

Can avian functional traits predict cultural ecosystem services?

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Abstract

1. The functional trait diversity of species assemblages can predict the provision of ecosystem services such as pollination and carbon sequestration, but it is unclear whether the same trait-based framework can be applied to identify the factors that underpin cultural ecosystem services and disservices.
2. To explore the relationship between traits and the contribution of species to cultural ecosystem services and disservices, we conducted 404 questionnaire surveys with birdwatchers and local residents in Guanacaste, Costa Rica.
3. We used an information-theoretic approach to identify which of 20 functional traits for 199 Costa Rican bird species best predicted their cultural ecosystem service scores related to birdwatching, acoustic aesthetics, education and local identity, as well as disservices (e.g. harm to crops).
4. We found that diet was the most important variable explaining perceptions of cultural ecosystem service and disservice providers. Aesthetic traits such as plumage colour and pattern were important in explaining birdwatching scores. We also found people have a high affinity for forest-affiliated birds.
5. The insight that functional traits can explain variation among cultural perspectives on values derived from birds offers a first step towards a trait-based system for understanding the species attributes that underpin cultural ecosystem services and disservices.

KEYWORDS

avian conservation, conservation psychology, ecosystem services, human-nature interactions, Neotropical birds, questionnaire surveys

1 | INTRODUCTION

Ecosystem functions and services are provided by a suite of biodiversity components ranging from species traits to ecological communities (Daily, 1997; Díaz & Cabido, 2001; Kremen, 2005). Indeed, biodiversity provides numerous benefits to humans, such as sequestering carbon, providing water, and supporting cultural values (Millennium Ecosystem Assessment, 2005), which enhance

human well-being (Díaz, Fargione, Chapin-III, & Tilman, 2006). The concept of ecosystem services is often associated with a broadly instrumental view of human–ecosystem relations (i.e. that nature is valuable because it is useful to people), yet the *cultural ecosystem services* (CES) concept has inspired a relational turn to understanding values (Chan et al., 2016; Fish, Church, & Winter, 2016). CES encapsulate the many important ways that people relate to ecosystems and are defined as ‘ecosystem’s contributions to the

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non-material benefits, such as capabilities and experiences, that arise from human-ecosystem relationships' (Chan, Satterfield, & Goldstein, 2012).

Some components of biodiversity are more directly related to ecosystem services than others (Balvanera et al., 2006). In particular, functional traits—features of 'an individual or a species that potentially affect performance or fitness' (Cadotte, Carscadden, & Mirotchnick, 2011)—offer a predictive link between biodiversity and ecosystem processes (e.g. decomposition and nutrient cycling). As such, functional diversity (e.g. the kind, range, and relative abundance of functional traits present in a community; Díaz et al., 2007) is often considered the component of biodiversity with the most potential to explain variation in ecosystem processes and services (de Bello et al., 2010; Díaz & Cabido, 2001; Kremen, 2005; Luck, Lavorel, McIntyre, & Lumb, 2012). Relationships between functional traits and ecosystem services have been empirically documented for a range of organisms and ecosystem services (de Bello et al., 2010; Hevia et al., 2017), for example, relationships between plants, soil invertebrates and mineralization, nutrient retention and pollination (e.g. Brown et al., 2013; Kimball et al., 2016; Lavorel et al., 2011; Storkey et al., 2013). However, relationships between functional traits and cultural services have rarely been evaluated (Goodness, Andersson, Anderson, & Elmqvist, 2016; Hevia et al., 2017).

Researchers have argued that CES transcend biophysical attributes of ecosystems because they are tied to places and memories, and cannot be treated as economic functions where a given number of species or biophysical attributes yields a certain number of CES units (Klain, Satterfield, & Chan, 2014). Daniel et al. (2012) argued that CES incorporate social constructs, and that identifying concrete features of the ecosystems independent of culture is therefore challenging. Indeed, the study of CES goes beyond the domain of ecology because it must take into account worldviews, identities, languages and folklore, which fall under the domain of many other academic subfields (Echeverri, Karp, Naidoo, Zhao, & Chan, 2018).

Nonetheless, previous studies have shown that specific ecological or evolutionary attributes can play an important role in explaining CES, as well as detrimental attributes of biodiversity (i.e. disservices). For example, forests with larger and denser trees are preferred for their scenic beauty (Ribe, 2009), while visitors in parks, zoos, and aquaria tend to prefer more colourful animals (Garnett, Ainsworth, & Zander, 2018; Lišková, Landová, & Frynta, 2015; Stokes, 2007), with larger body sizes (Woods, 2000), and those that are phylogenetically closer to humans (Batt, 2009). In urban environments, people prefer plants with diverse colours, fragrances and utilities (e.g. in terms of food and medicine) (Goodness, 2018). The trait–service approach therefore offers a way to explore the recognition and appreciation of biodiversity, which is inextricably linked with CES provisioning (Goodness et al., 2016). Perhaps most importantly, these observations suggest that a trait-based predictive framework for CES is feasible, although development of such a framework requires a deeper understanding of how cultural services are generated.

The lack of a general framework for predicting CES is problematic because ecosystem service assessments typically ignore cultural factors, partially because it is unclear which species or attributes of ecosystems are most important to safeguard or prioritize (Goodness et al., 2016; Plieninger, Dijks, Oteros-Rozas, & Bieling, 2013). Moreover, the vital connection between people and ecosystems appears to be changing. In some parts of the world, people are spending less time outdoors, minimizing their interactions with wildlife (Knapp, 2066), a phenomenon referred to as the "extinction of experience" (Soga & Gaston, 2016). It is also postulated that urbanization has led to an increased alienation from and a decreased focus on natural ecosystems and biodiversity (Manfredo, Teel, & Bright, 2003). Managing landscapes for CES that foster human–nature relationships is one way of reversing the extinction of experience and reconnecting people to the non-human world (Cox & Gaston, 2018). Therefore, understanding which characteristics of biodiversity are valued by different stakeholders is critically important for clarifying the basic mechanisms that underpin cultural services, and designing conservation planning initiatives that consider these services.

