Forest protected 2015 (km^2)	Forest protected 2015 (%)	Additional forest protected (km^2)	$USD billion	$USD/$km^2$ protected	Additional forest retained (km^2)	$USD/$km^2$ retained
BAU	BAU	115,040	17.5	0	0	0	0	0
Risk-prevention	20	166,321	25.3	51,281	11.8	229,608	20,388	577,522
Risk-avoidance	20	160,369	24.4	45,329	7.2	158,220	4205	1,705,573
Risk-neutral	20	158,459	24.1	43,419	7.9	181,680	6533	1,207,466
Risk-prevention	30	213,745	32.5	98,705	21.0	212,533	32,331	648,852
Risk-avoidance	30	205,764	31.3	90,724	13.0	142,815	6099	2,124,406
Risk-neutral	30	202,803	30.8	87,763	14.2	161,403	10,230	1,384,675
Risk-prevention	40	270,044	41.0	155,004	28.9	186,747	40,173	720,548
Risk-avoidance	40	266,805	40.5	151,765	20.4	134,477	10,743	1,899,736
Risk-neutral	40	262,655	39.9	147,615	22.7	153,764	16,472	1,377,970
Risk-prevention	50	330,121	50.1	215,081	37.7	175,242	48,793	772,473
Risk-avoidance	50	326,609	49.6	211,569	27.7	130,849	14,723	1,880,302
Risk-neutral	50	323,221	49.1	208,181	30.5	146,399	21,880	1,392,939
Risk-prevention	60	390,827	59.4	275,787	45.7	165,688	54,026	845,791
Risk-avoidance	60	390,431	59.3	275,391	36.1	131,132	21,400	1,687,502
Risk-neutral	60	385,984	58.6	270,944	39.2	144,521	28,497	1,374,074

