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Varied abundance and functional diversity across native forest bird communities in the Mariana Islands

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ABSTRACT—The Mariana islands have a species-poor but functionally diverse and largely endemic bird assemblage that varies due to biogeographic legacy and anthropogenic impacts. The largest island in the chain, Guam, is the setting for one of the most extreme examples of recent avian population declines, indicating the capacity for avifaunal collapse and loss of function in neighboring islands. We performed a systematic survey of resident land birds in remnant karst forest on the Mariana Islands' 3 largest islands following Guam to assess the status of the avifauna in this habitat, characterize inter-island heterogeneity in bird communities, and consider the resulting differences in the functional roles of birds across the archipelago's native forests. We identified significantly greater functional diversity on Rota than either Saipan or Tinian, but lower bird population densities, species richness, and Shannon diversity. We recommend continued monitoring of avian population trends across the archipelago and assessments of ecosystem functions like pollination, seed dispersal, and food web dynamics. *Received 18 July 2017. Accepted 13 November 2019.*

Key words: conservation, functional diversity, island birds, karst forest, Mariana Islands, population density

Variación en abundancia y diversidad funcional en comunidades de aves de bosque nativas en las Islas Marianas

RESUMEN (Spanish)—Las Islas Marianas tienen un ensamble pobre en especies, aunque funcionalmente diverso, que varía en respuesta a su historia biogeográfica e impactos antropogénicos. La isla más grande de esta cadena, Guam, es el escenario de uno de los ejemplos recientes más extremos de declines en poblaciones de aves, indicando la capacidad para el colapso avifaunístico y pérdida de funciones en islas vecinas. Hicimos un reconocimiento sistemático de las aves terrestres residentes en remanentes de bosque de karst en las 3 islas más grandes después de Guam para determinar el estatus de la avifauna en este hábitat, caracterizar la heterogeneidad de comunidades de aves entre islas y considerar las diferencias resultantes en los papeles funcionales de las aves en todos los bosques nativos del archipiélago. Identificamos una diversidad funcional significativamente mayor en Rota que en Saipan o Tinian, aunque menores densidades de población, riqueza de especies y diversidad de Shannon. Recomendamos el monitoreo continuo de tendencias en las poblaciones de aves en todo el archipiélago y la determinación de funciones ecosistémicas como la polinización, dispersión de semillas y dinámicas de redes tróficas.

Palabras clave: aves insulares, bosque de karst, conservación, densidad de población, diversidad funcional, Islas Marianas

The near-complete extirpation of Guam's native forest birds due to the introduction of the brown tree snake (*Boiga irregularis*) is a textbook example of the unintended consequences of species invasions (Savidge 1987, Wiles et al. 2003) and the particular vulnerability of island avifaunas. Following its arrival in south-central Guam in World War II, the snake's rapid population growth and range expansion triggered the complete loss or functional extirpation of all 12 native forest bird species formerly found on the island (Savidge 1987). Because remnant populations of most of the genera or species extirpated from Guam persist on the nearby major islands of Saipan, Tinian, and Rota, the archipelago comprises a powerful natural experiment in which the ecological impacts of bird loss can be isolated from the signal of climate, biogeographic history, and geology (Rogers et al. 2012, 2017).

The endemism present in this system, its known capacity for avifaunal collapse, and the potential for accidental dispersal of the brown tree snake to other inhabited Mariana islands, motivates research to understand the status and inter-island heterogeneity of the Mariana Island avifauna. Although both conservation efforts and research on avian influence on forest ecosystems would benefit from simultaneous assessments of bird communities across the inhabited Mariana Islands, existing studies have assessed each island independently. Studies were conducted in different years by different observers, complicating retrospective cross-island comparisons. Nevertheless, these studies have suggested discordance in trends in forest birds across the archipelago. A study by Amar et al. (2008) examining trends in bird abundance from 1980 to 2004 raised concerns that Rota is experiencing an unexplained avifaunal decline. Similarly, Camp et al. (2015) reported declines in 7 of Rota's 13 forest bird species based on a series of island-wide transect surveys