We sought to explore the links between functional traits and CES using Costa Rican birds as a case study. We asked: (a) Can functional traits explain some variation in the CES and disservices associated with birds? (b) If so, which avian functional traits better explain CES and disservices? (c) Do these trait–service relationships differ among beneficiaries (here, birdwatchers vs. non-birdwatchers)?

We hypothesized that, akin to biophysical services, functional traits could explain some of the variation in CES provisioning. Based on previous research, we expected that for birdwatchers, the following traits would predict birdwatching (i.e. recreation) values: rarity (i.e. low abundance), restricted distribution ranges (i.e. endemic species), and evolutionary distinctness (ED; Gaston, Cox, et al., 2018; Verissimo, MacMillan, & Smith, 2011). Birdwatchers often focus on rare birds and are likely to be competitive with one another. Indeed, avid birdwatchers tend to spend substantial amounts of money and time seeking birds they have never seen before (Steven, Smart, Morrison, & Castley, 2017). On the other hand, for non-birdwatchers (farmers and urbanites), we predicted that birdwatching would be positively associated with abundance, total number of colours in the plumage and body mass. Previously, these traits have all been documented as being positively associated with people's perceptions of the aesthetic beauty of animals (Amiot & Bastian, 2015; Ward, Mosberger, Kistler, & Fischer, 1998; Woods, 2000). Given the few empirical studies on bird-related CES, we did not have a priori predictions for other CES categories such as education (i.e. benefits that people derive from studying or learning about birds).

2 | MATERIALS AND METHODS

2.1 | Study area

Surveys were conducted in North-western Costa Rica (Guanacaste and Puntarenas provinces), a biodiverse region encompassing a

multitude of habitats, including tropical dry forests, rainforests, natural savannahs, cattle pastures, melon/rice crop rotations, sugar cane pastures and fruit crops (Calvo-Alvarado, McLennan, Sánchez-Azofeifa, & Garvin, 2009; Hund, Allen, Morillas, & Johnson, 2018; Karp et al., 2018).

Bird-related CES are important to Costa Rica because the country is one of the top destinations for international birdwatchers in Latin America (Yonz Martínez, 2014) and biodiversity contributes significantly to its tourism industry (5%–7% GDP; World Travel Tourism Council, 2014). North-western Costa Rica has developed its ecotourism industry partially based on the tropical dry forests of Palo Verde, Santa Rosa and Barra Honda National Parks, which inspire tourists from all over the world to explore the dry forests' wildlife. Indeed, North-western Costa Rica receives ~10% of the total tourists visiting Costa Rica, and the tourism industry keeps rising as an important economic activity in the region (Hernández & Picón, 2011).

Moreover, the recent history of reforestation in Costa Rica and the development of the ecotourism industry as an important economic sector has created new social and political identities, including a strong environmentalist perspective (Vivanco, 2006). Nonetheless, local peoples' identities are still deeply associated with cattle ranching and farming, as agriculture remains the region's main economic activity (Dinat, Echeverri, Chapman, Karp, & Satterfield, 2019). Thus, human–nature relationships in North-western Costa Rica take various forms. For tourists and local birdwatchers, they engage with birds through recreation, while local residents and farmers engage with birds through agriculture. Hence, this case study allowed us to compare how human–bird relationships differ among beneficiaries.

2.2 | Survey

We conducted 404 in-person and online surveys with birdwatchers ($n = 115$) and non-birdwatchers (i.e. farmers and urbanites; $n = 289$) in the region. This study was conducted under the auspices of the University of British Columbia with Behavioural Research Ethics Board approval (#H16-00693); all survey respondents gave consent to participate in the study. We asked each person to rate 12 or 13 bird species on 13 Likert-scale items designed to measure CES and disservices (Table 1), building on the categories from Gould et al. (2014) and Belaire, Westphal, Whelan, and Minor (2015). Specifically we measured: (1) *Birdwatching* (i.e. an activity by which pleasure is derived from finding and watching birds); (2) *Acoustic aesthetics* (i.e. enjoyment people derive from hearing birds' songs/calls); (3) *Education* (i.e. benefits that people derive from studying or learning about birds); (4) *Identity* (i.e. benefits that people derive from birds that are representative of the study region); (5) *Disservices* (i.e. detrimental aspects associated with birds, such as causing harm to the crops or the built infrastructure in their surroundings), and (6) *Bequest* (i.e. the birds that people want to protect for future generations; Table 1). The complete methodology is described by Echeverri, Naidoo, Karp, Chan, and Zhao (2019).

TABLE 1 Likert scale items presented in the survey to measure different cultural ecosystem services and disservices

Construct	Survey item
Disservices (Cronbach's $\alpha = 0.77$)	This bird causes problems to other species that are important for me (reversed coded)
	This bird causes problems to the crops or the farms by for example eating the crop (reversed coded)
	I find this bird annoying because it is too noisy
	I dislike this bird because their droppings make a mess or they build nests in inconvenient places
Education (Cronbach's $\alpha = 0.83$)	I like learning about or studying this bird, where it lives and what it does
	I like teaching others about this bird and its habitat
Bequest (Cronbach's $\alpha = 0.84$)	This bird should be protected for future generations
	It would be sad if this bird would no longer exist
Birdwatching (Cronbach's $\alpha = 0.84$)	This bird is beautiful and I enjoy watching it
	I am excited to find this bird
Acoustic aesthetics (NA)	This bird has a beautiful song
Identity (Cronbach's $\alpha = 0.58$)	This bird is like my neighbour and makes me feel at home
	This bird helps make this place what it is

Surveys covered questions about 199 species detected in the region (Frishkoff et al., 2016; Karp et al., 2018). Of the 199 species in the region, each survey asked questions on a set of 12–13 species that were randomly generated (Table S1). Each species was represented by a visual illustration of a male individual (Garrigues & Dean, 2007) and an auditory clip of their song/call (xeno-canto.org; Table S2). Participants were then asked how familiar they were with the species, how frequently they saw the species in a given month, and whether they liked or disliked the species. If participants were familiar with the species, then they were asked the name of the species and their subjective agreement on 12 different 5-point Likert scale items (Table 1), ranging from strongly disagree (1) to strongly agree (5), that reflected important cultural service and disservice categories.