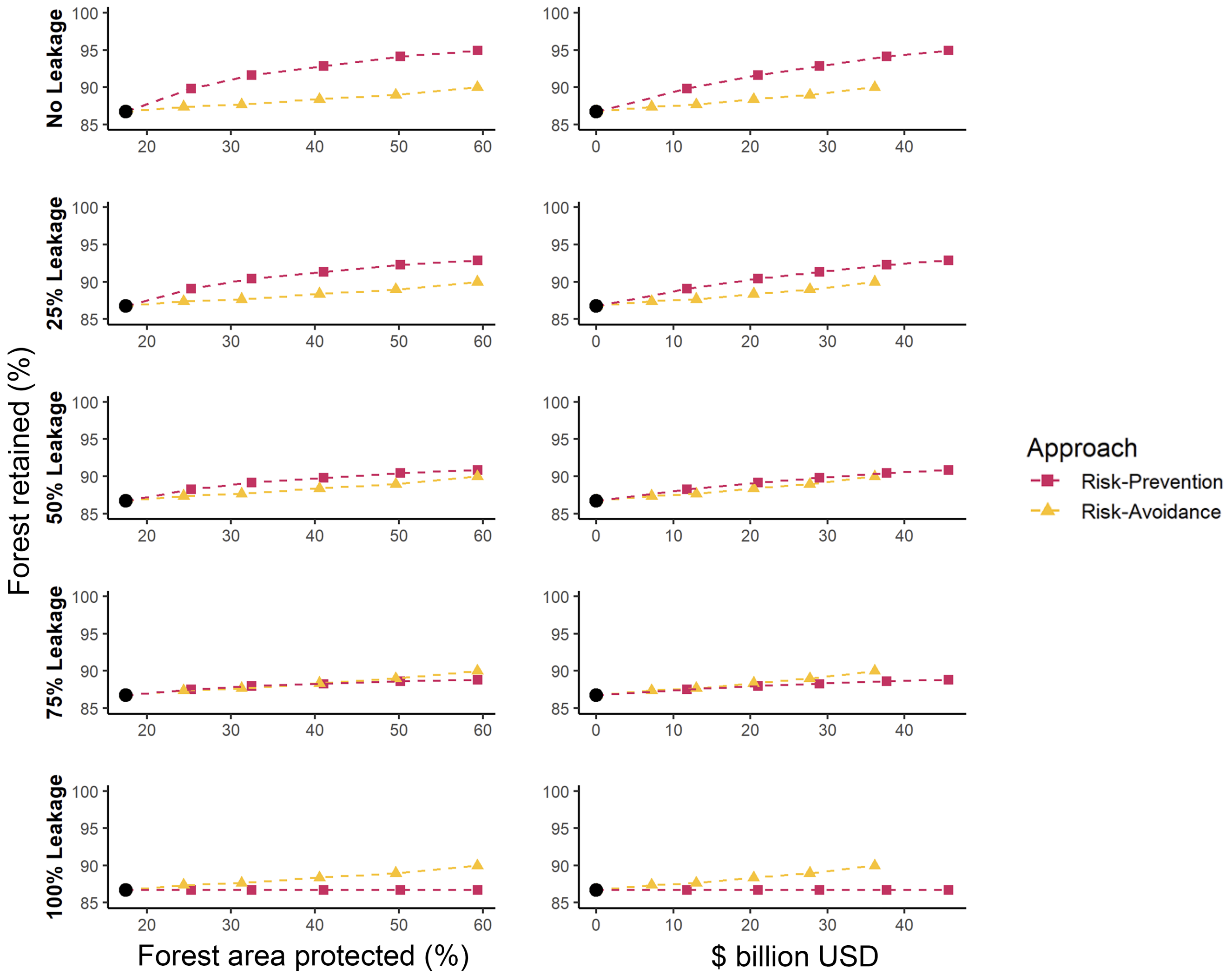

FIGURE 4 Sensitivity analysis of the effect of leakage attributing a percentage of 25%, 50%, 75% and 100% leakage to the proposed PAs under the risk-prevention approach only, for each species target, while maintaining a hypothetical 0% leakage for the risk-avoidance approach. Each panel shows the amount and cost of forest area protected and the proportion of forest retained in Colombia by 2050 under a BAU scenario of no PA expansion (black circles) and two different approaches of PA expansion. Favouring the selection of areas of low deforestation (yellow triangles) and favouring the selection of areas of high deforestation (red squares). The yellow and red figures represent the amount and cost of PA needed under each scenario to meet the prioritisation representation targets (20%, 30%, 40%, 50% and 60% of each species habitat protected). The black circle represents the amount and cost of PA in Colombia by 2050.

Some species had very large differences in the habitat retained between scenarios (Figures S4 and S5). For species present in areas of low deforestation risk the difference in retention between the BAU, the risk-prevention and the risk-avoidance scenarios was low. On the other hand, some species with very restricted distributions occurring in areas with particularly high deforestation risk also had low differences in habitat retention between scenarios as similar areas of their habitat were selected under both approaches, but any part of their habitat that was not protected was likely to be deforested. When assessing the retention of the current (2015) habitat of the regionally endemic species, the results showed similar patterns to that of historical habitat, but there was a greater difference among scenarios (Figure S5).

4 | DISCUSSION

Our results showed that in the case of Colombia, prioritising areas of high deforestation risk for protected area expansion was the most cost-effective approach when the objective was to maximise forest and bird habitat retention in the landscape. This remained the case even though high risk areas often had a higher cost per unit area (Figure S6). This approach outperformed approaches that ignored or avoided areas of high deforestation risk. Although the per km^2 land cost was 126%–149% higher when PA expansion was focussed on areas of higher deforestation risk, the cost per km^2 of avoided deforestation was much lower—by 50%–69%. To achieve retention of an average 88% of current forest bird habitat, expanding the PA system by prioritising places at lower deforestation risk required more than twice as much protected area, and cost more, than approaches that prioritised sites of high deforestation risk. Although it is intuitive that targeting protection to areas that most need it would be more effective, the extent to which the approach outperforms more commonly used approaches to prioritisation is often not quantified. We found strikingly large differences in the area required to achieve similar retention of forest bird habitat, and these differences were even greater when comparing the cost-effectiveness of the different strategies. More research in other countries and for other vertebrate groups is needed to determine if prioritising areas of high deforestation risk is consistently the most cost-effective approach to retain species habitat at the landscape level.

