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LETTER

Avian cultural services peak in tropical wet forests

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Abstract

The current biodiversity crisis involves major shifts in biological communities at local and regional scales. The consequences for Earth's life-support systems are increasingly well-studied, but knowledge of how community shifts affect cultural services associated with wildlife lags behind. We integrated bird census data (3 years across 150 point-count locations) with questionnaire surveys (>400 people) to evaluate changes in culturally important species across climate and land-use gradients in Costa Rica. For farmers, urbanites, and birdwatchers alike, species valued for identity, bequest, birdwatching, acoustic aesthetics, and education were more likely to occupy wetter regions and forested sites, whereas disliked species tended to occupy drier and deforested sites. These results suggest that regional climate drying and habitat conversion in the Neotropics are likely to threaten the most culturally important bird species. This study provides a novel and generalizable pathway for assessing the effects of environmental changes on cultural services and integrating the sociocultural and ecological dimensions of biodiversity.

KEYWORDS
biodiversity, birdwatching, conservation psychology, cultural ecosystem services, cultural values, human–avian interactions, Neotropical birds

1 | INTRODUCTION

Habitat loss and climate change are rapidly eroding biodiversity and its benefits to people (Díaz et al., 2019). Major progress has been made in monitoring, modeling, and managing biophysical ecosystem services from biodiversity, such as carbon sequestration and water regulation (Carpenter, Bennett, & Peterson, 2006). Yet, the impacts of global environmental changes on cultural ecosystem services remain poorly known (Bremer et al., 2018), in part due to the extreme multidisciplinary nature of the problem and the difficulties of integrating sociocultural and ecological data.

Nonetheless, international conservation policy efforts, such as the Intergovernmental Platform for Biodiversity and Ecosystem services (IPBES), are increasingly calling for plural valuation of ecosystems, integrating both ecological and cultural dimensions to better inform conservation planning (Pascual et al., 2017). Studies integrating social and ecological data to understand the linkage between ecological communities and cultural ecosystem services are nascent, and rarely evaluate how they are impacted by environmental changes (Arbieu, Grünewald, Martín-López, Schleuning, & Böhning-Gaese, 2017; Cumming & Maciejewski 2017; Kittinger et al., 2015; Naidoo & Adamowicz 2005; Tribot et al. 2018). Thus, practitioners seeking to comanage ecosystems for both species of conservation concern and culturally important species do not generally have the means to understand the effects of biodiversity change on cultural services. Moreover, several studies evaluating cultural services across species often analyze proxies for popularity rather than surveying people directly about the nonmaterial benefits they derive from species (Hirons, Comberti, & Dunford, 2016; Karp et al., 2015; Schuetz & Johnston 2019). Yet cultural services associated with species are often complex, context-dependent, and necessitate explicit study (Daniel et al., 2012).

Safeguarding cultural services provided by wildlife will ultimately require identifying which species people value and whether these species are vulnerable to global change. Ecologists are increasingly attempting to document which species will likely benefit or decline with ongoing habitat loss, habitat fragmentation, and climate change (Betts et al., 2019; Newbold et al., 2018). However, it is unclear whether the “winners” or the “losers” of global change are of equal cultural importance. On the one hand, the resilient “winners” that thrive in urban and agricultural areas may provide more cultural services, as they are more frequently encountered by local people (Cox et al., 2018). On the other hand, the “losers” restricted to protected, intact forests may provide more cultural services, as people perceive them as “more natural,” and perceived naturalness may correlate with cultural service provision (Martín-López et al., 2012).