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conducted from 1982. In contrast, studies on Saipan and Tinian (Craig 1996, Camp et al. 2009, 2012) have highlighted high bird densities, with Camp et al. (2012) suggesting populations on Tinian have remained stable over time despite near-complete loss of native forest. Engbring et al. (1986) provided useful comprehensive population estimates across all 3 islands in a single study, but these numbers were generated prior to reported declines on Rota and include non-forest bird communities. Further, the low species richness—and thus probable limited functional redundancy among bird species—in these islands means that species differences among islands and population declines on individual islands could lead to large differences in the ecological roles that birds play within these ecosystems. Functional differences across Mariana Island bird assemblages have not been assessed explicitly to date.

Here, we report the results of a systematic survey of native forest birds in limestone forest on the islands of Saipan, Tinian, and Rota. We complement previous surveys by generating comparable estimates of population densities, corrected species richness, and functional diversity and evenness. We describe drivers of differences in bird communities across islands, and discuss their conservation implications.

Methods

Bird surveys

We conducted point transect bird surveys (Hutto et al. 1986, Lee and Marsden 2008) between first light (~0530 h) and approximately 4 h later in karst limestone forest on Saipan, Tinian, and Rota (Rogers et al. 2017) in June and July 2011. These sites were originally selected for another ecological research project because they were within relatively large tracts of intact karst forest with similar tree composition. The sites did not include degraded forest types or ecotones. All 3 sites on Saipan, 3 sites on Tinian, and 2 out of 3 sites on Rota were located below 100 m elevation; one site on Rota was located at ~300 m elevation. We visited all 3 sites on a given island each day, and conducted surveys within sites along a transect containing 3 points situated 100 m apart. We changed the order of visitation daily to minimize bias associated with hourly variations in bird activity level, and so that each site was ultimately visited at least once during each time block. Counts lasted for 8 min, during which time all birds we detected by sight or sound were recorded and their distance from the observer estimated. We treated flocks as a single detection of an estimated number of individuals at a single distance, and did not conduct counts during periods of rain. In total, we performed 45 counts on Tinian and Rota, and 54 counts on Saipan, representing 5 repeat visits and 6 repeat visits to the former 2 islands and the latter island, respectively. All were conducted by EBL, who was trained in bird identification, practice censuses, and distance estimate calibration prior to starting fieldwork.

Abundance, diversity, and richness

We generated unbiased estimates of bird population densities on each island (accounting for detection probability and availability for detection) using the *gdistsamp* function of the R package *unmarked* (Fiske and Chandler 2011), excluding non-forest residents and species with fewer than 10 sightings. We estimated Shannon diversity and raw species richness using the R package *vegan* (Oksanen et al. 2017), and estimated functional diversity and functional evenness using the dendrogram-approach of Petchey and Gaston (2002). Our metrics of function were diet (i.e., portion of diet made up of invertebrates, vertebrates, fruit, nectar, seeds, or other plant material), foraging strata (classified as low, middle, or upper), and body mass. These data derive from estimates from the Elton Traits bird functional trait database (Wilman et al. 2014), vetted against the primary literature (Jenkins 1983; Craig 1990, 1996; Craig and Beal 2001) and our own extensive observations on the ecological roles of birds in the Mariana Islands (Fricke et al. 2017; Table S1). We assessed drivers of differences in the functional composition of bird communities using community-weighted means of each primary foraging guild and a canonical correspondence analysis implemented with abundance data and our functional trait matrix. To assess whether island and site-specific variables influenced population metrics, we fit linear mixed-effects models using the *lme4* package (Bates et al. 2015) and performed a likelihood ratio test between models with and without each variable of interest in R (R Core Team 2016). We used post hoc analyses with *glht* in the *multcomp* package to assess inter-island differences in each metric (Hothorn et al. 2008). All code and data matrices used in our analyses are available online (https://github.com/elinck/CNMI_bird_communities).