Surveys were administered in-person and online during November and December 2017. Participants were selected and sampled differently for each group. For farmers, we attended meetings of the Ministry of Agriculture and Cattle Ranching (MAG) in the towns of Nicoya and Hojanca. At the meetings, we invited farmers to participate in the study and explained that there was no compensation and that participation in the study was voluntary. We also visited farms to recruit more farmers. We sampled farmers who reared livestock and/or grew a variety of crops (e.g. sugar cane, rice). Even though women were less likely to farm in the region, we tried to sample as many women farmers as possible to minimize any bias in the

TABLE 2 Characterization of participants according to demographic information and attitudes/behaviour towards birds

Characteristics	Birdwatchers (n = 115)	Non-birdwatchers (n = 289)	
		Farmers (n = 140)	Urbanites (n = 149)
Age in years	39.34 (15.19)	49.79 (17.47)	34.93 (16.92)
Gender			
Male	67%	76%	49%
Female	33%	22%	51%
Prefer not to answer		2%	
Education level			
Primary school	3%	49%	22%
High school	15%	23%	27%
Technical or vocational school	8%	4%	3%
Bachelor's degree	41%	16%	35%
Specialization	8%	1%	1%
Master's degree	14%	2%	4%
Doctoral degree	9%		
Other	3%	4%	7%
Place considered home			
Costa Rica	77%	99%	95%
Asia	1%		
Central America		1%	1%
Europe	5%		1%
North America	13%		3%
Oceania			1%
South America	5%		
Attitudes and behaviours towards birds			
Gone birdwatching in the past 2 years	96%	37%	45%
Species that can identify	48.36 (15.04)	23.18 (2.65)	19.93 (2.43)

Note: Standard deviation is shown in parentheses.

data due to gender. Nevertheless, only 22% of the farmers surveyed were women (Table 2).

To recruit urbanites, we visited public spaces in urban areas across the peninsula, including central town parks, senior homes, universities, and schools. We approached people randomly and targeted people with a wide range of ages, different education levels, and 50% women, to gain a representative sample of the population (Table 2). Lastly, our criteria to select birdwatchers was to identify anyone who had gone birdwatching in North-western Costa Rica. We advertised the survey in Neotropical and European birdwatching forums and listservs (e.g. NEOORN- Neotropical Ornithology discussion list), in Facebook pages of Costa Rican birdwatching sites, and through the online bulletin of the Costa Rican ornithological association. We also attended two Christmas bird counts in Monteverde and Volcán Arenal (December 2017) and conducted in-person surveys during the meetings prior to the counts. Even though birdwatching is an activity that is mostly dominated by males over the age of 45 in North America and Europe

(>75%; Vas, 2017), we were able to cover a more demographically diverse sample (Table 2).

Surveys were available in Spanish and English and were administered by the first author and six local field assistants. On average, each survey took one hour to complete. All survey responses for farmers and urbanites were recorded in person, but birdwatchers' responses were recorded both online and in-person. Online responses ($n = 75$) were mostly composed of international birdwatchers who had been birdwatching in North-western Costa Rica in the past, but were not present at the time of sampling. All data were recorded in Qualtrics (a software for designing surveys).

2.3 | Functional traits

For all 199 species, we collected information on 20 functional traits (4 categorical, 16 numerical) from 6 trait families: acoustic traits ($n = 3$), morphological traits ($n = 5$), aesthetic traits ($n = 4$), ecological traits ($n = 3$) and life history traits ($n = 5$; Table 3).

TABLE 3 Avian functional traits used as predictor variables in the mixed-effects models with their description

Trait family	Trait	Name in models	Description	Source	Type of variable
Acoustic	Number of recording notes	Recording_notes_sc	Number of notes in the song/call. Refers to the quantity of the same musical syllable that has different notes	Sonograms analyzed in Raven Pro 1.5	Numerical, integer
Acoustic	Number of syllables	Recording_syllables_sc	Number of distinct musical syllables in bird's songs/calls	Sonograms analyzed in Raven Pro 1.5	Numerical, integer
Acoustic	Delta frequency (Hz)	Delta_freq_Hz_sc	Difference between the highest frequency and the lowest frequency of a bird's song/call	Sonograms analyzed in Raven Pro 1.5	Numerical, continuous
Morphological	Body mass (g)	Body_mass_sc	Geometric mean of body mass average values provided for both sexes	EltonTraits database, Wilman et al. (2014)	Numerical, continuous
Morphological	Hand-Wing Index	Hand_wing_index_sc	A ratio of the 'wing length' from the carpal joint to the tip of the longest primary feather; to the 'secondary length' from the carpal joint to the tip of the first secondary feather. The hand-wing index was developed by Claramunt, et al. (2011) as a metric of wing breadth	B10K trait project	Numerical, continuous
Morphological	Tarsus length (cm)	Tarsus_length_sc	A measure of the tarsus length from museum specimens	B10K trait project	Numerical, continuous
Morphological	Tail length corrected by body mass (cm)	Tail_length_BM_corr_sc	A measure of the tail length from museum specimens corrected by body mass (i.e. residuals of the regression of tail length by body mass)	B10K trait project	Numerical, continuous
Morphological	Bill total culmen corrected by body mass (cm)	Bill_total_culmen_BM_corr_sc	A measure of the total exposed culmen from museum specimens corrected by body mass (i.e. residuals of the regression of bill length by body mass)	B10K trait project	Numerical, continuous
Aesthetic	Crest	Crest_sc	A variable denoting whether the bird has a crest (1) or not (0)	Collected for this project	Binary
Aesthetic	Plumage, number of colours	Plumage_number_colors_sc	A variable denoting the number of colours seen in the illustration of the species in Garrigues & Dean (2007)	Collected for this project	Numerical, integer
Aesthetic	Plumage colour	Plumage_color_coded	A variable denoting whether the plumage colour is predominantly: - White ($n = 19$ species), - Cool colours (e.g. blue, purple, green) ($n = 39$) - Warm colours (e.g. yellow, orange, red) ($n = 37$) - Dull (e.g. brown, grey, black) ($n = 104$).	Collected for this project	Categorical
Aesthetic	Plumage colour pattern	Plumage_color_pattern	A variable denoting the pattern in the plumage coloration with four categories: - Blocks (if the plumage has blocks of colour e.g. Scarlett Macaw) ($n = 149$) - Spotted (if the plumage has spots or dots e.g. Spotted-breasted Oriole) ($n = 18$) - Striped (if the plumage has stripes e.g. Barred Antshrike) ($n = 16$) - Streaked (if the plumage has streaks e.g. Bright-rumped Attila) ($n = 16$)	Collected for this project	Categorical
Ecological	Diet	Diet5Cat	Assignment to the dominant diet type among five diet categories based on the summed scores of constituent individual diets calculated as percent usage of a resource in Wilman et al. (2014). Categories are: - Plant and Seeds ($n = 19$) - Fruits and Nectar ($n = 28$) - Invertebrates ($n = 79$) - Vertebrates and Carrion ($n = 37$) - Omnivore (score of $\leq 50\%$ in the 4 categories) ($n = 36$)	EltonTraits database, Wilman et al. (2014)	Categorical
Ecological	Groups	Groups_sc	A binary variable indicating whether the species forages in groups (1) or not (0). Groups include interspecific and intraspecific flocks	Stiles & Skutch (1989)	Binary