Neotropical bird communities represent a useful system for exploring how global changes may affect cultural services. Neotropical birds have occupied central positions in Latin American societies for centuries. They serve as regional and national symbols on flags and in currencies (Galloy, 2000), are sources of bushmeat for many Indigenous Peoples and Local Communities (Fernandes-Ferreira, Mendonça, Albano, Ferreira, & Alves, 2011), and are often mentioned in linguistic metaphors, similes, and slurs (Ibarra, Barreau, & Altamirano, 2013). At the same time, climate and land-use change are benefitting some Neotropical bird species and threatening others (Frishkoff et al., 2016). While we are unaware of any studies that have investigated the impacts of climate and land-use change on the cultural dimensions of birds, the results of such an analysis would be particularly important for biodiversity conservation in tropical areas, where biodiversity is suffering from intense deforestation and climate change (Tewksbury, Huey, & Deutsch, 2008).

Here, we ask three guiding questions: (a) How do avian cultural services vary across climate and land-use gradients?; (b) How does the presence of “iconic” and “highly charismatic” species impact cultural service provision across such environmental gradients?; and (c) What is the spatial distribution of culturally important birds? To answer these questions, we tightly coupled ecological and psychological methods to explore potential interacting impacts of climate and land-use change on multiple cultural services that Neotropical birds provide to different stakeholder groups in Costa Rica (Figure S1). Specifically, we first surveyed bird communities along land-use and climate gradients to identify the likely winners and losers from climate drying and habitat conversion. We then administered surveys to birdwatchers, farmers, and urbanites to determine which bird species are valued and for what reasons. Answers to our guiding questions help identify not only regional conservation practices and priorities, but also applications to other tropical areas facing climate change and deforestation.

2 | METHODS

2.1 | Stakeholder surveys

We surveyed stakeholders in dry forests, wet forests, pastures, and cropland of Northwest Costa Rica (Figure S2), a popular ecotourism destination with a long tradition of farming and cattle ranching. Across the region, we conducted in-person and online surveys with 404 people in total, including birdwatchers and birdwatching guides ($n = 115$), local farmers ($n = 140$), and urbanites ($n = 149$), during November and December 2017 (See Table S1 for participant demographics). We chose these stakeholder groups because they had varying degrees of relationships with birds. Birdwatchers tend to engage with birds through scientific and recreational purposes and their views and actions inform the large tourism industry in Costa Rica. Farmers are stewards of the land and have the power to modify landscapes, enabling some species to persist and causing others to decline. Urbanites were the most loosely defined group as they represent any person who lives in an urban town but who does not self-identify as a birdwatcher or farmer. This group encompassed people from many occupations and roles in society, for example, lawyers, nurses, waiters, and others.

For all analyses, we combined participants into two coherent categories based on their similarity in responses (Echeverri, Naidoo, Karp, Chan, & Zhao, 2019): birdwatchers and birdwatching guides (termed "birdwatchers") versus farmers and urbanites (termed "farmers and urbanites"). The survey asked participants to rate a subset of the region's 199 bird species (Table S2) on psychometric scales designed to capture *disservices* (i.e., species perceived as harmful/annoying) and five cultural services including *identity* (i.e., species viewed as emblematic of the study region), *bequest* (i.e., species people want to protect for future generations), *birdwatching* (i.e., species people enjoy watching), *acoustic aesthetics* (i.e., species people enjoy hearing), and *education* (i.e., species people enjoy studying) (Table S3). For complete information on participant recruitment, survey design, and survey analysis see Supporting Information.

2.2 | Avian surveys

From 2016–2018, we surveyed bird communities at 25 sites arrayed across the region's precipitation gradient, spanning ~1.5 m to ~3.5 m in total annual rainfall (Figure S2). Sites were chosen to vary in precipitation but not temperature or elevation, as we had previously identified that precipitation was the main environmental variable explaining avian ecological niches in Costa Rica (Frishkoff et al., 2016). Moreover, the region is expected to experience considerable climate drying in the future (Rauscher, Giorgi, Diffenbaugh, & Seth, 2008).

We chose study sites that were located in forest-adjacent farms (rearing cattle or growing rice, sugarcane, or Taiwan grass, a forage crop; $n = 20$) and protected areas ($n = 5$). In protected areas, four point-count locations were in reserve interiors and two were at reserve edges. In farming landscapes, half of the point counts were in agricultural areas and half were in adjacent forests (interiors, edges, and small fragments). Point count locations were selected so that local and landscape-level tree cover (hand-classified from Google Earth Imagery) varied independently (Karp et al., 2018).

