Contributed Paper

Change in avian functional fingerprints of a Neotropical montane forest over 100 years as an indicator of ecosystem integrity

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Abstract: Ecologically relevant traits of organisms in an assemblage determine an ecosystem's functional fingerprint (i.e., the shape, size, and position of multidimensional trait space). Quantifying changes in functional fingerprints can therefore provide information about the effects of diversity loss or gain through time on ecosystem condition and is a promising approach to monitoring ecological integrity. This, however, is seldom possible owing to limitations in historical surveys and a lack of data on organismal traits, particularly in diverse tropical regions. Using data from detailed bird surveys from 4 periods across more than a century, and morphological and ecological traits of 233 species, we quantified changes in the avian functional fingerprint of a tropical montane forest in the Andes of Colombia. We found that 78% of the variation in functional space, regardless of period, was described by 3 major axes summarizing body size, dispersal ability (indexed by wing shape), and habitat breadth. Changes in species composition significantly altered the functional fingerprint of the assemblage and functional richness and dispersion decreased 35–60%. Owing to species extirpations and to novel additions to the assemblage, functional space decreased over time, but at least 11% of its volume in the 2010s extended to areas of functional space that were unoccupied in the 1910s. The assemblage now includes fewer large-sized species, more species with greater dispersal ability, and fewer habitat specialists. Extirpated species had high functional uniqueness and distinctiveness, resulting in large reductions in functional richness and dispersion after their loss, which implies important consequences for ecosystem integrity. Conservation efforts aimed at maintaining ecosystem function must move beyond seeking to sustain species numbers to designing complementary strategies for the maintenance of ecological function by identifying and conserving species with traits conferring high vulnerability such as large body size, poor dispersal ability, and greater habitat specialization.

Keywords: Andes, birds, Colombia, ecological integrity, fragmentation, functional richness, functional uniqueness

Cambios en las Huellas Funcionales Aviarias en un Bosque Neotropical de Montaña durante Cien Años como Indicadores de la Integridad del Ecosistema

Resumen: Las características ecológicamente relevantes de los organismos que pertenecen a un ensamblaje determinan la huella funcional de un ecosistema (es decir, la forma, el tamaño y la posición del espacio multidimensional de la característica en cuestión). Por lo tanto, la cuantificación de los cambios en las huellas funcionales puede proporcionar información sobre los efectos que tiene la pérdida o ganancia de diversidad a lo largo del

tiempo sobre las condiciones del ecosistema; por esto se le considera una estrategia prometedora para el monitoreo de la integridad ecológica. Sin embargo, lo anterior es pocas veces posible debido a las limitaciones de los censos históricos y a la falta de datos sobre las características del organismo, particularmente en las diversas regiones tropicales. Con datos detallados de censos realizados durante cuatro periodos en más de un siglo, y utilizando las características morfológicas y ecológicas de 233 especies, cuantificamos los cambios en la huella funcional aviaria de un bosque tropical de montaña en los Andes de Colombia. Encontramos que el 78% de la variación en el espacio funcional, sin importar el periodo, estuvo descrito por tres ejes principales que resumen el tamaño corporal, la habilidad de dispersión (indicada por la forma de las alas) y la amplitud del hábitat. Los cambios en la composición de especies alteraron significativamente la huella funcional del ensamblaje y la riqueza y dispersión funcional disminuyeron en 35–60%. Debido a la pérdida de especies y a la adición de especies nuevas al ensamblaje, el espacio funcional disminuyó con el tiempo, pero, durante la década de 2010, al menos el 11% de su volumen se extendió a áreas de espacio funcional que no estaban ocupadas cien años antes. El ensamblaje ahora incluye menos especies de gran tamaño, más especies con buena habilidad de dispersión y menos especialistas de hábitat. Las especies que se perdieron eran funcionalmente únicas, lo que resultó en reducciones importantes en la riqueza y en la dispersión funcional después de su pérdida, e implicó consecuencias importantes para la integridad del ecosistema. Los esfuerzos de conservación enfocados en mantener la función del ecosistema deben ir más allá de la búsqueda de la preservación del número de especies y enfocarse también en el diseño de estrategias complementarias para el mantenimiento de la función ecológica por medio de la identificación y conservación de especies con características que otorgan una vulnerabilidad alta, como lo son el tamaño corporal grande, una habilidad de dispersión pobre y una mayor especialización de hábitat.

Palabras Clave: Andes, aves, Colombia, fragmentación, integridad ecológica, riqueza funcional, singularidad funcional

Introduction

Determining how changes in the natural world affect ecosystems and their biodiversity is essential, especially if ecosystem function is to be maintained and habitats restored to regain services they once provided (Cadotte et al. 2011; Dirzo et al. 2014). First, however, there is a need to understand ecosystems in terms of function and how they change naturally or in response to human intervention. Functional traits, defined as ecological, morphological, or behavioral traits influencing fitness and survival of organisms (Violle et al. 2007), mediate ecosystem processes and determine the responses of populations to environmental conditions, biotic interactions, and nutrient cycling in ecological assemblages (Bregman et al. 2016; Funk et al. 2017). Therefore, measures of diversity in functions provide information about ecosystem condition and stability because high functional diversity is associated with greater plasticity, productivity, and resilience in the face of disturbances or climatic fluctuations (Mason et al. 2005; Cadotte et al. 2011). Examining changes in functional diversity within assemblages known to have changed in species composition through time offers an opportunity to determine the consequences that such changes have on ecosystem functions and services, including seed dispersal, predation, pollination, and nutrient flow.