(Continues)

TABLE 3 (Continued)

Trait family	Trait	Name in models	Description	Source	Type of variable
Ecological	Foraging strata-weighted average	For_strata_w_avg	A numerical variable ranging from 1 to 7 indicating the weighted average of a species' foraging strata. It was calculated by multiplying the percentage of time spent at a given strata by the different strata treating 1 = ground and water surface, and 7 = forest canopy	Calculated with the data from EltonTraits database	Numerical, integer
Life history	Evolutionary Distinctness score	ED_score_sc	A species-level measure representing the weighted sum of the branch lengths along the path from the root of a tree to a given tip (species). The ED score metric from Jetz et al. (2014)	Jetz et al. (2014), EDGE website	Numerical, continuous
Life history	Distribution range (Km ²)	Distribution_range_sc	Distribution range of a species at the global scale	BirdLife International (2017)	Numerical, continuous
Life history	Population trend	Population_trend	A categorical variable denoting whether the population is: - Increasing (n = 48) - Decreasing (n = 63) - Stable (n = 66) - Unknown (n = 21)	BirdLife International (2017)	Categorical
Life history	Forest affiliation	ForestAff_sc	A numerical variable ranging from -2 to +2 indicating how affiliated a species is to a forest habitat. A score of +2 indicates high affiliation to forests and -2 indicates low affiliation to forests/high affiliation to agricultural lands	Calculated with the data from Karp et al. (2018) and Echeverri, Frishkoff, et al. (2019). Only for 150 species in the dataset	Numerical, continuous
Life history	Abundance	Abundance_sc	A numerical variable estimating the relative abundance of species ranging from -4.5 to +4. Positive numbers indicate species that are more abundant than expected by chance and negative scores indicate less abundant than expected	Calculated with the data from Karp et al. (2018) and Echeverri, Frishkoff, et al. (2019). Only for 150 species in the dataset	Numerical, continuous

To measure acoustic traits, we analysed one auditory clip (song or call) for each species. We always chose recordings from Costa Rica when available and prioritized songs over calls due to their greater distinctiveness. Moreover, when recordings from Costa Rica were not available, we used the next closest location (e.g. Nicaragua, Panama). All song/call information is presented in Table S2.

We analysed each auditory clip presented in the survey using the software Raven Pro 1.5 (Bioacoustics Research program 2014). We measured three acoustic traits: total note count, total syllables count, and total song frequency range (Hz) following Freeman and Montgomery (2017) (see Figure S1 for examples of acoustic trait data collection). With Raven, we used a Hann spectrogram window with 512 samples, a time grid with an overlap of 50% and a hop size of 256 samples, and a frequency grid with discrete Fourier transform set at 512 and grid spacing of 86.1 Hz (Freeman & Montgomery, 2017).

We compiled a dataset of eight biometric traits including body mass and linear measurements of an additional seven morphological traits. Body mass data were extracted from literature sources (primarily Wilman et al., 2014). Seven other traits—wing length, first secondary length, tarsus length, tail length, bill length (total culmen), bill width, bill depth—were assembled by measuring specimens of all 199 species stored in museums and research collections worldwide.

Measurements were taken by hand using callipers and rulers following a strict protocol (Bregman et al., 2016; Pigot et al., 2016) (see supporting information for further details of methods). For each species, we aimed to measure a minimum of two males and two females (4–39 specimens sampled per species). Our final trait data was calculated as the average value of the individuals measured. Measurements of wing length and first secondary distance (i.e. the distance from the carpal joint [bend of the wing] to the tip of the first [outermost] secondary feather) were not analysed directly but instead used to calculate hand-wing index (Claramunt, Derryberry, Remsen, & Brumfield, 2011), a measure of wing aspect ratio correlated with flight efficiency (Pigot et al., 2016). Hand-wing index reflects the pointedness of a bird's wing, providing a widely used index of avian dispersal ability and ranging behaviour, with relevance to ecosystem services including seed dispersal and pollination (Bregman et al., 2016; Pigot et al., 2016). Bill size and shape are associated with diet in birds (Luck et al., 2012).

Given that the three bill measurements (i.e. bill length, width, depth) were highly correlated with one another (Pearson's $r > .79$), we focused only on bill length in subsequent analyses. Body mass was correlated with both bill length and tail length (Pearson's $r > .5$). Thus, to avoid collinearity in subsequent analyses, we regressed tail length and bill length against body mass and extracted the residuals (Table 3, Figures S2 and S3).