Bird surveys consisted of 20 min, 50 m radius point counts, beginning at dawn and continuing for 5 hours. The same expert ornithologist (Jim Zook) conducted all counts, recording all birds as well as variables that affect bird detection (e.g., time of day, presence of loud noise, number of people nearby, and wind speed). Data were collected from May–August of 2016, 2017, and 2018, with the exception of reserve sites, which were surveyed only in 2017 and 2018. Each year, half the sites were surveyed once, and half were repeatedly surveyed three times within the same week to enable multispecies occupancy modeling.

2.3 | Statistical analysis

We used a spatial scale selecting, multispecies occupancy model that accounted for variability in species' detection probabilities to estimate species occurrences at each point count location (Frishkoff, Mahler, & Fortin, 2019) (see Supporting Information for model specification). Then, for each stakeholder group and each cultural service category ($n = 12$), we calculated the average cultural service score across all bird species predicted to occur at each point count location. To address the contention that cultural services may be driven by peoples' positive interactions with a few iconic species (Belaire, Westphal, Whelan, & Minor, 2015; Graves, Pearson, & Turner, 2019), we also assessed spatial trends in the number of iconic species detected at each site. We defined a species as iconic for any given service if, on average, survey participants strongly agreed that it provided that service (category average on the Likert-scale > 4.5). Finally, to evaluate where the most iconic species were located, we quantified the number of "highly charismatic" species at each site, defined as species that survey participants agreed provided all cultural services but no disservices (category average on the Likert-scale > 4 for cultural services and <3 for disservices). See Supporting Information for more details about quantifying average cultural service scores, iconic species, and highly charismatic species.

We implemented linear mixed-effect models (LMMs) to explore effects of environmental gradients on average cultural ecosystem service scores, iconic species richness, and numbers of highly charismatic species (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Fixed effects included linear and quadratic effects of precipitation, local tree cover (within 50 m), and landscape tree cover. Because the occupancy model indicated that tree cover within 670 m explained