Functional diversity is often quantified based on a multidimensional volume, where each species occupies a position depending on its similarity to others. In this volume, species with similar trait values (i.e., functionally redundant species) are located near the centroid close to other species, whereas functionally distinctive species exist separately in the periphery (Mason et al. 2005; Ricklefs 2012; Kuebbing et al. 2018). The shape, size, and position of the multidimensional trait space formed by organisms inhabiting an ecosystem hence determines a unique functional fingerprint. Quantifying changes in functional fingerprints can therefore provide information about the effects of changes in species composition on ecological integrity and is a promising monitoring tool for conservation (Carmona et al. 2016; Pigot et al. 2016; Cooke et al. 2019b).

In response to environmental changes, the functional fingerprint of an assemblage may remain unchanged, move in different directions, or change its shape and volume. One may use various metrics to assess such changes. For instance, if an assemblage loses or gains species that are distinct in functional space, then its functional richness (i.e., the total functional space it occupies) would change more drastically than if it lost or gained species occupying areas near the centroid (Carmona et al. 2016; Grenié et al. 2017; Kuebbing et al. 2018). Similarly, whether lost or gained species are located close or far from the centroid of trait space, defined by the most abundant traits and whether such species are abundant or rare, will determine the effect of changes on functional dispersion (FDis) (i.e., the mean distance of each species to the centroid of trait space) (Laliberte & Legendre 2010). Because losses (or gains) of abundant species in the periphery of functional volume cause greater decreases in FDis than changes at the center (Laliberte & Legendre 2010; Carmona et al. 2016), combining measures of functional richness and

dispersion provides a clear picture of the effects of shifts in species composition on functional fingerprints.

Birds are good indicators of ecosystem integrity because they rapidly respond to environmental changes and because variations in bird assemblages can be assessed readily by human observers (e.g., Gregory & van Strien 2010; Bregman et al. 2016). Furthermore, the link between avian functional traits and ecosystem processes is well documented (Maglianesi et al. 2015; Ikin et al. 2019; Pigot et al. 2020). Although studies have explored changes in bird assemblages through time as a response to habitat or climate change (e.g., Renjifo 1999; Freeman et al. 2018), determining whether ecosystem integrity is affected by changes in species diversity and abundance requires assessing whether such changes extend to functional fingerprints.

Studies of the temporal dynamics of functional diversity in ecological assemblages indicate that extirpations and colonizations of species are not random because some traits make species more susceptible to being lost or gained than others (Petchey et al. 2007). Accordingly, changes in functional diversity after climate or landscape change often tend to homogenize traits within assemblages, implying loss of unique functions (Clavel et al. 2011; Jarzyna & Jetz 2017) and likely altered ecosystem integrity (Chalmandrier et al. 2015; Jarzyna & Jetz 2018; Stouffer 2020). However, there are very few studies quantifying long-term changes in the functional fingerprints of tropical assemblages (Hendershot et al. 2020).

The avifauna of San Antonio, a montane cloud forest in the western Andes of Colombia, poses an unprecedented opportunity to examine shifts in functional fingerprints through time in a highly diverse tropical ecosystem and thereby to infer how species extirpations and recolonizations may have influenced ecosystems. San Antonio was first surveyed by naturalists in the 1910s (Chapman 1917). Since then, exhaustive resurveys conducted in the 1950s, 1990s, and 2010s have documented substantial changes in composition of the bird assemblage over more than a century of landscape change, comprising a period of intense forest loss followed by recent regeneration (Kattan et al. 1994; Palacio et al. 2019). We combined morphological and ecological data for the complete bird assemblage of San Antonio, comprising 233 species, to test the hypothesis that functional fingerprints change as a result of gains, losses, and shifts in abundance of functionally distinctive species. We expected functional richness and dispersion to have decreased from the early 1910s and the 1990s, when several species extirpations occurred (Kattan et al. 1994), and to have increased following recovery of some species and colonization by formerly absent species in the 2010s (Palacio et al. 2019). We also evaluated whether colonization by novel species caused changes in the functional fingerprint of the San Antonio assemblage if these species filled areas of functional space not occupied by the set of species coexisting in the area in the 1910s. If extirpated species were functionally unique, then this system may have lost functions provided by those species and potentially gained others from novel colonizers. Alternatively, if extirpated species or novel colonizers were functionally redundant, then the overall functionality of the system may not have changed significantly.

Methods

Study Site

The *Bosque de San Antonio* is a midelevation mountain ridge (1700–2200 m) in Colombia's Western Andes (3.4960 N, −76.6305 W) approximately 15 km west of Cali, Valle del Cauca (Kattan et al. 1994; Palacio et al. 2019). This region (covering approximately 8000 ha) originally harbored extensive tropical montane cloud forests, for which widespread fragmentation in the 1920s to the 1960s resulted in an approximately 46% reduction of forest cover (Kattan et al. 1994; Palacio et al. 2019). Since then, the remaining matrix of forest fragments and farms has remained stable, and there was an estimated approximately 10% increase in forest cover from 1995 to 2016 (Palacio et al. 2019).

Historical and Contemporary Bird Survey Data

We analyzed data from published bird lists for San Antonio compiled by Palacio et al. (2019). From 1907 to 2016, 233 species were detected (Appendix S1). We divided data into 4 periods: the 1910s, including surveys led by Frank M. Chapman and Mervin G. Palmer; the 1950s (surveys by Alden H. Miller); the 1990s (surveys by Gustavo Kattan et al.); and the 2010s (surveys by Ruben Palacio et al.). Detailed methods for these surveys are in the original publications, and they range from specimen collection, to mist-netting, to standardized transect and point count censuses carried out throughout multiple months and years (Chapman 1917; Miller 1963; Kattan et al. 1994; Palacio et al. 2019). Details on methodological differences and changes in the avifauna during these periods are in Appendix S3.

