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# Confronting and resolving competing values behind conservation objectives

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**Diverse motivations for preserving nature both inspire and hinder its conservation. Optimal conservation strategies may differ radically depending on the objective. For example, creating nature reserves may prevent extinctions through protecting severely threatened species, whereas incentivizing farmland hedgerows may benefit people through bolstering pest-eating or pollinating species. Win-win interventions that satisfy multiple objectives are alluring, but can also be elusive. To achieve better outcomes, we developed and implemented a practical typology of nature conservation framed around seven common conservation objectives. Using an intensively studied bird assemblage in southern Costa Rica as a case study, we applied the typology in the context of biodiversity's most pervasive threat: habitat conversion. We found that rural habitats in a varied tropical landscape, comprising small farms, villages, forest fragments, and forest reserves, provided biodiversity-driven processes that benefit people, such as pollination, seed dispersal, and pest consumption. However, species valued for their rarity, endemism, and evolutionary distinctness declined in farmland. Conserving tropical forest on farmland increased species that international tourists value, but not species discussed in Costa Rican newspapers. Despite these observed trade-offs, our analyses also revealed promising synergies. For example, we found that maintaining forest cover surrounding farms in our study region would likely enhance most conservation objectives at minimal expense to others. Overall, our typology provides a framework for resolving the competing objectives of modern conservation.**

agriculture | bird | conservation | ecosystem services | multifunctionality

For at least the last century (1, 2), there has been fierce debate over whether nature should be conserved primarily to benefit people or for its own sake. Recently, conservation scientists and practitioners have called for the adoption of a more holistic and inclusive conservation ethic that accepts diverse motivations for conservation (3). In practice, however, limited funding and resources precipitate conflict between individuals and institutions with different motivations for conserving nature. Such conflicts often arise because the best intervention for achieving a chosen conservation objective may fail to achieve another. For example, the influential "biodiversity hotspots" concept directs conservation resources to areas with high rates of habitat loss and high densities of endemic species (4). But hotspots could be delineated using criteria related to virtually any conservation objective. Targeting conservation efforts only on hotspots of extinction or endemism could overlook other species and ecosystems that deliver vital benefits to people (e.g., wetlands that purify water and mitigate floods) (5, 6; but see ref. 7).

Because conservationists have disparate and diverse values (8), measuring trade-offs is critical. A typology of conservation objectives could help identify trade-offs. In the past, scientists have created typologies to promote multiple components of biodiversity for monitoring and consideration in conservation decisions. For example, biodiversity has been divided across scales (α, β, and γ diversity) (9), into different species groupings (functional, phylogenetic, taxonomic, or morphological diversity) (10), and into compositional, structural, and functional attributes (11). Typologies have also been used to manage ecosystem services; for example, dividing services into "provisioning," "regulating," "cultural," and "supporting" categories (12). A benefit of typologies is that multiple categories of biodiversity and ecosystem services can be analyzed simultaneously to identify and compare trade-offs. For example, one recent study reported low congruence between bird functional, phylogenetic, and taxonomic diversity, and underrepresentation of functional diversity in existing protected areas (13). Another showed that most regulating ecosystem services decline in areas where provisioning services increase (14).

Early attempts to monitor and manage nature focused on developing indicators that reflected aspects of biodiversity that were widely valued (10, 15, 16). We drew from this work to define a typology for nature conservation that is explicitly linked to conservation objectives, rather than attributes of biodiversity or ecosystem services per se. Specifically, we delineated seven common objectives for nature conservation: (*i*) preventing global extinctions: extinction risk; (*ii*) conserving local populations or regional species pools: extirpation risk; (*iii*) preserving the legacy of past evolution by sustaining biodiversity across the tree of life (15, 17): evolution; (*iv*) restoring historic species assemblages: naturalness; (*v*) securing the flow of material resources from nature to people: provisioning services; (*vi*) maintaining ecological processes that benefit people: regulating services; and

## Significance

Conservationists have become embroiled in debates over different motivations for conserving nature. One path forward is to acknowledge that nature is valued for many reasons and that managing for one objective can fail to achieve others. We categorize conservation objectives and provide a framework for comparing trade-offs between alternative strategies for conserving Costa Rican birds. Specifically, we focus on mitigating species extinction risk, preventing population extirpations, restoring historic assemblages, and conserving evolutionarily unique, culturally significant, and ecosystem-service providing species. Our approach pinpoints strategies for resolving trade-offs and achieving multiple conservation objectives; for example, by maintaining forest cover surrounding tropical farms. These insights demonstrate the advances needed in conservation strategy to design multifunctional interventions.