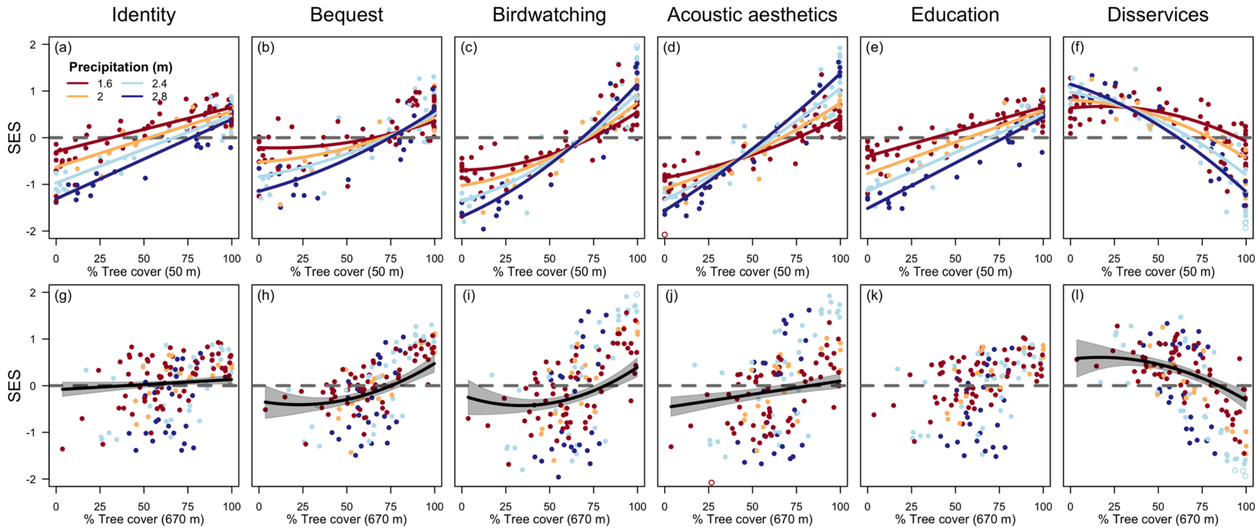

FIGURE 1 Wetter and more forested sites house more culturally important bird communities. Panels show variation in standardized effect sizes of average cultural services scores (SES, see Supporting Information) at each site across tree cover gradients at *local scales* (within 50 m; panels a-f) and *landscapes scales* (within 670 m; panels g-l). Sites (points) are colored by annual precipitation values (1.6 m[red] –2.8 m [dark blue]). Graphs show the results for farmers and urbanites; results were qualitatively similar for birdwatchers. Colored lines (panels a–f) depict interactive effects between precipitation and local tree cover. Black lines (panels g–l) show fitted models; grey bands are 95% confidence intervals

the most variation in species occupancy (95% CI: 563–782 m; Figure S3), we defined landscape-scale tree cover to be tree cover within 670 m of survey locations. Models also included two-way interactions between precipitation and local tree cover and between tree cover at local and landscape scales. Prior to analysis, all fixed effects were scaled by subtracting the mean and dividing by the standard deviation. We included a random intercept of site (i.e., specific farm or protected area) to account for spatial autocorrelation. For analyses of iconic species richness and highly charismatic species, we included an additional nested random intercept of point-count location (as point counts were repeatedly visited over the three-year study period).

Model selection was determined through a backwards selection process, using likelihood ratio tests evaluated against a chi-squared distribution. Figures depict results from the "best" model, as determined through backwards model selection. Nonetheless, to ensure results were robust to analysis procedures, we also used the MuMIn package in R for model averaging; specifically, averaging only over models that included each fixed effect to obtain the non-shrinkage variance estimates for each fixed effect (Bartoń, 2020). All analyses were conducted separately for farmers/urbanites versus birdwatchers, and for each cultural service ($n = 12$ final models). We respected hierarchy and checked residuals to ensure the models conformed to assumptions. If residuals were not normally distributed, we applied transformations (e.g., raising response variables to the power of 0.75) and then reran models.

Finally, to evaluate the spatial distribution of culturally important birds, we used our best-supported model to map the number of highly charismatic species that would likely be encountered during a 20 min, 50 m point-count across a 300 m grid encompassing our study region. As inputs for our model, we calculated precipitation, local forest cover, and landscape forest cover values at each grid point from regional precipitation and land-use maps (Karp et al., 2019). Areas with precipitation values greater than the maximum or less than the minimum values observed at our study sites were excluded from analyses.

3 | RESULTS

Over three years of bird censuses, we detected 157 species in our point counts, most of which were viewed positively by farmers, urbanites, and birdwatchers. All cultural services were strongly positively correlated with one another across sites, whereas disservices exhibited strong negative spatial correlations with services (Figure S4). Answering our first research question, which evaluated how avian cultural services vary across climate and land-use gradients, we found that cultural service scores peaked in forests for birdwatchers (Figure S5 and Tables S4 and S5) as well as farmers and urbanites (Figure 1 and Tables S6 and S7). Specifically, we found that tree cover at a local scale (within a 50 m radius) was the strongest predictor of cultural-service scores. Though effects were more muted at the landscape scale (within 670 m), sites in more forested