Results

Bird surveys and abundance estimates

We detected a total of 15 species during the survey period, with 8 species occurring on all 3 islands; 12 species were detected on Saipan, 10 on Tinian, and 11 on Rota. After dropping Micronesian Megapode (*Megapodius laperouse*), Mariana Crow (*Corvus kubaryi*), and White Tern (*Gygis alba*) from analyses due to insufficient data, we found total abundance ranged from ~30 to ~55 birds per hectare across islands and from less than 2 to greater than 9 birds per hectare for each species (Fig. 1, 2; Table S2). Broad confidence intervals for White-throated Ground Dove (*Alopecoenas xanthonura*), Philippine Collared-Dove (*Streptopelia dusumieri*), and feral chicken (*Gallus gallus*) may reflect inaccurate estimation of distant calls.

Mixed-effects models

We identified island as a significant predictor of functional diversity (likelihood ratio test, $P < 0.001$), abundance ($P < 0.001$), species richness ($P = 0.006$), and Shannon diversity ($P = 0.006$), but not functional evenness ($P = 0.203$) (Fig. 1). Community-weighted means showed wide variation in the relative importance of foraging guilds across islands, with island describing significant variation in community-weighted mean diet composition values (likelihood ratio tests; all $P < 0.05$). While frugivore and nectarivore values were highest on Saipan, insectivore values were higher on both Rota and Tinian, and carnivore values were significantly higher on Rota than either Saipan or Tinian (Fig. 3A). Canonical correspondence analysis largely corroborated these results, implicating differential abundances of foraging guilds and body mass across islands in driving differences in functional diversity and evenness (Fig. 3B).

Discussion

Conducting systematic surveys in comparable native forest habitat on Saipan, Tinian, and Rota, we found island was a significant predictor of avian abundance, richness, Shannon diversity, functional evenness, and functional diversity. Overall bird abundance varied widely, with roughly one-third fewer birds per hectare on Rota than either Saipan or Tinian (Fig. 1). This can partially be attributed to small understory species (such as the 3 white-eye species) found at high densities on Saipan and Tinian but absent or not detected in our surveys on Rota. Additionally, median abundance estimates of 3 other species—Micronesian Myzomela (*Myzomela rubratra*), Philippine Collared-Dove, and White-throated Ground Dove—shared across all 3 islands were lower on Rota than Saipan or Tinian (Fig. 2), consistent with a declining trend identified by Camp et al. (2015). The native Micronesian Starling (*Aplonis opaca*), on the other hand, was the most common native forest bird species on Rota, consistent with an increasing population trend identified by Camp et al. (2015).

Anthropogenic impacts interact with biogeographic history to explain higher values for species richness and Shannon diversity on Saipan and Tinian than on Rota. Three smaller-bodied native species were found in the highest density on Saipan and Tinian: the Bridled White-eye (*Zosterops conspicillatus*), the Golden White-eye (*Cleptornis marchei*), and the Tinian Monarch (*Monarcha takatsukasae*). These 3 were absent from our surveys on Rota due to biogeographic history, in the case of the Tinian Monarch and Bridled White-eye, or population declines since human colonization, in the case of the Golden White-eye (Steadman 1999). The Rota White-eye (*Zosterops rotensis*), sister to Bridled White-eye and similar in functional traits, was also undetected in our study, although this may be an artifact of a patchy distribution and low abundance in its expected upland habitat. Conversely, the nonnative Black Drongo (*Dicrurus macrocercus*) is found in high abundance on Rota, but is absent from Tinian and Saipan.