Surveys in the 1910s consisted exclusively of collecting expeditions (Chapman 1917), whereas the 1950s survey involved both collecting and observations (Miller 1963). The 1990s surveys combined mist netting and standardized transects (Kattan et al. 1994), and in the most recent 2010s surveys point counts and citizen science data were used (Kattan et al. 1994; Palacio et al. 2019). Methodological differences between surveys imply that we have strong certainty about species extirpations occurring over time but are less certain about novel species colonizations because the older surveys were

more likely to have missed species that were actually present but were not identified or collected. To address this issue, we analyzed our data based on 2 scenarios. The first is based on the assumption that all surveys accurately describe the avifauna present and that any records of species not detected in prior surveys of San Antonio represent real colonizations. The second scenario is based on the assumption that all the novel species (i.e., those detected for the first time after the 1910s) were false absences. Thus, changes in the avifauna in this scenario consisted exclusively of extirpated species or recolonization of previously extirpated species. What actually occurred likely lies somewhere in the middle of our 2 scenarios.

Functional Traits

For all 233 species, we compiled information on 9 traits describing functional morphospace and avian ecological strategies (Cooke et al. 2019b; Habel et al. 2019; Pigot et al. 2020; Sheard et al. 2020): body mass, bill length, bill width, wing chord, tail length, tarsus length, hand-wing index (a measure of wing shape), habitat breadth (number of habitats listed in International Union for Conservation of Nature accounts), and generation time (years) (IUCN 2018). For additional details on functional trait selection and compilation, see Appendix S3.

Estimation of Functional Diversity Metrics and Temporal Comparisons

Body mass was $\log_{10}$ transformed, and all traits were scaled and centered to have 0 mean and unit variance (Cadotte et al. 2011; Carmona et al. 2016; Cooke et al. 2019a). To obtain a reduced set of uncorrelated variables explaining variation in functional traits, we ran a principal components analysis with data from all species (R Development Core Team 2019). Out of 9 principal components (PCs), the first 3 explained 78% of the variation in functional trait values. Loadings suggested that PC1 described mostly variation in body size (55%), PC2 was related to dispersal ability through the hand-wing index (13%), and PC3 described habitat breadth (11%) (Appendix S3). The first 3 PC scores were then used as axes to compare functional spaces among periods and groups of species (Carmona et al. 2016; Cooke et al. 2019b). An additional discussion of PC4, which correlated with bill morphology and explained 9% of the variation, is included in Appendix S3.

We adopted methods from Cooke et al. (2019b) to construct functional spaces and evaluate temporal shifts in the San Antonio avifauna. Two and 3-dimensional trait spaces were constructed by comparing different combinations of trait space values; in this case, PC1, PC2, and PC3 (Cooke et al., 2019b). Multivariate kernel density estimates (Duong 2019) were used to calculate the 0.50, 0.95, and 0.99 probability contours for trait spaces (Cooke et al. 2019b). Scores from PCs comprising approximately 95% of variance were used to construct a trait hypervolume to visualize temporal shifts in functional space and to calculate changes in volume and overlap between time periods. The hypervolume was constructed following Cooke et al. (2019b), who used a "one-class support vector machine (SVM)" method (Blonder & Harris 2019). Because migratory species may differ morphologically and ecologically from residents, we conducted separate analyses including and excluding Neotropical migrants ($n = 13$ species) to assess their influence on our inferences Appendix (S3).

Historical and contemporary relative abundances of species from San Antonio were extracted from Palacio et al. (2019). We assigned a value from 0 to 1 to each abundance category (0, absent or extirpated; 0.2, rare; 0.4, uncommon; 0.6, fairly common; 0.8, common; 1, abundant). We constructed a period-by-species matrix with these values, and a species-by-trait matrix with the standardized values of our 9 functional traits. We then estimated functional richness and dispersion with the function dbFD in R package FD (Villeger et al. 2008; Laliberte & Legendre 2010; Laliberté et al. 2014). Functional richness (FRic) was estimated as the volume of the minimum convex hull (Villeger et al. 2008). For ease of interpretation, the functional richness of each time period was standardized by the global FRic; thus, values were constrained to range from 0 to 1 (Laliberté et al. 2014). Functional dispersion is the mean distance of each species to the centroid of trait space, weighted by its relative abundance (Laliberte & Legendre 2010). FDis increases as the most abundant trait values get farther from the centroid of trait space (Laliberté et al. 2014). The relative abundance categories for the historical data sets may be inaccurate because they do not account for collecting bias (i.e., an uncommon species in the collection may have been common in the assemblage). We therefore also estimated FDis without considering abundances.

To evaluate whether functional metrics for each period were different from what might be expected through random processes, we compared observed values with those generated by null models. We randomly reordered the species identity column of the abundance matrix 999 times (thus breaking associations between traits and species' identities) and then recalculated FRic and FDis for each random assemblage (Van de Perre et al. 2020). To assess the magnitude of the difference between observed and null values of FRic and FDis, we estimated standard effect sizes (SES) as $\text{SES} = \frac{\text{obs} - \text{meanNull}}{\text{SD Null}}$ (Van de Perre et al. 2020) and assessed significance with p values as $\frac{(\text{number } F_{\text{null}} \le F_{\text{obs}} + 1)}{(999 + 1)}$ (Cooke et al. 2019a).

Functional Characteristics of Extirpated Species and Novel Colonizers

To describe functional differences among extirpated species, novel additions to the assemblage as of the 2010s, and shared species maintained through time, we constructed trait probability density curves (TPD) based on the first 3 PC axes as traits and the aforementioned species groups as ecological units for comparison in package TPD (Carmona et al. 2016, 2019). We used a 2-sample Kolmogorov–Smirnov test to assess whether there were differences between TPDs of extirpated species and novel additions to the assemblage.