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**Table 1. Definition of conservation objectives, strategies and policies that address those objectives, and the indicators and metrics implemented in this study**

| Objective | Definition/justification | Strategies and policies | Indicators | Case study metrics |
|---|---|---|---|---|
| Extinction risk | This objective highlights a desire to prevent global extinctions through focusing conservation on endangered, range-restricted, or otherwise globally at-risk species. | Convention on International Trade in Endagered Species of Wild Flora and Fauna; Endangered Species Act; Endemic Bird Areas; Global Species Program; global biodiversity hotspots; International Union for Conservation of Nature and Natural Resources Red List; watch list; important bird areas | Endemism | Total captures and number of species endemic to Costa Rica and Panama |
| | | | Elevation restriction | Average elevational range among species (multiplied by −1) |
| | | | Rarity | Total captures and number of infrequently observed species |
| Extirpation risk | This objective seeks to prevent the regional or local loss of populations, and thereby preserve the aspect of diversity most often observed and measured. | Mean species abundance; Biodiversity Intactness Index; Centers of Plant Diversity; conservation planning algorithms (e.g., C-Plan, Marxan) | Richness | Estimated species richness (Chao) |
| | | | Abundance | Total captures |
| | | | Irreplaceability | Number of times a site appears in the suite of sites that conserve the most species (see *Methods*) |
| Evolution | This objective seeks to protect both ancient lineages to preserve evolutionary history and diversifying lineages to perpetuate diversity in the future. | Evolutionary distinct, globally endangered (EDGE) (17) | Evolutionary history | Phylogenetic diversity; Rao's PD; mean phylogenetic distance |
| | | | Evolutionary potential | Average diversification rate over last 5 or 10 million y |
| Naturalness | Many aspire to recreate a precolonial or prehuman state of nature. | Pleistocene rewilding; restoration; wilderness areas | Historical baseline | Chao similarity to forest community; no. of forest species |
| Provisioning services | Conserving nature can benefit people directly by providing material resources such as food, fuel, and water. | Catch shares; certification (e.g., Rainforest Alliance or bird-friendly coffee); seed banks; sustainable forestry | Not included in this case study | Not included in this case study |
| Regulating services | From water filtration to pollination, many ecological processes support human lives. The suite of functional traits present in a biological community may regulate the flow of these services to people. | Ecosystem-based management; ecosystem function conservation areas; payment for ecosystem services; Redusing Emissions from Deforestation and Forest Degradation (REDD)/REDD+ | Functional diversity | Petchey's FD; Rao's FD; functional divergence |
| | | | Pollination | No. of plant-pollinator interactions; no. and diversity of species pollinated |
| | | | Seed dispersal | No. of plant-seed disperser interactions; no. and diversity of species dispersed |
| | | | Pest control (providers) | Number and total captures of species that consume the coffee berry borer beetle |
| Cultural services | Nature also provides benefits that enrich human lives, often expressed in rituals, art, vocabulary, national symbols, myths, and in other ways. | Community-based ecotourism; game reserves; indigenous preserves; traditional use conservation areas; recreation areas | Popular press | No. of mentions in newspapers; abundance-weighted mentions |
| | | | Birdwatching | Average and abundance weighted average desirability to birders; mentions on birding tour websites |

(*vii*) conserving species or landscapes of cultural significance: cultural services (Table 1). Extinction and extirpation risk categories can be differentiated from the evolution category in that neither accounts for evolutionary relationships among species nor their potential to generate new species into the future. Moreover, unlike the other objectives, all species are equivalently valued in the extinction and extirpation risk categories unless the species is threatened.