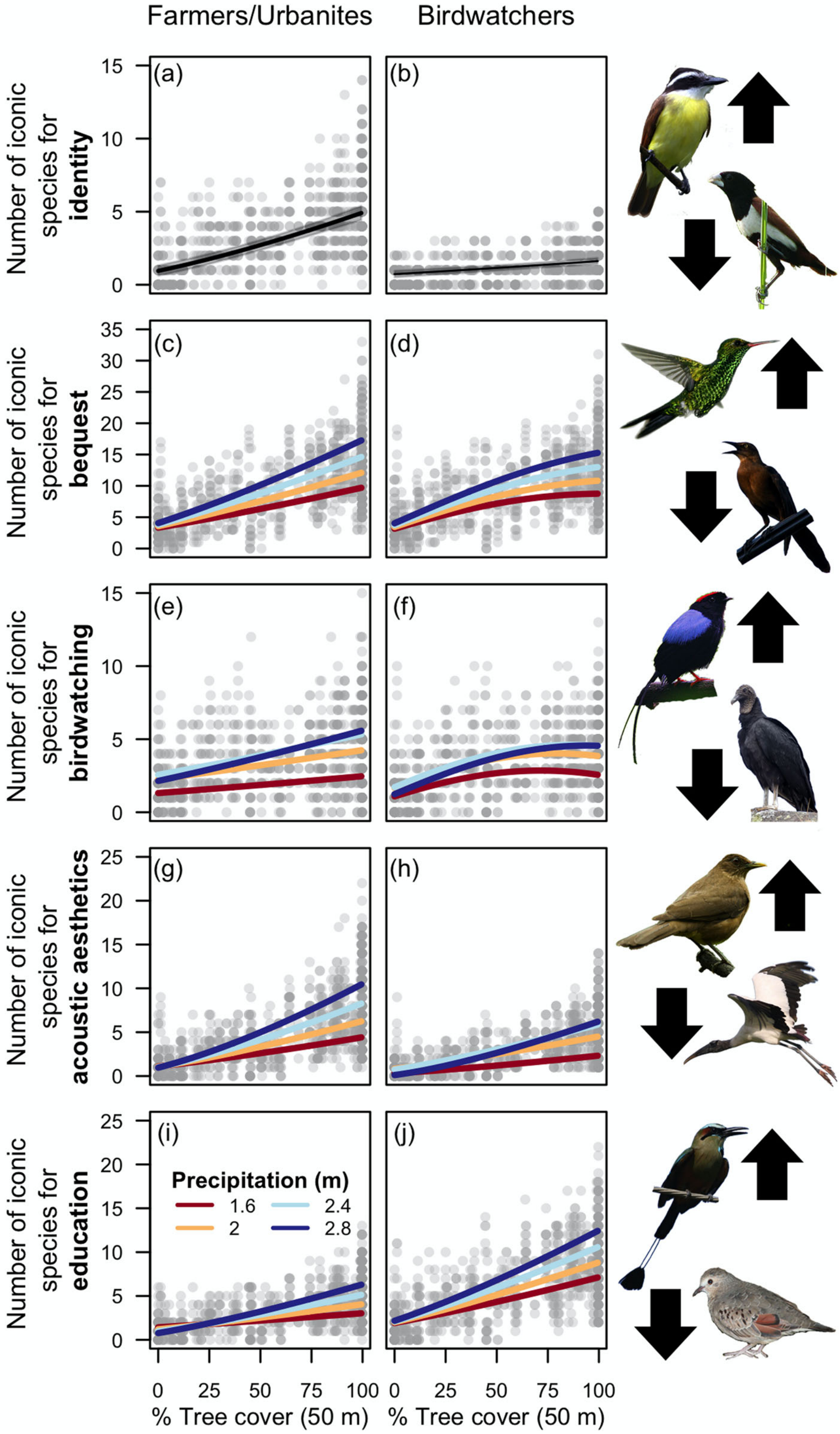

FIGURE 2 More iconic species are found in wetter, more forested sites. Each point represents the number of iconic species detected in one point-count census. Colored lines show effects of local tree cover (within 50 m) for different levels of total annual rainfall. Left and right panels correspond to cultural services for farmers/urbanites and birdwatchers, respectively. To the right, we indicate iconic species for each service (arrows pointing upwards) and species that were unimportant or even detrimental for each service (arrows pointing downwards). From top to bottom, the species presented are as follows: Great Kiskadee (*Pitangus sulphuratus*), Tricolored Munia (*Lonchura malacca*), Canivet's Emerald (*Chlorostilbon canivetii*), Great-tailed Grackle (*Quiscalus mexicanus*), Long-tailed Manakin (*Chiroxiphia linearis*), Black Vulture (*Coragyps atratus*), Clay-colored Thrush (*Turdus grayi*), Wood Stork (*Mycteria americana*), Turquoise-browed Motmot (*Eumomota superciliosa*), and Common Ground-Dove (*Columbina passerina*)