To evaluate whether extirpated species and those establishing new populations in San Antonio were functionally redundant or unique, we calculated functional distinctiveness and uniqueness with package funrar in R (Grenié et al. 2017; Pimiento et al. 2020). Functional distinctiveness (D_i) measures how uncommon a species' trait value is compared with other species in the assemblage, weighted by the species' relative abundance. Functional distinctiveness has values from 0 (high functional redundancy) to 1 (low functional redundancy) (Grenié et al. 2017). Functional uniqueness (U_i) is the distance of each species to its nearest neighbor in the assemblage; the closer U_i is to 1, the farther species i is from its nearest neighbor (Grenié et al. 2017). We ran permutation tests to evaluate whether extirpated species and new additions to the assemblage were more functionally unique or distinctive than expected by chance (Pimiento et al. 2020) and carried out pairwise comparisons to assess differences between time periods (Cooke et al. 2019a).

Results

Under both scenarios (1, novel species colonized the assemblage; 2, no novel colonizers), the centroid of the morphospace described by PC1 (body size) and PC2 (dispersal ability) has remained in the same position, but both the shape and extent of trait space have changed over >100 years (Fig. 1 & Appendix S3). Extirpated species (both scenarios), as well as novel colonizers (scenario 1), were spread over functional space, but those located toward the periphery were responsible for the most noticeable shape changes in functional space (Fig. 1 & Appendix S3).

Changes in functional space were also evident in trait density curves used to compare extirpated species, novel additions, and shared species through time. Trait density curves for scenario 1 showed that the San Antonio assemblage shifted toward smaller sized birds (Kolmogorov–Smirnov test $D = 0.34$, $p = 0.03$) (Fig. 2a), species with higher dispersal ability, as indicated by the hand-wing index ($D = 0.48$, $p < 0.001$) (Fig. 2b), and wider habitat breadths (i.e., fewer habitat specialists) ($D = 0.44$, $p < 0.01$) (Fig. 2c). These shifts resulted in 34% of the functional hypervolume present in the 1910s being absent from the 2010s. In turn, 11% of the volume occupied by the 2010s assemblage was not occupied in the 1910s and 55% has remained constant (Fig. 2d). Trait density curves for body size and dispersal ability in scenario 2 showed shifts similar to those of scenario 1. The assemblage lost larger sized birds ($D = 0.39$, $p < 0.001$) and some species with relatively low dispersal ability ($D = 0.43$, $p < 0.001$), but showed no significant shifts in habitat breadths of species (PC3) ($D = 0.24$, $p = 0.08$) (Appendix S3). Under scenario 2, 29% of the trait hypervolume from the 1910s was lost, 1% of the hypervolume was unique to the 2010s, and 70% remained constant across periods.

Changes in the hypervolume of all traits were comparable to measures of functional richness (FRic) based on the minimum convex hull. Under scenario 1, from the 1910s to the 1950s, functional richness decreased by approximately 36% and then recovered approximately 22% from the 1990s to the 2010s for an approximately 14% net loss (Table 1 & Fig. 3a). Under scenario 2, there was an approximately 66% decrease in functional richness from the 1910s to the 1990's (Table 1) and then a recovery of 12% during the 2010s resulting in a net loss of approximately 54% (Table 1). Functional dispersion followed a similar pattern in both scenarios (Table 1). There was a decrease of approximately 8% from the 1910s to the 1950s and then an increase of approximately 3% from the 1990s to the 2010s (Table 1; Fig. 3b). The difference between values of FDis estimated with and without weighting for abundance was negligible (mean difference = 0.02, range = 0.003–0.05). All observed values of FRic and FDis were lower than expected by chance; negative standard effect sizes ranged from −0.87 to −2.81 (Fig. 3c). Excluding Neotropical migrants did not change any of these patterns (Appendix S3).