Aesthetic traits included the presence of a crest as well as plumage colour, plumage pattern, and the number of colours in the plumage (Table 3). We collected this information through examining illustrations of each species (Garrigues & Dean, 2007). Examples of these classifications are presented in Table S3.

We also collected a range of ecological and life history traits such as foraging strata, diet, ED score, distribution range, and others from different sources (BirdLife International, 2014; Jetz et al., 2014; Wilman et al., 2014; Table 3). Lastly, we obtained two traits (forest affiliation and abundance) from modelled point count data conducted in the same region (Echeverri, Frishkoff, et al., 2019; Karp et al., 2018). Only 150 of 199 species were surveyed on point counts; thus, 49 species did not obtain forest affiliation and abundance estimates.

2.4 | Statistical analyses

First, we calculated pairwise correlations between all numeric traits and narrowed our trait list to those that were uncorrelated with one another (Pearson's $r < .5$) for all subsequent analyses (Figures S2 and S3). Next, we fitted linear mixed-effects regression models with traits as predictor variables, using 'participant' as a random effect, and with the Likert score for each CES/disservices as the response variable. We modelled the five response variables separately: *birdwatching*, *acoustic aesthetics*, *education*, *identity* and *disservices*. We decided to exclude *bequest*, because there was very little variation in respondents' scores across species (see Echeverri, Naidoo, et al., 2019). We also conducted separate analyses for birdwatchers and non-birdwatchers (i.e. after pooling the data from farmers and urbanites). Finally, all analyses were conducted twice, once for the full range of species ($n = 199$) and again for the 150 species for which we also had information about abundance and forest affiliation. Thus, in total we constructed 20 full models (5 CES x 2 social groups x 2 trait groups, see supporting information).

To quantify the relative effects of each functional trait on all 5 CES/disservices categories, we used an information-theoretic approach, which compares regression models based on how well they account for the information in the data (Burnham & Anderson, 2002). For these analyses, we used the 'dredge' function instituted in the MuMIn package (Barton, 2011) and extracted model-averaged regression coefficients and relative importance using the function 'model.avg' (Barton, 2011). We averaged models across a subset of all possible models ($n = 1,048,576$ models when 20 traits were included in the analyses, and $n = 262,144$ when 18 traits were included) that accounted for 95% of the total weight of all models based on Akaike weights (Akaike's Information Criterion AICc), a metric that balances model fit and complexity (Burnham & Anderson, 2002). The best models for each of the 20 mixed-effects models are presented in the supporting information (Tables S4-S43). Results were summarized by plotting the model-averaged coefficient estimates for each predictor variable with the 95% confidence intervals. All numeric variables were scaled by subtracting the mean and dividing by the standard deviation, so that regression coefficients were directly comparable.

3 | RESULTS

3.1 | Which functional traits predict bird-related CES?

Our results showed that traits from all trait families (acoustic, morphological, ecological, aesthetic and life history) were significant predictors of some CES categories. Below, we show which traits were important predictors of different CES categories.

3.1.1 | Acoustic traits

For acoustic aesthetics and identity CES categories, the number of syllables in a bird's song was a strong positive predictor for birdwatchers (Figure 1). Moreover, the frequency range in a birds' song was a positive predictor for the identity services for both groups, and a positive predictor of disservices for non-birdwatchers (Figure 1).

3.1.2 | Morphological traits

Each of the five morphological traits we measured impacted CES provisioning. Specifically, body mass, hand-wing index, bill length corrected by body mass and tail length corrected by body mass were important negative predictors of acoustic aesthetics for birdwatchers and non-birdwatchers ($RVI > 0.95$, $p < .05$). Tail length was also a strong positive predictor of disservices scores for both groups (Figure 1). Among the five morphological traits, tarsus length was the one with the lowest importance in CES provisioning (see supporting information).

3.1.3 | Aesthetic traits

Traits related to a bird's aesthetic appeal were significant predictors of birdwatching and identity scores ($RVI > 0.95$, $p < .05$). For instance, for both birdwatchers and non-birdwatchers, having more colours in their plumage explained perception of beauty. Also, a spotted plumage pattern was a strong positive predictor of birdwatching, acoustic aesthetics, and education for non-birdwatchers. Moreover, having a crest was a positive predictor of birdwatching scores for birdwatchers.

3.1.4 | Ecological traits

Diet was the most important trait in predicting all five CES categories ($RVI > 0.95$ in most models, $p < 2e-16$, Tables S4-S43). We found that for birdwatchers and non-birdwatchers, diet categories were the strongest negative predictors of birdwatching, acoustic aesthetics, education, and identity. Moreover, diet categories were also the strongest positive predictors of disservices among non-birdwatchers. For instance, we found that relative to frugivores/nectarivores, insectivorous birds had significantly lower scores on birdwatching, acoustic aesthetics, education, and identity, and significantly higher scores on disservices for both groups. We also found that carnivore