We applied our typology to a focused case study of the effects of the primary driver of global biodiversity loss—habitat conversion—on tropical bird assemblages. Rather than attempting to reveal general trends, which would require a broader focus on other taxa and locations and preclude a more in-depth analysis, we combined a series of comprehensive data sources to illustrate how a conservation objective typology could be used to guide local conservation decisions. Specifically, we used the typology to identify locations to target for conservation and conservation strategies for those locations.

Our case study focused on an intensively studied bird assemblage in the Coto Brus Canton of southern Costa Rica. The case study leveraged 6 y of bird surveys at 18 field sites located in agricultural fields ($n = 6$), tropical forest fragments ($n = 9$ sites), and a forest reserve ($n = 3$). The dataset comprised ~70,000 mist-net hours of effort from 2007 to 2012, for a total of 32,861 different individuals captured across 239 species (18). Survey data were supplemented with (*i*) a complete avian phylogeny, (*ii*) conservation status and functional traits acquired from literature and field measurements, (*iii*) surveys of species appearances in national newspapers and ecotourism websites, and (*iv*) direct observations of species interactions. These data were used to quantify 15 indicators of most of the conservation objectives outlined above (the provisioning service objective was not quantified in this case study).

We leveraged our typology to answer three interrelated questions. First, how does habitat conversion affect each conservation objective? Second, would creating forest reserves maximize all conservation objectives or are there trade-offs between objectives; for example, in managing for threatened species versus species that provide ecosystem services? Finally, are there conservation strategies that would likely enhance most conservation objectives at once?

## Results

We found that conservation objective indicators exhibited distinct responses to habitat conversion (Fig. 1 and Tables S1 and S2), in part because bird assemblages in agriculture were not nested subsets of assemblages in forest (Fig. S1). Instead, bird assemblages shifted in composition along the land-use gradient, with some species increasing and others declining in agricultural sites (Fig. S2). Sites with similar levels of forest cover contained similar species (Table S3), and thus achieved similar conservation objectives (Fig. S3 and Table S4).

Assuming that tropical forest predominated in the region before human influence, habitat conversion caused a reduction in naturalness because the composition of agricultural and forest assemblages differed so markedly (Fig. 1, row l). Approximately 40% of the 239 species ever captured were either found only in forest reserves and fragments or were captured >10 times more frequently in forest than in agriculture. Conversely, 25% of species were either only found in agriculture or were captured >10 times more frequently in agriculture. Overall, agriculture maintained total abundance and richness of species on a par with forest (Fig. 1, rows m and n). (Agricultural species are considered native species, whose habitat affinities and ranges before human influence are not known.) Given such varied responses of different species to land-use change, maintaining a mosaic landscape of forest reserves, fragments, and agricultural sites would likely help mitigate regional extirpation risk (Fig. 1, row b).

The compositional shift between forest and agriculture bird assemblages could be characterized by a decline in species with higher species-level extinction risks (endemic, rare, and elevation-restricted species) (Fig. 1, rows a, e, and k). Forest-affiliated species belonged to older evolutionary lineages; therefore, evolutionary history (phylogenetic diversity) was higher in forest reserves and fragments than in agriculture (Fig. 1, row d). In contrast, species from recently diversifying clades were more agriculture affiliated (evolutionary potential) (Fig. 1, row o).

We also observed varied effects of land conversion on regulating and cultural services. Functional variety and the abundance of birds previously shown to consume agricultural pests (19) were higher in agriculture than forest, but bird-mediated pollination and seed dispersal did not differ among land uses (Fig. 1, rows f–i). Species of higher value to international birdwatchers were more abundant in forested sites, but the forty species mentioned in three Costa Rican newspapers thrived in agricultural sites (Fig. 1, rows c and j).