The San Antonio assemblage lost a higher number of functionally unique and distinctive species than would have been expected by chance (Figs. 4a & 4b), and pairwise comparisons between groups of species showed significant differences in functional distinctiveness and uniqueness between extirpated species and species remaining in the assemblage across time periods. Large frugivores, a group especially sensitive to extirpation, were among the highest ranked in functional distinctiveness and uniqueness (Fig. 4 & Appendix S3), yet other groups also lost >50% of species, including aquatic insectivores, canopy omnivores, and ground insectivores. Reestablished species belonged to various functional groups and were more likely to be habitat generalists. Approximately 65% of the species that reestablished populations and that were novel additions had below-average
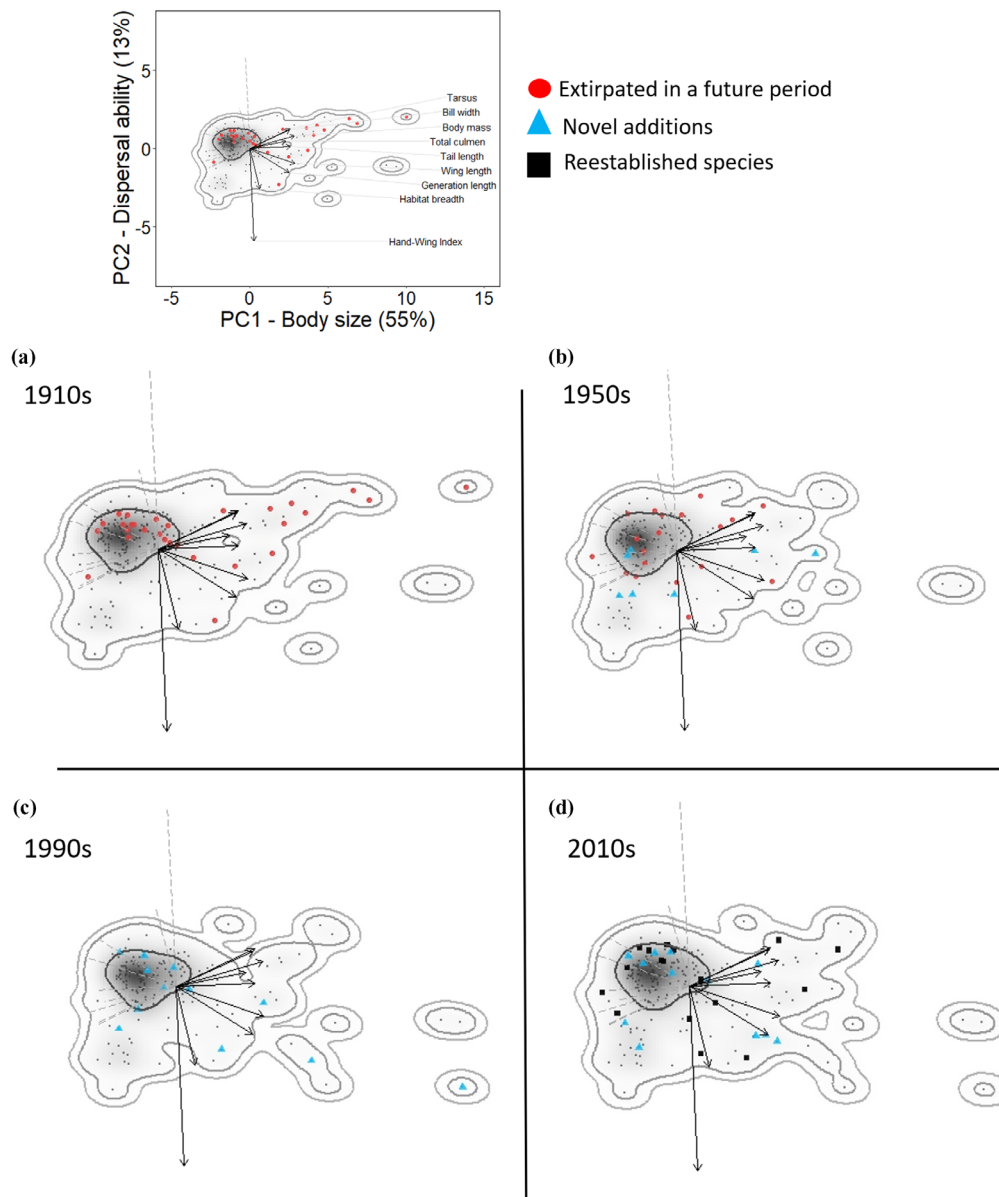
Figure 1. Changes in shape and extent of the functional fingerprint of the San Antonio avian assemblage over more than 100 years. Two-dimensional functional space is represented by principal component (PC) scores of functional traits in the (a) 1910s, (b) 1950s, (c) 1990s, and (d) 2010s. The PC1 axis reflects largely variation in body size, whereas PC2 correlates with dispersal ability of birds and habitat breadth (small black dots, species present in each period; red dots, species extirpated in a future period; blue triangles, new species absent in previous periods; black squares in panel d, species that reestablished after extirpation; arrows, scaled to represent loadings and direction of each trait in functional space). Insert shows the scale and traits represented by each arrow (gray shading, kernel density estimates for each period; curved lines, 50%, 95%, and 99% probability contours).

values of functional distinctiveness and uniqueness (Appendix S3). However, novel additions, such as the Ornate Hawk-Eagle (*Spizaetus ornatus*), stood out for having the highest overall values of uniqueness and distinctiveness (Fig. 4).

Discussion

We found that changes in species composition caused significant shifts in the functional fingerprint of a montane bird assemblage from the Western Andes of
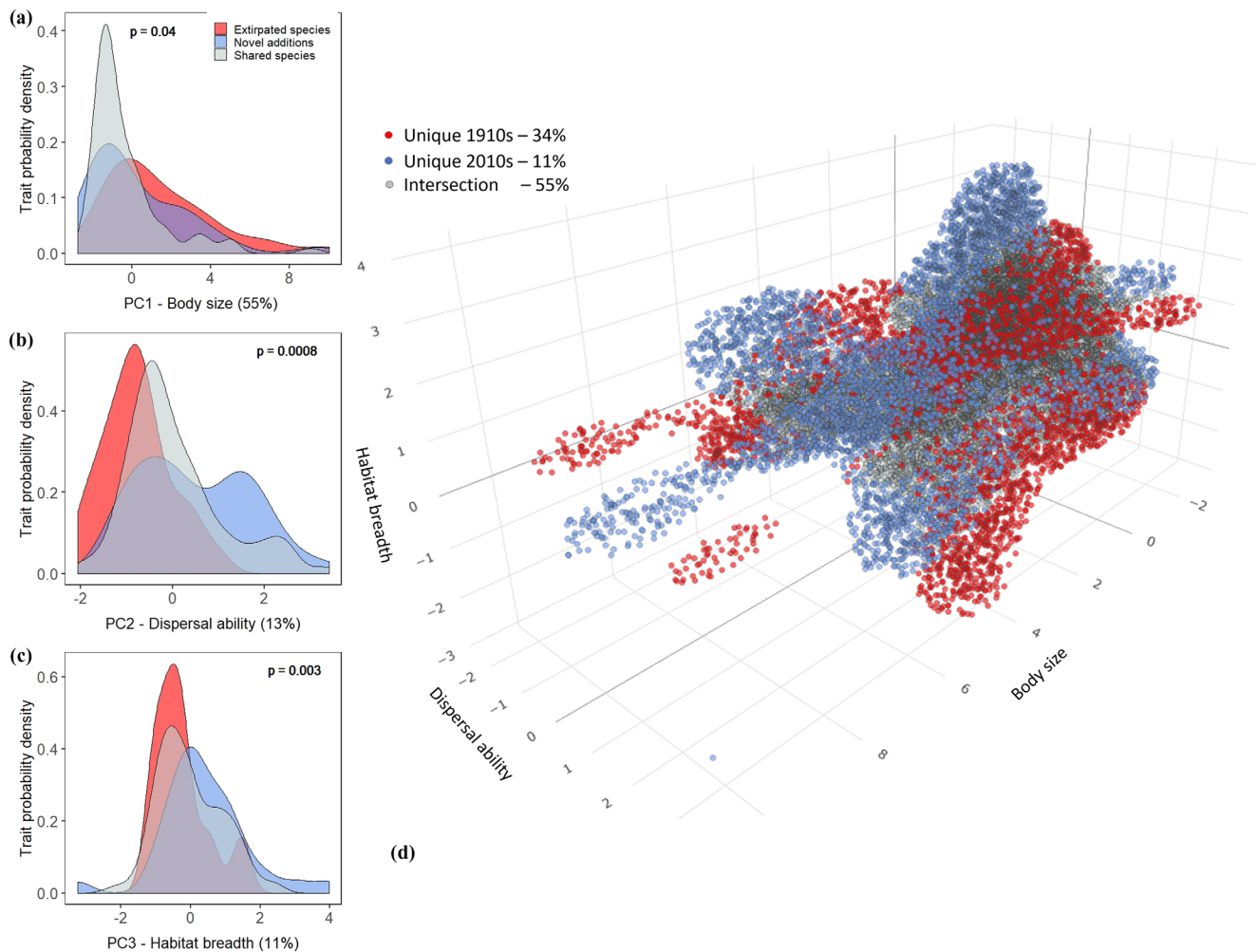
Figure 2. Trait probability density curves of extirpated species and novel additions to the avifauna of San Antonio, Colombia, from 1910s to (scenario 1): (a) the 2010s assemblage had smaller birds relative to the 1910s, (b) species with higher dispersal ability, and (c) species with wider habitat breadths (p-values from Kolmogorov–Smirnov tests comparing distributions of extirpated and novel species). (d) Overlap of the 9-dimension hypervolumes of the 1910s and 2010s (red, volume occupied solely in 1910s; blue, new functional space provided by the novel additions to the assemblage in the 2010s).