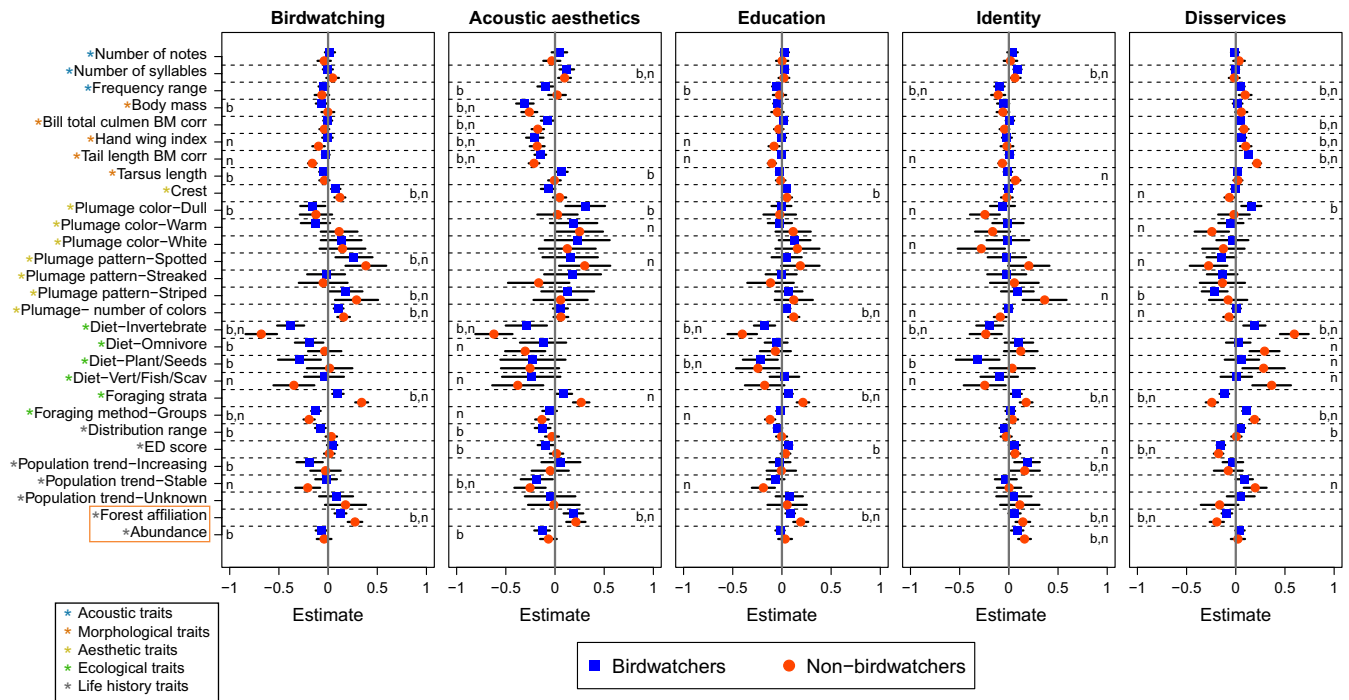


FIGURE 1 The 20 functional traits predicting cultural ecosystem service and disservice categories. On the Y axis are the traits organized by trait family (denoted by coloured stars). The X axis shows the model-averaged standardized regression coefficients (estimates) for all 20 traits with 95% confidence intervals based on the subset of models that accounted for 95% of the total weight of all models (based on Akaike weights). Significant variables are those whose confidence intervals do not cross zero. The estimates presented here are for the models with 18 traits and 199 species, except for the last two estimates which refer to forest affiliation and abundance derived from the models with 20 traits and 150 species (surrounded by an orange box). Blue squares depict estimates for birdwatchers, and orange circles those for non-birdwatchers (farmers/urbanites). The letters on each side of the trait indicate statistical significance ($p < .05$) for b = birdwatchers, n = non-birdwatchers, b, n = both groups (letters are on the right side of the graph indicate significantly positive estimates, while letters on the left indicate significantly negative estimates). Baseline categories for which all categorical traits are compared against, are as follows: Plumage colour-Cool, Plumage pattern-Blocks, Diet-Fruit/Nectar, Population trend-Decreasing

and scavenger birds were perceived as having lower birdwatching scores and as causing higher levels of disservices among non-birdwatchers, relative to frugivores/nectarivores (Figure 1).

Foraging strata was the second most important trait in predicting CES positively for birdwatchers and non-birdwatchers (RVI >0.95 in most models, $p < 2e-16$, Tables S4-S43). Birds that forage in higher foraging strata were perceived as having high birdwatching and identity scores and low disservices for birdwatchers. Additionally, they were perceived as positively impacting acoustic aesthetics, birdwatching, and education scores and low disservices for non-birdwatchers. Lastly, foraging in groups was a positive predictor of disservices for non-birdwatchers and negative predictors of the other CES categories (e.g. having cacophonous songs, or generating lower identity scores; Figure 1).

3.1.5 | Life history traits

Life history traits were also significant predictors of various CES. For instance, ED scores were positive predictors of education scores for birdwatchers and negative predictors of disservices for birdwatchers and non-birdwatchers alike (Figure 1). Contrary to our expectations, distribution range was only a positive predictor for acoustic aesthetics for birdwatchers, but not for the other services (Figure 1).

Population trend was also an important predictor for most CES. Specifically, for non-birdwatchers, stable population size was a negative predictor of a species' birdwatching, acoustic aesthetics, education, identity, and disservices relative to birds with declining population trends. For the two traits with point-count specific data, we found that forest affiliation was a strong positive predictor of birdwatching, acoustic aesthetics, and identity for both groups, and a negative predictor of disservices for both groups. Lastly, abundance was a negative predictor of acoustic aesthetics for birdwatchers, but a positive predictor of local identity scores for birdwatchers and non-birdwatchers (Figure 1).

4 | DISCUSSION

Our study is the first to directly test whether the same trait-based approaches that underpin biophysical services can be applied to multiple cultural services and disservices via a quantitative approach. Charles & Linklater (2013) evaluated which functional traits made birds prone to avian-human conflicts in urban landscapes in New Zealand. Building on their findings, with more cultural service categories and in a different geographical location, we showed that

functional traits pertaining to all trait families (i.e. acoustic, morphological, aesthetic, ecological and life history) can indeed help to explain variation in CES and disservices among species, as has been proposed (de Bello et al., 2010; Kremen, 2005; Luck et al., 2012).

Contrary to our predictions, we found no evidence that rarity (i.e. low abundance), ED scores and restricted distribution ranges were strongly associated with birdwatching scores (i.e. the average of 2 Likert scale items per person, Table 1). One explanation could be that in a country like Costa Rica where avian species richness is high, overall familiarity with rare, evolutionary distinct or range-limited species may be lower compared to other species. Indeed, familiarity has been proposed as an important factor that determines peoples' attitudes towards species (Echeverri, Callahan, Chan, Satterfield, & Zhao, 2017).