Protected area spillover can influence deforestation patterns in the landscape. Evidence shows that in the case of South America, the effect of blockage can be more prevalent than that of leakage (De Assis Barros et al., 2022; Fuller et al., 2019). Additionally, a recent study done in Colombia found that deforestation increased both inside and in the surroundings of PAs after the peace agreement with FARC, but it was higher inside PAs (Clerici et al., 2020). If blockage is the dominant form of spillover effect in Colombia, the difference between approaches would be higher than we estimated. On the other hand, our sensitivity analysis showed that leakage in the risk-prevention approach would have to be at least 75% higher than for the risk-avoidance approach for our substantive conclusions to be changed. Further research into PA spillover, its extent, its magnitude and its impact on deforestation patterns at a landscape scale is needed. Protected Area Downgrading, Downsizing, and Degazettement (PADDD) can also influence PA effectiveness. In the Colombian context, there have been PADDD propositions, but most have not been successful (Conservation International & World Wildlife Fund, 2022) and there have been no PADDD events since 1991 (Golden et al., 2019). Due to this we did not simulate potential PADDD events in our analysis. However, PADDD events should be taken into account where possible, specially in places where they are a high risk, as this could affect the benefit of establishing PAs.

Several studies have assessed the benefits and disadvantages of taking risk-avoidance or risk-prevention approaches in conservation (Brooks et al., 2006; Cardador et al., 2015; Mokany et al., 2020; Watson et al., 2018; Wilson et al., 2019). Targeting protection in areas that are at higher risk of being lost is the most intuitive approach if the main conservation objective is the retention of conservation features (e.g., species) in the landscape. However, many global and local conservation planning exercises are focused on increasing the representation of conservation features only within the PA network without accounting for what happens to the rest of that conservation feature in the landscape (Butchart et al., 2015; Forero-Medina & Joppa, 2010; Rodrigues et al., 2004; Venter et al., 2014). Our results show that the risk-prevention approach was more expensive and needed more area than the risk-avoidance one to achieve a particular representation target within the PA system, but in terms of the ultimate outcome of interest—retention of bird habitat in Colombia—it was always the most cost-effective approach. These results show that focussing only on representation of conservation features within PA systems can lead to conservation plans that perform poorly in contributing to habitat retention in the landscape. Moreover, this approach of focusing on representation does not take into account that PAs are not 100% effective (Geldmann et al., 2019; Jones et al., 2018), and that this effectiveness varies through space (Geldmann et al., 2019; Graham et al., 2021; Negret et al., 2020).

At a global scale, PAs have been disproportionately established in areas of high elevation and slope, far away from roads and cities and with low suitability for agriculture (Joppa & Pfaff, 2009; Pressey et al., 1996). The greater cost of protection in areas where multiple alternative land-uses compete is part of the reason for this, as it is financially and politically easier to protect land with low financial value (Ando et al., 1998; Joppa & Pfaff, 2009; Margules & Pressey, 2000; Pressey et al., 1996). Despite this, several studies have shown that accounting for the economic costs in the planning process markedly increases the efficiency of resulting conservation strategies (Naidoo et al., 2006; Naidoo & Iwamura, 2007). For Colombia, forested areas with higher deforestation risk tend to be more expensive (Figure S6). Our results show that despite this, the approach that prioritised areas of high deforestation risk for PA expansion was still the most cost-effective in terms of forest bird habitat retention in the landscape. Therefore, the benefit of the risk-prevention approach for forest bird habitat retention in Colombia is high enough to compensate the elevated cost of acquiring that land.

The protection of species habitat is often necessary to avoid their extinction (Barnes et al., 2016; Geldmann et al., 2013). However, for some species habitat destruction might not be the primary driver of extinction risk (Allan et al., 2019; Maxwell et al., 2016). Also, increasing the proportion of habitat that is protected may not be the most cost-effective conservation action for some species, especially if the cost of purchasing the land is high. We found that for some species that are present in areas of low deforestation, the difference in projected retention of habitat between the different conservation approaches was low. For those species, little deforestation was expected regardless of the amount of habitat protected. In those cases, understanding better the species distribution and ecology, as well as other threats like hunting (Benítez-López et al., 2017), wildlife trade (Symes et al., 2018) and disease (Thomas et al., 2007) is potentially more important than protecting their habitat. It is important to identify species for which interventions other than tenure change are more important, as conservation funds for those species could be invested in conservation actions focused on other threats. Further, including them within PA prioritisation exercises may dilute the effectiveness of solutions. On the other hand, for species that have very restricted distributions and that are present in areas with particularly high deforestation risk, protection of the remaining habitat is essential and urgent.