Table 1. Values of functional richness and functional dispersion estimated for 2 possible scenarios of changes in bird assemblages over 100 years in San Antonio, Colombia*.

	Functional richness		Functional dispersion	
Period	*scenario 1*	*scenario 2*	*scenario 1*	*scenario 2*
1910s	0.60	1.00	2.39	2.45
1950s	0.24 (−36%)	0.41 (−59%)	2.19 (−8%)	2.28 (−7%)
1990s	0.28 (+4%)	0.34 (-7%)	2.27 (+3%)	2.32 (+2%)
2000s	0.46 (+18%)	0.46 (+12%)	2.35 (+3%)	2.35 (+2%)

*For scenario 1, it is assumed there are novel species that joined the assemblage, extirpations, and recolonizations. For scenario 2, it is assumed there are no novel species, just extirpations and recolonizations. Numbers in parentheses are percent change from the previous period.

Colombia. Due mostly to species extirpations, functional space in the 2010s was considerably smaller and at least 11% different from what it was 100 years before. This space contained fewer large-sized species, more species with wing shapes correlating with greater dispersal ability, and fewer habitat specialists. However, the core of functional space, which holds most of the species (approximately 65%), remained in the same position,
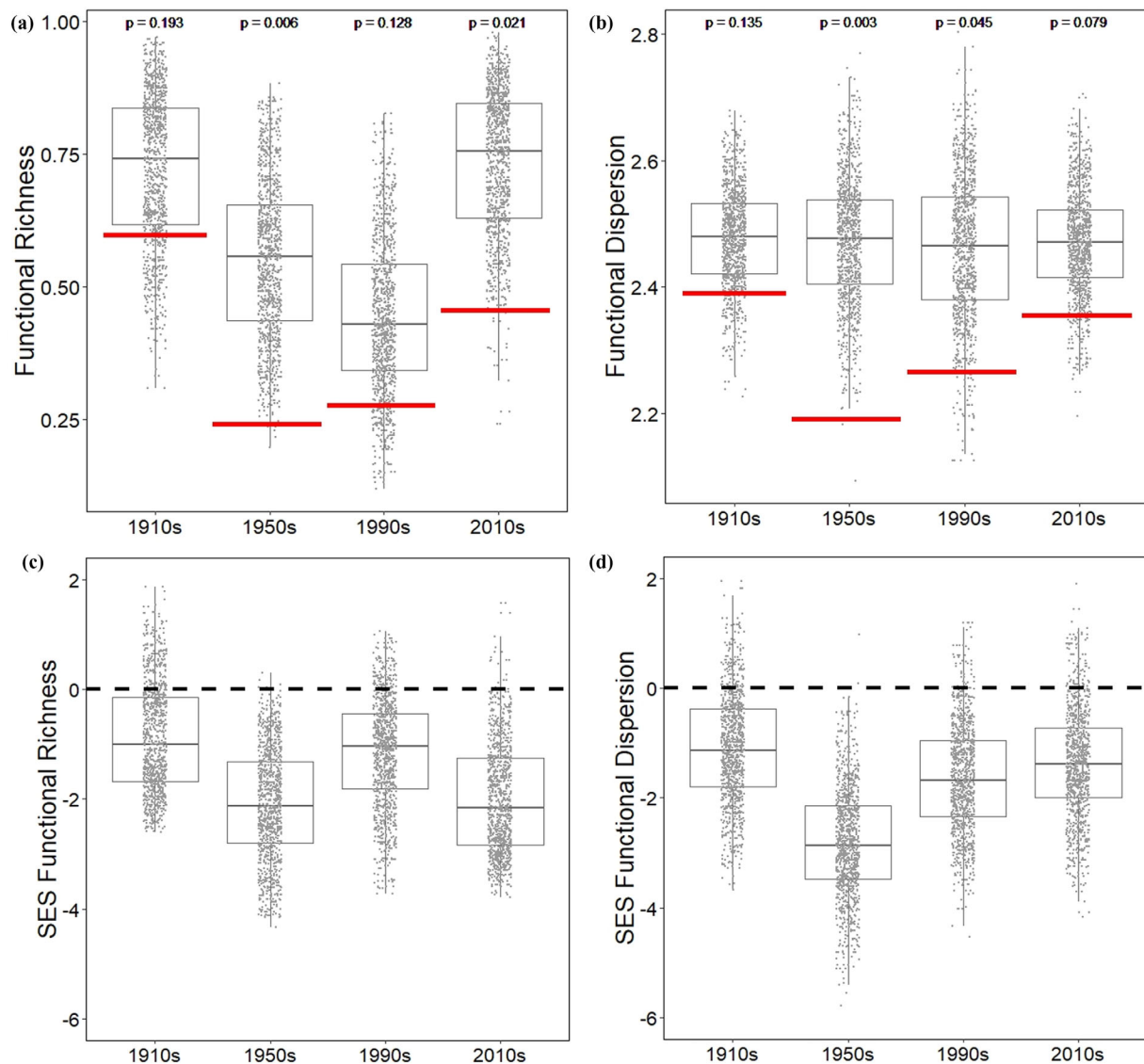
Figure 3. Changes in (a) functional richness and (b) dispersion from the 1910s to the 2010s in San Antonio, Colombia (red lines, empirical values of functional richness and dispersion estimated for each period; boxes, distribution of these values generated by 999 iterations of a null model with randomized species identities). (c and d) Deviances from random expectation (dashed line) measured as standard effect sizes (SES).