Instead, we found that plumage pattern, foraging strata, forest affiliation and having a crest were the most important variables for explaining birdwatching scores among birdwatchers (Figure 1). Empirical studies linking functional traits with CES have shown that aesthetic traits relating to visual appearance (e.g. colour) were the most frequently mentioned factor regarding the plant species people kept in their gardens (Goodness, 2018). Here, we demonstrated that traits pertaining to the physical appearance of birds are important in explaining birdwatching scores for birdwatchers and non-birdwatchers. These results are consistent with previous research showing that people prefer more colourful birds (Garnett et al., 2018) and birds with patterns in their plumage coloration (Lišková et al., 2015).

We found that diet was the strongest predictor for all CES categories (including disservices) and for both groups. In New Zealand, generalist birds (i.e. birds without a specialized diet) were more likely to cause human conflicts compared to birds with more specialized diets (Charles & Linklater, 2013). Here, we found that that non-birdwatchers perceived carnivores and scavengers as less attractive and more likely to cause disservices than other birds. On the one hand, these results were surprising given that human fascination towards raptors has induced cultural practices like falconry in other geographies (Negro, 2018). Also, since raptors feed on vertebrate pests, which can benefit farmers (Kross, Tylianakis, & Nelson, 2012), we expected farmers and urbanites (i.e. non-birdwatchers) to exhibit positive attitudes towards raptors. However, in our study, farmers reported harm due to raptors preying on their chickens (a primary food source for people), which may explain the results we found. In addition, as in other parts of the world (see Campbell, 2009), local Costa Ricans often victimize scavengers/carnivores such as vultures, hawks, and owls. In our sample, people often talked about vultures as being ugly and stinky ($n = 23$ non-birdwatchers; 5 birdwatchers), and in other parts of the country, people hold the superstition that these birds spread diseases and represent evil spirits (Enríquez Rocha & Rangel Salazar, 2004; Sault, 2010).

We also found that insectivores scored poorly on birdwatching, acoustic aesthetics, education, and identity values relative to other birds. Moreover, we found that frugivores/nectarivores (e.g. hummingbirds, toucans) scored relatively higher on all CES categories except disservices compared to other birds, suggesting frugivores/nectarivores are perceived as benevolent, despite frugivores

being more likely to damage some crops (Kross et al., 2012). These results are consistent with the 'personalised ecology' framework, which suggests that people experience human–nature relationships based on the ecological communities in their surroundings. People are more likely to interact with species that are diurnal, common, and apparent, such as birds that are common in urban feeders (Gaston, Soga, et al., 2018). Frugivores/nectarivores tend to be more common in urban areas and gardens as people place hummingbird feeders and put out ripe plantains to attract them. Thus, the increased familiarity with these birds may lead to more positive perceptions.

Our finding that diet can influence CES is non-trivial and may have major conservation implications for the design of conservation programmes. For instance, in Costa Rica, insectivores are the most vulnerable group to deforestation (Sekercioglu et al., 2002). Moreover, vultures have experienced the most rapid decline in conservation status over the past decade and comprise the most threatened avian functional guild in the world (Buechley & Sekercioglu, 2016), though two of the three vultures studied here (Black Vulture, *Coragyps atratus*, and Turkey Vulture, *Cathartes aura*) are hyperabundant. Nonetheless, because insectivores and scavengers are, in general, the most endangered and the least-liked, our work suggests further research is needed to encourage support for conservation of these groups. Specifically, educational campaigns attempting to counteract negative perceptions of these birds, and highlighting their ecological importance, might be appropriate in this region.

After diet and plumage colours, forest affiliation and foraging strata played important roles in explaining birdwatching and identity services for birdwatchers, and education, birdwatching, identity and acoustic aesthetics for non-birdwatchers. Hence, our findings suggest that in general, people have high affinity for forest-associated species. In our study region, forest-affiliated birds are expected to be sensitive to climate drying and deforestation (Karp et al., 2018). To our knowledge, our study is the first to demonstrate human preferences for forest-associated wildlife. We interpret these results by drawing parallels with research on urban ecosystem services which has demonstrated perceived naturalness to be a strong predictor of aesthetic and recreation values (Sandifer, Sutton-Grier, & Ward, 2015). Perhaps forest-associated species are perceived as "more natural" and thus as having more education and birdwatching values.

Human–bird relationships have the potential to impact physical, mental and social comfort and happiness (Millennium Ecosystem Assessment, 2005; Cox & Gaston, 2016). For instance, studies have shown that urban settings are appreciated more if bird songs are heard (Hedblom, Heyman, Antonsson, & Gunnarsson, 2014). Indeed some bird songs are commonly associated with perceived stress recovery (Ratcliffe, Gatersleben, & Sowden, 2013) and have the potential to decrease anxiety and depression felt by people as a result of the massive environmental changes that our planet is experiencing (Clayton, Litchfield, & Geller, 2013). Our study also sheds light on the kinds of birds people derive benefits and disservices from. Thus, designing landscapes, cities, infrastructure, and human activities to foster human–nature relationships could help reverse the extinction

of experience and connect people more to the non-human world (Cox & Gaston, 2018).

All trait-based studies have important shortcomings, and our study is no exception. Previously, scholars have claimed that, for example, morphological traits are important predictors of human attitudes towards animals (e.g. Serpell, 2004). We decided to analyse traits separately to evaluate the relative importance of the trait families in explaining CES variation. However, we recognize that different traits may be autocorrelated, driving some spurious associations, such as plumage coloration coinciding with feeding guilds.