The varied responses to land-use change among indicators highlight potential management trade-offs (Fig. 2 and Table S5). We found that sites with high numbers of pest predators, rapidly diversifying species, and species mentioned in the popular press contained significantly fewer species that international birdwatchers value and fewer endemic, elevation-restricted, and evolutionarily distinct species (Fig. 2). On the other hand, species providing regulating services (pollination, pest control, and seed dispersal) tended to increase in abundance at the same sites (Table S5). Functional variety also correlated with these processes.

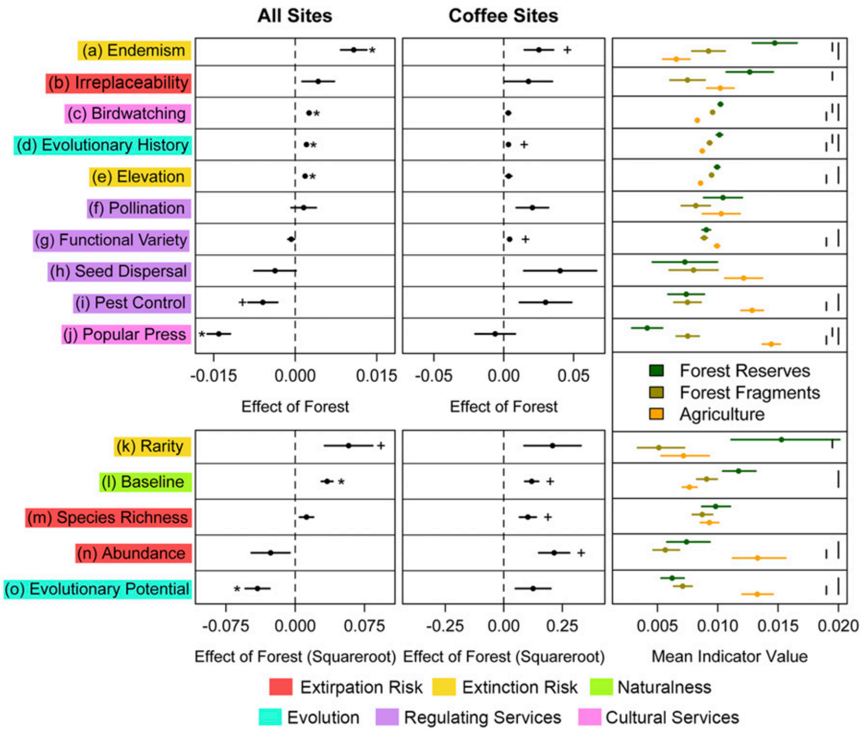

**Fig. 1.** Effect of land use on 15 indicators of common conservation objectives. (*Left*) Varied responses of indicators to increases in forest cover, measured as the fraction of forested area within 150 m of bird survey sites. Indicators that were square root-transformed to meet normality assumptions (*Lower*) are separated from those that were not transformed (*Upper*). Asterisks denote significance ($P < 0.05$, $n = 108$ site-years) after multiple test correction; plus signs denote significance without multiple test correction. (*Center*) The effect of increasing forest cover only at agricultural (coffee) sites ($n = 36$ site-years). (*Right*) Effects partitioned by land-use treatments. Vertical lines denote significance after multiple-test correction ($P < 0.05$, $n = 108$). For example, significantly more endemic species were found in reserves than in agriculture or fragments.

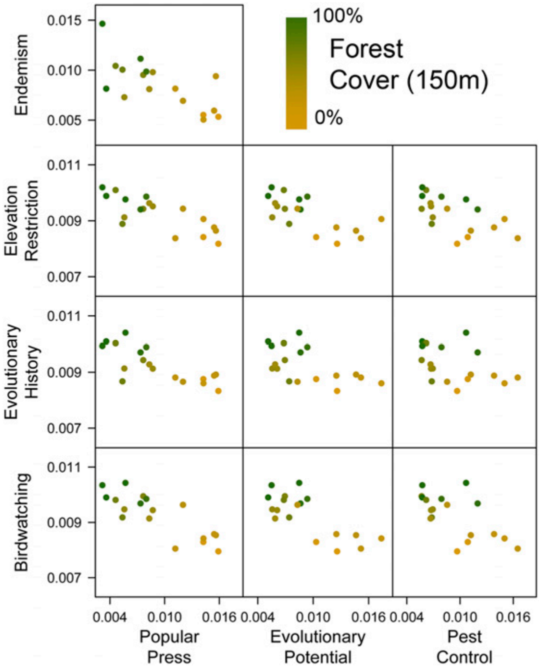

**Fig. 2.** Trade-offs among conservation objective indicators. All significant negative correlations between indicators after multiple test correction ($P < 0.05$; $n = 18$ sites) are shown. Points correspond to the 18 survey locations, colored according to surrounding forest cover, and depict average standardized values of each indicator (Table 1).