It is important to highlight that there are multiple benefits that can be obtained from expanding the extent of the PA network in addition to increasing the retention of ecosystems and species habitat. However, adequate funding and management is essential if the benefits of PA expansion are to be realised (Leverington et al., 2010). PA designation can be a useful tool to enable focussed management to improve the condition of the habitat in an area. For example, in Costa Rica, an estimated 13.5% of previously unforested lands inside PAs reforested because they were afforded protection (Andam et al., 2013). Fire (Rodríguez et al., 2013) and invasive plant and vertebrate management (Foxcroft et al., 2017; Gallardo et al., 2017) can all be facilitated by PA designation. Also, PAs can make it easier to directly manage particular species populations. This can be especially important for populations of range restricted and threatened species. For example, both gorillas and chimpanzees persistence in the Congo Basin depend heavily in the management of the populations inside PAs (Tutin, 2001), and waterfowl populations globally are benefited by PAs when management interventions are targeted at those taxa (Wauchope et al., 2022). These additional purposes for PA expansion are often just as important as a focus on the retention of ecosystems and species habitat. As such, the role of PAs will vary in different contexts, and the full range of expected benefits and how different management actions affect them has to be considered when planning PA expansion to ensure multiple objectives are achieved (López-Cubillos et al., 2022; Nelson et al., 2009; Williams et al., 2020).

The main objective of this research was to examine the importance of considering retention of forest habitat in the landscape, as opposed to just representation inside PA networks, as a key outcome relevant to effectively achieve national and international conservation goals. For this reason, the areas defined through our analysis are not intended as specific recommendations of where to expand PAs in Colombia as they represent a virtual scenario based on assumptions including: (a) protected areas are expanded independently of the location of current protected areas; (b) establishing a protected area has zero spillover effects on deforestation; (d) the spatial configuration of habitat in the landscape does not affect species persistence; and (e) agricultural opportunity costs are the only financial costs of protected area expansion. Decisions about the location of PAs must take into account multiple ecological, social, geographical, political, environmental and historical factors that are not included in this analysis (Margules & Pressey, 2000; Pressey et al., 2007). Conflicts between socioeconomic and conservation objectives may arise because of PA establishment (Schleicher et al., 2019) and in many cases the establishment of strict PAs (Categories I & II) is not appropriate; instead, PAs that allow sustainable use of natural resources (Category VI) could be more acceptable to local communities. Moreover, in certain places PA establishment might not be possible or appropriate, due to existing land tenures. In such areas, implementation of codesigned conservation solutions with the landowners through a prior informed consultation can be an alternative (Chambers et al., 2021). Indigenous territories in particular have high overlap with protected and forested areas globally (Garnett et al., 2018), and Indigenous-led management of such areas can reduce deforestation under certain conditions (Sze et al., 2022). Similar results have been found for afro-Colombian territories (Vélez et al., 2020).

Defining clearly the purpose and objectives of local and global area-based conservation actions is critical (Pressey et al., 2021). When the objectives of such conservation actions are based only on representation of conservation features in the PA network, the often-large contribution of these features outside PAs is overlooked. While it is important to acknowledge that resources for PA establishment are limited, making it difficult to always purchase the land under higher risk of deforestation, our results highlight the importance of expansion of PA networks to be directed, when possible, towards areas and for species that are at higher risk of disappearing, and not only at areas that are poorly represented within reserve networks.

AUTHOR CONTRIBUTIONS

Pablo Jose Negret: Conceptualization; methodology; formal analysis; writing initial draft; writing - reviewing and editing. **Ruben Venegas:** Formal analysis; methodology; writing – review and editing. **Laura J. Sonter:** writing – review and editing. **Hugh P. Possingham:** Conceptualization; writing – review and editing. **Martine Maron:** Conceptualization; methodology; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

Forest cover maps and the spatial layers to generate the deforestation risk layers as well as those deforestation risk layers from Negret et al. (2019) are available at https://doi.pangaea.de/10.1594/PANGAEA.899573. Data from Guerrero-Pineda et al. (2022) and Bird Life international used in this study as well as the Marxan protected area expansion scenarios and the resultant forest cover projections for Colombia in 2050 are available from Zenodo at https://zenodo.org/records/10672391.

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SUPPORTING INFORMATION

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