For certain traits, variation within species may be stronger than variation between species (Laughlin, 2014). Thus, trait scores calculated from only a few individuals may not be representative of the entire species. For instance, vocalizations from oscines (songbirds) are often learned through imitation and can be quite complex. Their song repertoires are informed by their social networks, and exhibit strong regional variations (e.g. the Rufous-and-white Wren in our study system, Graham, Sandoval, Dabelsteen, & Mennill, 2016). As we could only analyse one call/song per species, our acoustic trait scores do not account for this variation. Moreover, there are other traits that could influence CES provision. Some birds (e.g. Great Kiskadee, *Pitangus sulphuratus*; White-throated Magpie-Jay, *Calocitta formosa*; Great-tailed Grackle, *Quiscalus mexicanus*) are very aggressive, particularly during their nesting periods (Stiles & Skutch, 1989), which may cause people to form negative perceptions towards these species. Future work could profitably focus on exploring the role of behavioural traits- like aggression- in explaining variation in CES.

Similarly, species dimorphism (i.e. when males look and act different from females) might influence CES provisioning because in many cases, people prefer the vibrant appearance and behaviours of male birds over females birds (Batt, 2009). Species under intense sexual selection, may have polygamous mating systems (e.g. manakins, hummingbirds), which also may play a role in the cultural perceptions of birds. Moreover, it is possible that sexual selection driving dimorphism affects perceptions towards birds. However, we did not present illustrations for the females of dimorphic species in our survey because we did not want to bias responses by having some species presented once versus twice. We acknowledge that this might have influenced our results. People did mention, however, in the open-ended questions that they liked some species because the males and females looked different (e.g. Long-tailed Manakin, $n = 57$ people). Thus, our method was able to capture to some extent the dimorphism for species that people recalled well. Future research might compare sets of dimorphic versus non-dimorphic species to evaluate the extent to which dimorphism drives bird-related CES provisioning, and to test whether dimorphism elevates the perceived species richness, as some people might perceive dimorphic species as two different species.

We approached human–bird relationships with a post-positivist epistemology rooted in Western science, which posits some limitations. We used the CES framework to operationalize human–bird relationships, but we recognize that many other theoretical frameworks exist (Echeverri et al., 2018). In Costa Rica, as well as in other

Latin American countries, current human–bird relationships are partially shaped by the place of birds in Indigenous worldviews. Indeed, some folk stories that are still told about the birds have pre-Hispanic Indigenous roots (Jacques-Coper, Cubillos, & Ibarra, 2019; Sault, 2010). Thus, our study could be complemented with an ethno-ornithological analysis that draws from Indigenous epistemologies and delves into other factors that are also important in shaping cultural connections between people and nature such as values, emotions, unconscious motives, cultures, and worldviews (Martín-López, Montes, & Benayas, 2007; Peterson, Russell, West, & Brosius, 2010).

Lastly, a caveat of these type of studies is the correlation versus causation problem. In fact, preferences are informed by implicit biases, which are more difficult to measure (Echeverri et al., 2017). More work is needed to disentangle the role of explicit versus implicit preferences that affect peoples' perceptions of species-related CES and disservices (Echeverri et al., 2017). Implicit preferences, defined by psychologists, explain wherein a person's judgements are said to be based on preconscious automatic evaluations conducted without intentions (Greenwald & Banaji, 1998). In contrast, explicit preferences represent conscious judgements that can be assessed through self-reported measures (e.g. surveys; Echeverri et al., 2017).

5 | CONCLUSIONS AND CONSERVATION IMPLICATIONS

Conservation planning, resource management and urban planning efforts often ignore CES because they are difficult to capture, quantify, and assess in comparison to the other ecosystem service categories (Hernández-Morcillo, Plieninger, & Bieling, 2013). However, considering CES in such decision-making realms would be beneficial because they are more directly linked to people's motivations to care for nature (Chan, Guerry, et al., 2012). Researchers have pushed to include CES in decision-making and have consequently developed methods to capture and map CES at the landscape level (Gould et al., 2014; Klain & Chan, 2012; Plieninger et al., 2013), but CES provided by species remain difficult to capture, measure, or assess (Hevia et al., 2017).

Regarding global avian policy, our study can help inform the design and delineation of Important Bird and Biodiversity Areas (IBAs). The IBAs represent the largest global network of important sites for biodiversity (Devenish, Díaz Fernández, Clay, Davidson, & Yépez Zabala, 2009). IBAs are best suited to ensuring the survival of viable populations of many of the world's bird species. Broadening the mandate of IBAs to include socio-cultural considerations, particularly those of local stakeholders, might help to mainstream a socio-ecological perspective of bird conservation and result in more effective and inclusive conservation.

Moreover, stakeholders who prioritize the ecological dimensions of bird conservation may not always agree with those who prioritize the socio-cultural dimensions of birds. In our study we found that scavengers and insectivores, some of the most endangered bird taxa, were also the least-liked groups of birds. Thus, improving local conservation efforts for insectivores may involve highlighting

their role in pest control; this information may help change public attitudes towards these birds, which in turn may translate into more support for their conservation. For carnivores and scavengers, their respective roles in controlling pests and carcass removal/disease prevention (Kross et al., 2012; Markandya et al., 2008) could form the basis of educational campaigns.

We recognize that campaigns may not always be sufficient to foster tolerance and acceptance of the conservation of endangered species, and that conflict can remain an important issue (e.g. raptors feeding on people's chickens). Additional compensation mechanisms may be needed when the goal is to conserve an endangered species that also induces human-wildlife conflict (e.g. Jabiru, *Jabiru mycteria*, which is endangered in Costa Rica and feeds on fish from tilapia ponds). Paying attention to public perceptions of species while addressing their ecological vulnerability is not easy, but in our paper, we have demonstrated that functional traits can indeed help to explain variation across CES and disservices. These findings might also occur with other taxa and in other geographical regions. Our method may help identify broad trade-offs between cultural preferences and ecological aspects of species.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.E., D.S.K., R.N. and K.M.A.C. designed research; A.E. and J.A.T. collected data; A.E., D.S.K., R.N., and J.Z. analysed data; A.E. wrote the manuscript. All authors contributed to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

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 Behavioural Research Ethics Board for researchers who meet the criteria for access to confidential data. Contact the authors for information regarding access. Functional trait data are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.cjsxk5n1p> (Echeverri, Karp, et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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