On average, conservation objectives did not change across the land-use gradient because some indicators of conservation objectives increased while others declined (Fig. 3 and Table S1). Restricting analyses to solely focus on agricultural sites, however, pointed the way toward synergistic management interventions that could simultaneously increase several aspects of nature that people value at once. Coefficients relating almost every indicator to the amount forest cover surrounding farms were positive at every spatial scale considered (except for popular press mentions) (Fig. 1 and Table S6). Therefore, increasing forest cover surrounding farms significantly increased all conservation objectives on average (likelihood ratio tests: $P = 0.01$, $n = 30$) (Fig. 3).

## Discussion

Our case study demonstrates that land managers must contend with trade-offs between common conservation objectives when seeking to enhance the conservation value of farming landscapes. Specifically, we found that creating forest reserves in farming countryside would cause a dramatic shift in bird assemblage composition, which would help achieve some conservation objectives but not others. For example, we found that sites with many elevation-restricted, evolutionarily unique, endemic, and rare species were not especially rich in ecosystem-service providing species because pest-consuming, pollinating, and seed-dispersing species were no more abundant in forested than agricultural sites. Although some studies have identified win-win opportunities in which ecosystem-service conservation also results in biodiversity conservation (20), our findings align with a growing body of literature that suggests that focusing on ecosystem services alone will not adequately protect at-risk species (21).

Our work demonstrates how a typology of conservation objectives could not only help identify trade-offs but also facilitate their resolution. First, explicit quantification of multiple objectives could lead to the discovery of exceptional areas deserving of special conservation attention. For example, we found that one site in the reserve and another in a fragment of secondary forest ranked in the top third for all but two to three indicators of conservation objectives. Second, a conservation objective typology could be used to identify targeted strategies for enhancing multiple conservation objectives that would usually be in conflict. For example, although we documented several concrete trade-offs between indicators (e.g., sites with many elevation-restricted species hosted few pest predators) (Fig. 2), we also found that increasing forest cover within and surrounding agricultural plots would increase almost every indicator considered (except popular press mentions). Thus, there is scope for pursuing conservation within agricultural landscapes, as incentivizing farmers to maintain tropical forest cover would likely benefit most conservation objectives, at least for tropical birds.

Future application of our typology could enhance its utility by further development in four areas. First, the typology could be applied across multiple locations and taxa to elucidate which trends are general and which are context dependent. For example, studies on multiple taxa and from other regions support our observation that agriculture can maintain biodiverse assemblages (22) of rapidly diversifying, but not evolutionary unique, lineages (23). On the other hand, although we found that biodiversity-driven ecosystem processes were largely unresponsive to the land-cover gradient, many regulating services not measured here are likely more dependent on forests. For example, tropical forests increase the supply of water for hydropower production (24).

Second, new indicators could be developed to better characterize progress toward achieving the conservation objectives. For example, a focus on monitoring wild and cultivated genetic diversity could provide insights into how to increase the adaptive evolutionary potential of wild species (25) and crop resilience against future pests or diseases. Similarly, methods for quantifying and integrating cultural services into land-use decisions are emerging, and future analyses would benefit from more inclusive consideration of social benefits (26).

Third, our typology could be used to balance multiple conservation objectives with other goals for agricultural landscapes. For example, stakeholders may seek to conserve nature in areas where agriculture is expected to expand or intensify to meet growing food needs (27). Optimal strategies for doing so may depend on the conservation objective considered (28). For example, although conserving species-rich assemblages on farms can be possible without compromising farm yields (29), intensifying production and preserving nature elsewhere may be a better strategy for increasing mean species abundances (27), especially for species at risk for global extinction.