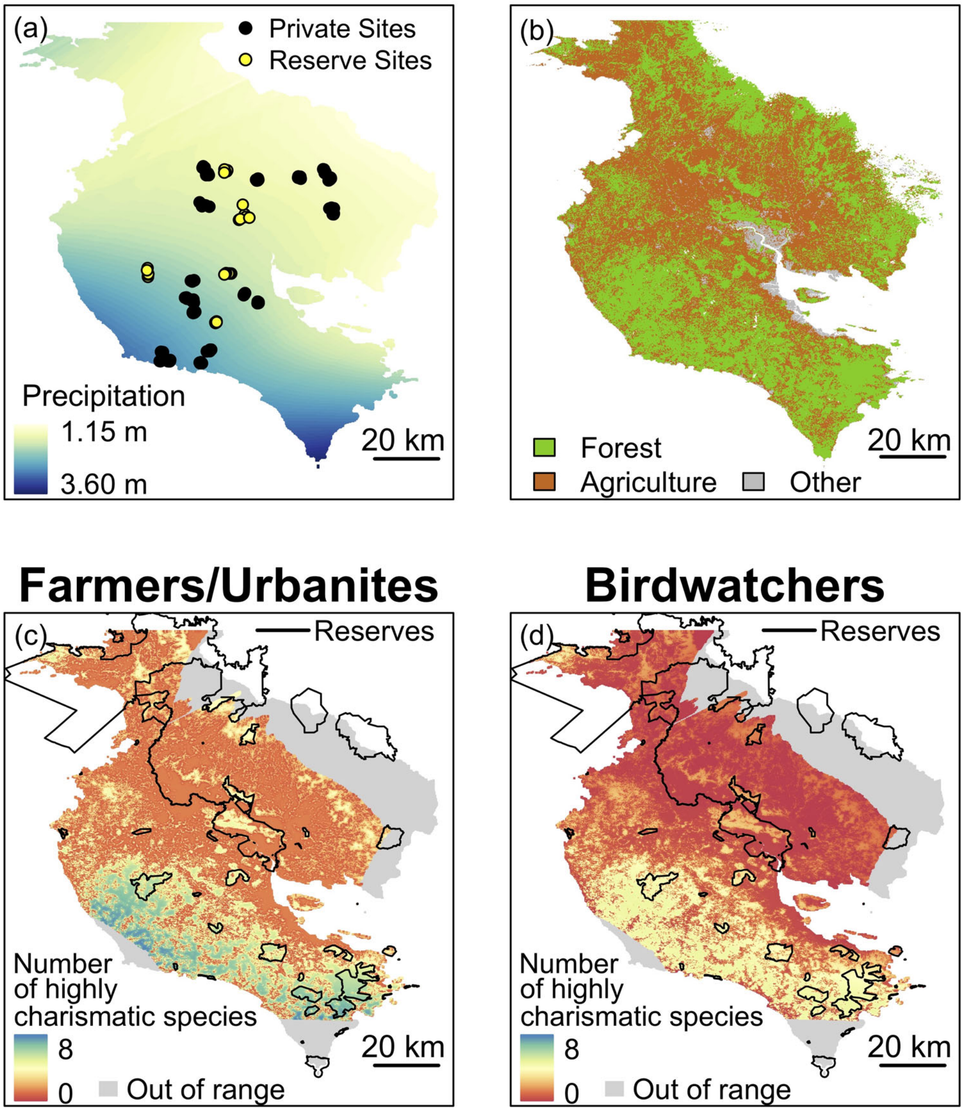

FIGURE 3 Highly charismatic species are found near the Pacific coast, in wetter and more forested areas. (a) Modeled annual precipitation across Northwest Costa Rica ranges from 1.15 m to 3.6 m near the coast. Black and yellow points represent point-count locations on forest-adjacent farms and in reserves, respectively. (b) Land-use map of the region, where green represents forest and orange represents agriculture. Predicted distribution of the number of highly charismatic species—species that provided all cultural services but no disservices—for (c) farmers/urbanites and (d) birdwatchers that would be encountered in one 20 min point count. Nature reserves are outlined in black; gray regions are areas with annual precipitation outside the range of our survey sites

landscapes tended to have higher cultural services scores and lower disservices for farmers, urbanites, and birdwatchers (Figures 1 and S5). While main effects of precipitation were mixed (Figure S6), we observed significant interactive effects of local tree cover and precipitation, such that the strong positive effects of local tree cover on cultural services (and negative effect on disservices) were amplified at wetter sites. As a result, most cultural services peaked (and disservices plummeted) at the wettest and most forested sites for both stakeholder groups (Figures 1 and S5).

With respect to our second research question, which studied how the presence of "iconic" and "highly charismatic" species impacts cultural service provision across such environmental gradients, we found that, as with the full avian community, iconic species synergistically increased with local tree cover and precipitation, suggesting that wetter and more forested sites housed the most iconic species. This was found for nearly all cultural services and across both stakeholder groups (Figures 2, S7 and S8, and Tables S8–S13). Nonetheless, there were important differences in which and how many species were considered iconic across cultural services and stakeholder groups. For example, ~3× more species were perceived as being worth conserving for future generations (i.e., bequest) versus those that were perceived as beautiful for birdwatching (Figure 2). Similarly, farmers and urbanites perceived nearly ∼3× more species to be iconic for identity services than birdwatchers did in any avian community. Consistently, farmers and urbanites considered many more species to be highly charismatic (by our definition) than birdwatchers (55 vs. 25 species), with only 9 species shared among both groups (Table S14).