suggesting a portion of the system's original functionality remains intact. On average, extirpated species had higher values of functional distinctiveness and uniqueness relative to the whole assemblage, and groups known to be globally prone to extirpation (e.g., large frugivores) ranked high in uniqueness and distinctiveness. Therefore, despite the stability of the centroid of functional space, important ecological functions performed by relatively few species may have been disproportionately affected by changes in assemblage composition.

We detected substantial (i.e., 30−60%) declines in functional richness in the San Antonio assemblage over 100 years. These values are high given that declines in functional richness in the 11−25% range

may cause substantial loss of functionality in highly diverse ocean and forest assemblages (Mcwilliam et al. 2018; Newbold et al. 2020; Pimiento et al. 2020) and that some systems with approximately 40% difference in tree cover (e.g., agriculture vs. old-growth forest) differ by only approximately 5% in the functional richness of their bird assemblages (Ikin et al. 2019). Furthermore, we found that extirpated species had higher than expected values of functional uniqueness and distinctiveness, and therefore their loss was mostly responsible for the decreasing trend in functional diversity over 100 years. The joint substantial reduction in functional diversity and loss of unique species suggests that the San Antonio assemblage has likely lost important ecological functions.
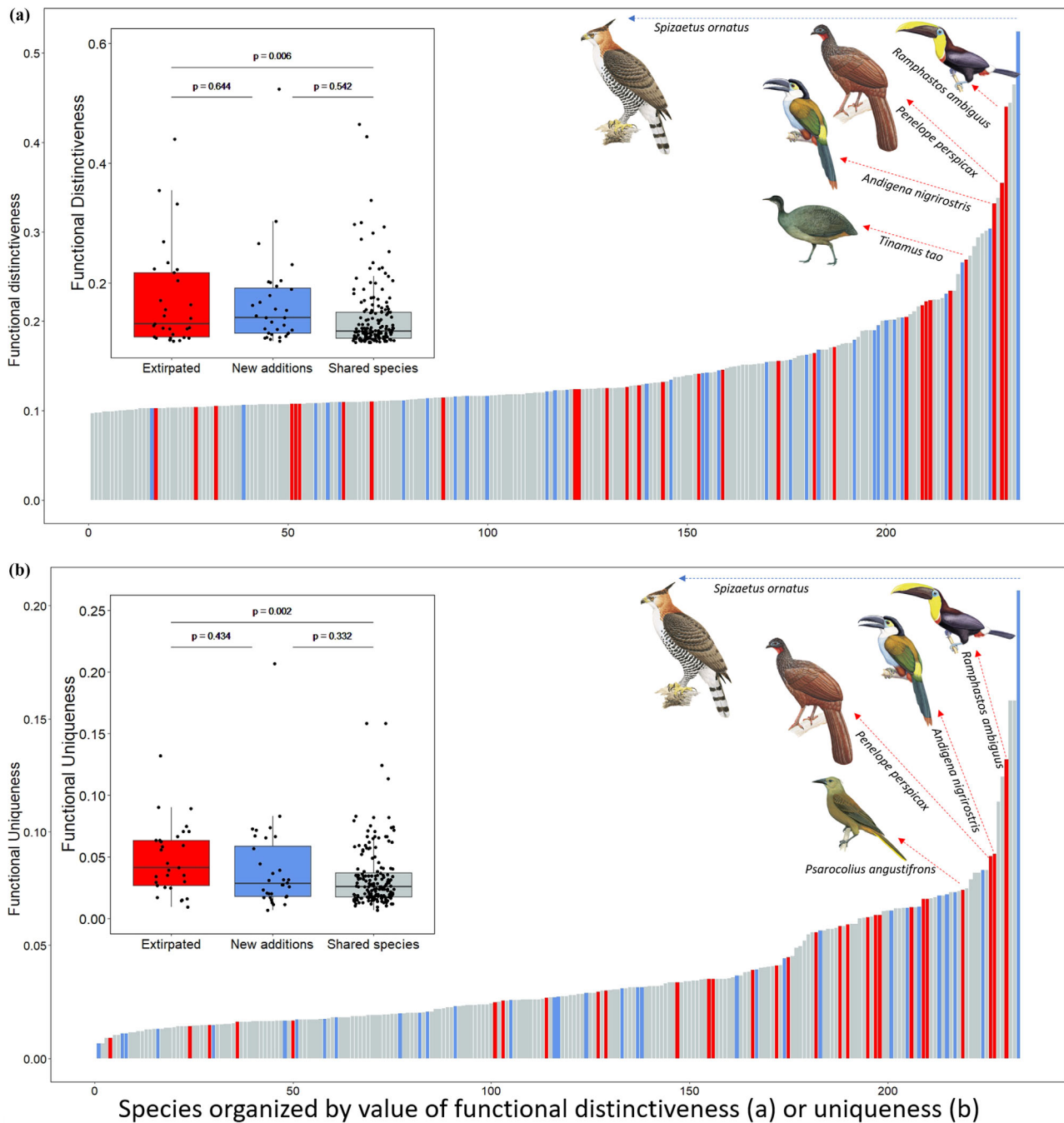
Figure 4. Functional (a) distinctiveness ($p_{ext} = 0.009$, $p_{new} = 0.002$) and (b) uniqueness ($p_{ext} = 0.002$, $p_{new} = 0.017$) of extirpated (red), new (blue), and shared (gray) bird species between periods in San Antonio, Colombia. Differences between pairs of groups were significant between extirpated and shared species (top p-value) but not the other pairs (lower p-values). The extirpated species with the highest values of distinctiveness and uniqueness (as ordered on the x-axis) are all large frugivores, but the Ornate Hawk-Eagle (Spizaetus ornatus), a novel addition that appeared in the 1990s, had the highest overall value. Species illustrations reproduced by permission from Lynx Edicions.