Finally, the typology could be implemented across regions to strategically prioritize conservation interventions. Although our case study uncovered strategies for achieving multiple conservation objectives within a landscape, trade-offs may still exist in defining conservation priority areas at larger scales (30). Conservationists often implement systematic conservation planning to identify sets of complementary protected areas that conserve the greatest collection of species or biomes (31). Applying these techniques to our typology could help target interventions on sets of sites that are irreplaceable for achieving multiple objectives.

Conservation interventions in human-dominated landscapes will likely determine which components of biodiversity will be shepherded through the ongoing mass extinction (32). Our results demonstrate how considering alternative conservation objectives can identify potential trade-offs, as well as locations and strategies for achieving multiple conservation objectives. In agricultural landscapes, where sustaining rural livelihoods and local economies are critical, ensuring that interventions address multiple motivations for conservation could garner widespread support. Admitting the complexity and multidimensionality of nature conservation will undoubtedly complicate conservation planning. However, it would also yield the synergistic outcomes for people and nature that are essential to achieving success.

## Methods

**Study Sites.** We quantified spatial patterns in bird assemblages in the Coto Brus Valley of Southern Costa Rica (~1,000 m above sea level). The valley

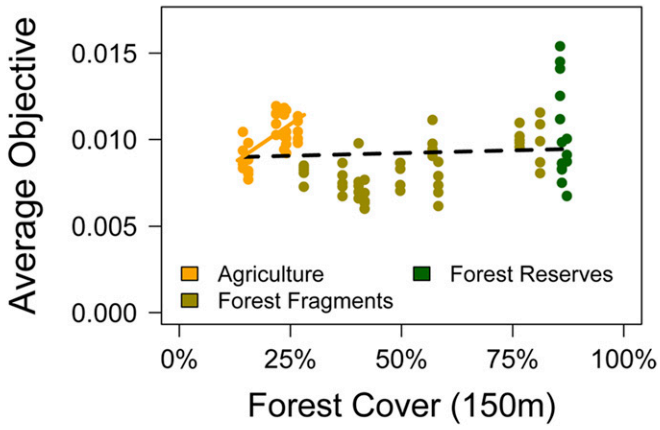

**Fig. 3.** Shifts in conservation objectives on average across the land-use gradient. Increasing forest cover within 150 m of a site caused no change in conservation objectives on average ($n = 90$ site-years; $P = 0.80$); however, increasing forest cover on coffee plantations resulted in a significant increase ($n = 30$; $P = 0.01$). Seed dispersal was not included, as it was surveyed only in 2011. Pollination was not surveyed in 2007; therefore, analyses were limited to the subsequent 5 y.

experiences an annual precipitation of 3,600 mm, daily temperatures of 17–24 °C, and is a mosaic of coffee plantations, pastures, small rural settlements, and forest fragments (18). We studied bird assemblages with 6 y of mist-net surveys (2007–2012) at 18 sites, representing a land-use gradient ranging from the Las Cruces Forest Reserve to intensive coffee plantations. We used three sites in the reserve, nine in forest fragments, and six sites in coffee plantations. All coffee plantations were classified as "sun coffee," with ∼5–25% seasonal canopy cover directly over the coffee.

At each site, we haphazardly placed 20, 12 m × 2.5 m mist nets in 3–5 ha plots, and followed standard mist-netting protocols. Surveys took place over 6 h beginning at sunrise and in the dry season, between January 25 and May 12. Each of the 18 sites was visited six times per year. Each bird was marked with a unique leg band and released onsite shortly after processing and data collection.