Finally, the spatial distribution of culturally important birds was consistent across all analyses, indicating that iconic birds and highly charismatic species are found in wetter, more forested sites, especially near the Pacific Coast of the Nicoya peninsula (Figure 3). Across all analyses, results were highly robust to model selection versus model averaging procedures.

4 | DISCUSSION

Our analyses suggest that Neotropical deforestation and climate drying would likely, on average, trigger declines in culturally important birds and increases in harmful/annoying ones (Figures 1 and S5). This result contradicts previous studies that show that farmers and urbanites derive cultural services from birds found in human-dominated areas such as cities and gardens (Belaire et al., 2015; Cox et al., 2018). Our findings emphasize that most cultural services were derived from birds in wetter forests. Therefore, a conservation focus on wetter forests could maximize avian cultural services to multiple beneficiaries.

The "forest scarcity hypothesis" (Satake & Rudel 2007) suggests that as with other economic goods, an increasing scarcity of forest-affiliated birds (due to increased deforestation) renders these species more economically and culturally valuable. This hypothesis may explain why people preferred forest-affiliated birds. If scarcity underpins cultural services, then promoting reforestation to increase cultural services could induce a paradox: increasing forest cover should benefit rarer, forest-restricted species, making them less scarce and therefore potentially less valued (Courchamp et al., 2006). Indeed, prior work in our study system and elsewhere suggests that birdwatchers do place greater value on rarer species, especially for birdwatching and acoustic aesthetics (Booth, Gaston, Evans, & Armsworth, 2011, Echeverri et al., 2020). However, rarity did not drive cultural services for urbanites and farmers (Echeverri et al., 2020), indicating reforestation would likely increase bird-mediated cultural services for urbanites and farmers without inducing any paradoxes.