Our approach can enable conservation practitioners to move beyond simple quantifications of losses and gains of species through time, to identify areas of functional space in need of attention owing to potentially negative effects on ecosystem function. For example, the loss of functionally unique large frugivores from the San Antonio assemblage likely increased the potential for collapse of mutualistic networks of bird and plant species

in which previous work revealed they play a critical role (Palacio et al. 2016). Loss of large frugivores can further have negative cascading effects on ecosystems by reducing seed dispersal, which affects the survival of native trees, influences the potential for forest regeneration, and even constrains the ability of vegetation to respond to climate change (Moran et al. 2009; McConkey et al. 2012; Mokany et al. 2014; Ribeiro da Silva et al. 2015; Bovo et al. 2018). Similarly, loss of insectivores can result in increased herbivory rates that may reduce forest resilience and regeneration (Peter et al. 2015).

Although the San Antonio bird assemblage changed in functional volume, the core of its functional fingerprint (concentrating species that are arguably functionally redundant) retained its position. High functional redundancy may be just as important to ecosystem integrity as richness extending to the periphery of functional space because it is one of the mechanisms that help maintain high diversity and ecosystem function (Wohl et al. 2004), reduce negative effects of natural enemies of species (Philpot et al. 2012), and facilitate niche packing within assemblages (Ricklefs 2012; Pigot et al. 2016; Cooke et al. 2019a). Our finding that the core of the San Antonio bird assemblage has seemingly not lost functions or shifted in position suggests that there are still important attributes of the system's functionality that mirror the predisturbance assemblage of over 100 years ago. We hope, given the right conditions (i.e., time, continued forest recovery, and increased connectivity between remaining forest fragments), San Antonio may recover more of its lost functionality provided by extirpated species, some of which still occur in the wider region (Palacio et al. 2016, 2019). It has taken some species over 100 years to reestablish populations in San Antonio, and we found that those that did were more likely to be forest generalists with relatively low values of functional uniqueness and distinctiveness. Therefore, reestablishing the species that contribute most to increase functional diversity in this system may take even longer and may depend on the reconfiguration of interspecific interaction networks that existed in the past (Palacio et al. 2016, 2019).

Our study provides one of the few examples of an assessment of temporal changes in functional fingerprints from a highly diverse tropical ecosystem over more than 100 years, and both our findings and the methods we employed have wide applications particularly for tropical ecosystem study and conservation (Stroud & Thompson 2019). For instance, restoration objectives aimed at replicating previous states of a system or at recovering functionality could use measures of functional fingerprints to inform efforts to recover particular areas of functional space (Meli et al. 2014). Our use of the term *functional fingerprint* to describe functional diversity and its many associated metrics helps to relate somewhat abstract concepts in functional diversity to the ecology and condition of ecosystems and assemblages. In so doing, via its link to management practices, use of the term may aid ecologists, conservation scientists, and practitioners overall.

Certain species traits, such as being large, specialized, social, having low dispersal ability, and being at the top end of food webs, make animal species more vulnerable to extirpation (Kattan et al. 1994; Davies et al. 2000; Pearson et al. 2009; Habel et al. 2019). Our results highlight that some of these traits, namely, body size, dispersal ability, and habitat breadth, are responsible for approximately 78% of the variation in functional diversity over time within a tropical bird assemblage. This means that species with trait values at the extremes of these axes of variation (size, dispersal, and habitat specialization) likely also account for a large proportion of the functional richness and dispersion in ecological assemblages. Thus, when a system loses species at the extremes of these axes, it likely also loses unique functionality. In San Antonio, the extirpation of species combining some of these traits associated with vulnerability resulted in significant decreases in functional richness and dispersion, hence arguably making the assemblage less healthy and potentially more susceptible to further changes (Mouillot et al. 2013). In agreement with our results, species vulnerability to extinction is positively correlated to functional uniqueness and specialization in a wide range of organisms (Pimiento et al. 2020), and the functions provided by these unique species may be particularly prone to disappear (Mouillot et al. 2013). Therefore, conservation efforts aimed at maintaining ecosystem integrity must move beyond just maintaining species numbers to designing strategies for the maintenance of ecological function by identifying and conserving species with traits conferring high vulnerability (Cadotte et al. 2011; McConkey et al. 2012; Pimiento et al. 2020).

Acknowledgments

Supporting Information

Additional information is available online in the Supporting Information section at the end of the online article. Authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Supplementary Material

Appendix S1: Excel file with complete trait dataset, PC scores, functional uniqueness and distinctiveness values by species

Appendix S2: R code used for all analyses

Appendix S3. Supplementary methods and results.

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