From 2008 to 2012, we collected pollen loads from hummingbirds and other nectarivorous birds to document bird-mediated pollination. We acquired pollen by rubbing tape across heads and bills. Pollen grains were identified to species, genus, or morphospecies using a reference collection ($n = 2,297$ pollen loads). In 2011, we also collected bird fecal samples to quantify seed dispersal. Birds defecated in the sterilized cotton bags that we used for transport to the banding station. We collected these feces with sterilized tweezers, and deposited them in glass vials filled with 95% (vol/vol) ethanol. Seeds were counted and identified to species, genus, family, or morphospecies using a reference collection ($n = 584$ fecal samples from 58 bird species). All captured animals were treated humanely, in accordance with the Institutional Animal Care and Use Committee (IACUC) guidelines and approved by the Administrative Panel on Laboratory Animal Care (APLAC) of Stanford University (assurance number A3213-01; protocol ID 26920).

### Indicators of Conservation Objectives.

***Extinction risk.*** We quantified metrics for three indicators of extinction risk: endemism, elevation restriction, and abundance. First, we identified species endemic to southern Costa Rica and Northern Panama using the Map Of Life (www.mol.org), and computed the species richness and total detections of endemic species at each site. We then calculated the mean and abundance-weighted mean elevation range of the species present at each site using data from Stiles and Skutch (33). To express elevation restriction, we multiplied elevation range values by −1. Finally, we identified which species were captured fewer than 10 times over all sites and years, and calculated the species richness and total detections of these rare species at each site.

***Extirpation risk.*** Preventing regional extirpations requires both conserving local populations and identifying sets of sites that complementarily conserve regional species pools. We estimated the number of species (Chao metric that algorithmically accounts for unseen species) and individuals (unique individual bird captures) present at each site. We also designed a metric of site "irreplaceability" to identify which sites were essential for safeguarding the regional species pool. For each year, we asked which portfolios of sites housed the maximum number of species, given varied constraints of how many sites could be conserved (from one to all sites). Sites were given one point for every time that they appeared in a portfolio. If multiple site combinations produced the same maximal species richness, then sites were scored according to their relative presence across all combinations.

***Evolution.*** We generated indices for both the evolutionary history and potential of bird assemblages using multiple metrics. Measures of evolutionary history included phylogenetic diversity (PD), Rao's PD, and mean phylogenetic distance, both accounting for and not accounting for species abundances (15, 23, 34). In calculating these metrics, we took the mean over 500 possible species-level phylogenies (35). For evolutionary potential, we assumed that the diversification rates of the past reflect potential diversification of the future. Specifically, we calculated diversification rates for each species as the number of tree splits over the last 5 or 10 million y that gave rise to each species, averaged over the 500 possible phylogenies. For each site, we then calculated the average and abundance-weighted average diversification rate among detected species over the last 5 or 10 million y.

***Naturalness.*** We traded space for time and considered the forest bird assemblage a natural baseline. We thus computed the average similarity (Chao, abundance-weighted) of bird assemblages at each study site to the bird assemblage in the reserve (18). We also calculated the species richness of "forest species," or the number of species at each site that were also found in the reserve.

***Regulating services.*** We measured how birds contribute to regulating services through directly quantifying three ecosystem functions: pollination, seed dispersal, and pest control. For pollination, we calculated the number of distinct plant–pollinator connections, the number of plant species pollinated, and the Simpson diversity of plant species pollinated at each site, using pollen incidence across samples as a measure of relative abundance. For seed dispersal, we calculated the number of distinct plant–bird connections, the number of plant species dispersed, and the Simpson diversity of plant species dispersed, using the total number of seeds detected as a measure of relative abundance. For pest control, we calculated the number and total captures of pest-eating birds, identified through molecular analyses of 1,430 bird fecal samples (19).

We also calculated metrics of functional variety because the suite of functional traits present in a biological assemblage may regulate ecological processes (36). First, for each detected bird species, we compiled functional trait data from the literature pertaining to bird resource use and acquisition (body mass, body length, sociality, preferred foraging strata, diet breadth, diet, foraging strategy) (33). Next, we quantified the trait dissimilarity between every pair of detected bird species using a Gower dissimilarity metric that equally weighted each functional trait. Finally, for each site and year, we calculated three indicators of functional variety using the package "FD" in R: functional diversity (FD), functional divergence, and Rao's FD (37).