Regardless, as global environmental changes reshape diversity patterns across landscapes, our work demonstrates that it will be imperative to not only understand which species may be extirpated, but also how shifts in species' composition of ecological communities may alter the existing cultural connections between people and nature. We have previously shown that the bird species that occupy wetter, more forested sites tend to have smaller distributional ranges and tend to be more vulnerable to climate and land-use change (Frishkoff et al., 2016; Karp et al., 2019). Thus, our results are encouraging in that they suggest conserving wetter forests in Northwest Costa Rica would align with both ecological and cultural conservation priorities. However, our findings are also discouraging in that they suggest that human-induced changes to the environment are threatening the most culturally important avian species. Of course, it is unclear how transferable our findings would be to other locations, given that peoples' attitudes towards wildlife are extremely context dependent (Dinat, Echeverri, Chapman, Karp, & Satterfield, 2019) and species' responses to deforestation can vary across their ranges (Orme et al., 2019).

5 | CONCLUSIONS

By combining sociocultural and ecological data across environmental gradients (via wildlife censuses and social surveys administered to various stakeholders), our work provides a roadmap for integrating cultural services into global change impact assessments. Our approach also provides a pathway for identifying community-driven flagship species that could be used in conservation campaigns to garner public support for local conservation efforts (Veríssimo, MacMillan, & Smith, 2011). Since we showed that all stakeholder groups preferred the same wet-forest affiliated species, despite differences in livelihoods and demographic characteristics, the "highly charismatic species" that we identified here could be used to support conservation efforts aimed at reducing deforestation and raising awareness of predicted climate drying in the region.

More broadly, our findings align with a nascent literature showing that, as ecosystems get modified, so too do the interconnections between people and ecosystems, threatening social structures, cultural practices, and traditional knowledge systems (Adger, Barnett, Brown, Marshall, & O'Brien, 2013). While our study does not document temporal changes in bird communities with land-use or climate change, it does suggest that people tend to place higher cultural values on the species that are more likely to be threatened by habitat conversion and ongoing climate drying in our study region (Rauscher et al., 2008). As such, protecting and restoring wet forests will be critical for safeguarding both ecological vulnerable and culturally important species (Karp et al., 2019). Ultimately, our work suggests that preventing bird declines in the Neotropics is not only important for biodiversity conservation, but could also buffer against the erosion of cultural, emotional, and social connections that people have historically constructed and continue to foster with birds.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICS STATEMENT

This work was conducted under the auspices of the University of British Columbia with UBC Animal Care Committee approval (A15-0109), Behavioral Research Ethics Board approval (H16-00693), and Costa Rican government approval (SINAC- SE-CUS-PI-R-036-2016; SINAC-SE-CUS-PI-R-030-2017; ACT-OR-DR-048-18).

AUTHOR CONTRIBUTIONS

Alejandra Echeverri, Daniel S. Karp, Luke O. Frishkoff, Robin Naidoo, Jiaying Zhao, and Kai M.A. Chan designed research; Alejandra Echeverri, Daniel S. Karp, and Jim Zook collected data; Alejandra Echeverri, Daniel S. Karp, Luke O. Frishkoff, Robin Naidoo, and Jaya Krishnan analyzed data; Alejandra Echeverri and Daniel S. Karp wrote the manuscript. All authors contributed to drafts and gave final approval for publication.

DATA ACCESSIBILITY STATEMENT

Data from the ecological surveys (including avian point count data, land-use, and precipitation data for all sites) are stored in Dryad data repository: https://doi.org/10.5061/dryad.pzgmsbcj6. Data on the mean scores for cultural services per species and per point count location are also stored in Dryad. Raw questionnaire survey data are available from the University of British Columbia and are stored in the Institute for Resources, Environment and Sustainability following the guidelines of the Behavioral Research Ethics Board for researchers who meet the criteria for access to confidential data. Contact the authors for information regarding access.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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