***Cultural services.*** We developed two indicators of cultural services: birds' value to international birdwatchers and their prevalence in mainstream Costa Rican media.

We used two methods to assess birdwatching value. First, an expert ornithologist and birdwatching guide in Costa Rica, Jim Zook, scored all detected bird species from 1 to 5 according to their desirability to North American and European birdwatchers. At each site, we computed the average and abundance-weighted average of bird desirability across all species. Second, assuming that birdwatching tour companies highlight desirable species, we searched the Internet for companies leading bird tours in our study region and tallied the proportion of websites ($n = 25$) that mentioned each bird species in our study region. We then computed the average and abundance-weighted average of birdwatching website mentions across all species at each site.

Finally, we used the LexisNexis search engine (www.lexisnexis.com/en-us/gateway.page) to quantify the number of times each species was mentioned in the three major national, daily Costa Rican newspapers (*La Nación*, *Al Día*, and *El Financiero*) since the year 2000. We searched both scientific and local names, gathered from Stiles and Skutch (33). We read each possible entry to ensure that the species was indeed the subject of discussion, and then calculated the average and abundance-weighted average number of mentions for each bird assemblage.

**Statistical Analysis.** We first tested whether land use caused a shift in bird assemblage composition. We calculated differences in assemblage composition between sites using the Chao abundance-based metric that accounts for unseen species. We then used permutational multivariable ANOVA (PERMANOVA) and nonmetric multidimensional scaling (nMDS) to assess whether sites that were more similar in forest cover were also more similar in their bird assemblage composition. We also used the function "nestedtemp" in the "vegan" package in "R" to determine whether bird assemblages in agriculture were nested subsets of bird assemblages in forests.

We then analyzed how different land-use practices affect conservation objectives, focusing on 15 indicators (Table 1). Although differences in detection probabilities between habitat types could confound analyses, to our knowledge there is no method for accounting for detection in all of the indicators considered here. Therefore, we calculated effects of land-use type on raw values from each indicator. First, we standardized each metric by dividing the metric's value at a given site in a given year by the summed value of the metric across all years and sites. For indicators that were composed of multiple metrics, we then calculated the average metric value for each site in each year. For example, the indicator "functional variety" was computed through averaging standardized Petchey's FD, functional divergence, and Rao's FD. We then modeled differences between the forest reserve, forest fragments, and coffee plantations, using linear mixed models with Gaussian error terms. Indicators that failed normality assumptions were square root-transformed. Years and sites were included as random effects. Nested models, with and without land-use treatments, were compared through backward model selection (38), using likelihood ratio tests and Akaike Information Criteria (AIC). *P* values were adjusted for multiple tests ($n$ = 15, one for each indicator) using false-discovery rates. Because data were only collected for 1 y, we analyzed changes in seed dispersal using ANOVA.

We also tested whether forest cover in the surrounding landscape influenced each indicator. We used a 2-m resolution, manually digitized land-use map to calculate the fraction of forested area in 70-m to 450-m buffers surrounding all of the mist-nets at each site (18). We then used linear mixed models to relate forest cover to the 15 indicators. Seed dispersal data were analyzed with linear regression. We repeated all analyses after restricting our focus to the six coffee plantations to examine the effects of increasing forest cover on coffee plantations explicitly.

Next, we determined how forest cover affected conservation objectives on average. First, for each conservation objective in each year we averaged the constituent indicators, omitting seed dispersal. We then averaged the conservation objectives and used linear mixed models to quantify the effect of forest cover as above.

Finally, we assessed trade-offs and synergies among indicators. We tested whether each pair of indicators was positively or negatively correlated using Spearman correlation coefficients. To avoid pseudoreplication, we computed the average value of each indicator over the 6 y of data collection and used individual sites as replicates, again using false-discovery rates for multiple test correction. We then calculated the Gower dissimilarity between pairs of sites with respect to their suite of indicators. We visualized differences between sites using nMDS, and tested whether forest cover at multiple spatial scales explained variation among sites using PERMANOVA. All statistical analyses were conducted in "R" (39).

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