Previous researchers (Amar et al. 2008, Camp et al. 2015) have identified bird declines on Rota, and suggested the cause is predation by introduced feral cats (*Felis domesticus*), mangrove monitor (*Varanus indicus*), and rats (*Rattus* spp.), compounded by ongoing reductions in forest cover for agriculture and by typhoon disturbance. However, cats, monitors, and rats are also common on Tinian

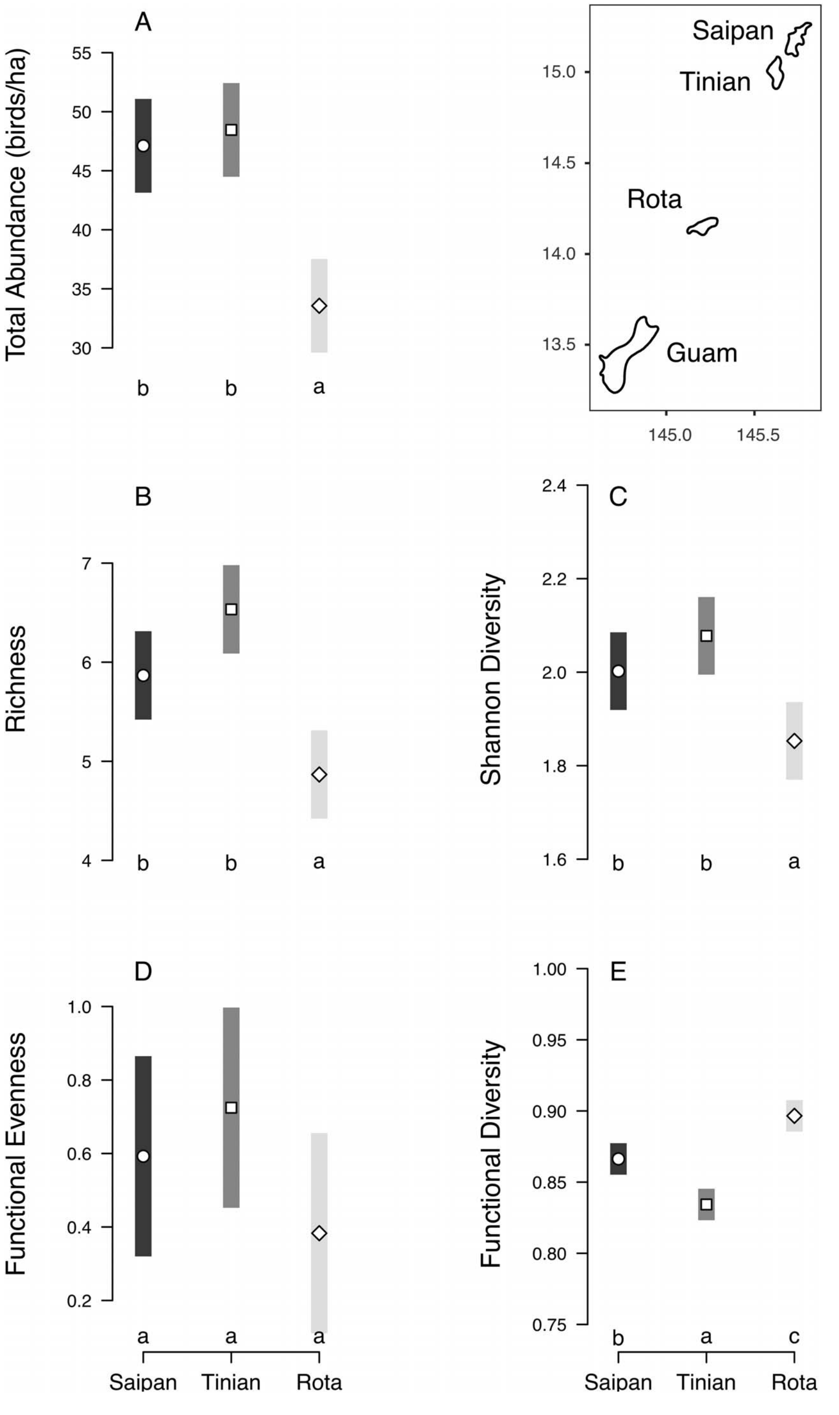

Figure 1. Bird population indices compared among Saipan, Tinian, and Rota (pictured to scale upper right). Likelihood ratio tests of linear mixed effects models implicated island as a significant predictor of abundance, richness, Shannon diversity, and functional diversity, but not functional evenness. Points represent model estimates and bars represent 95% confidence intervals. Letters at panel bottoms indicate statistically significant inter-island differences.

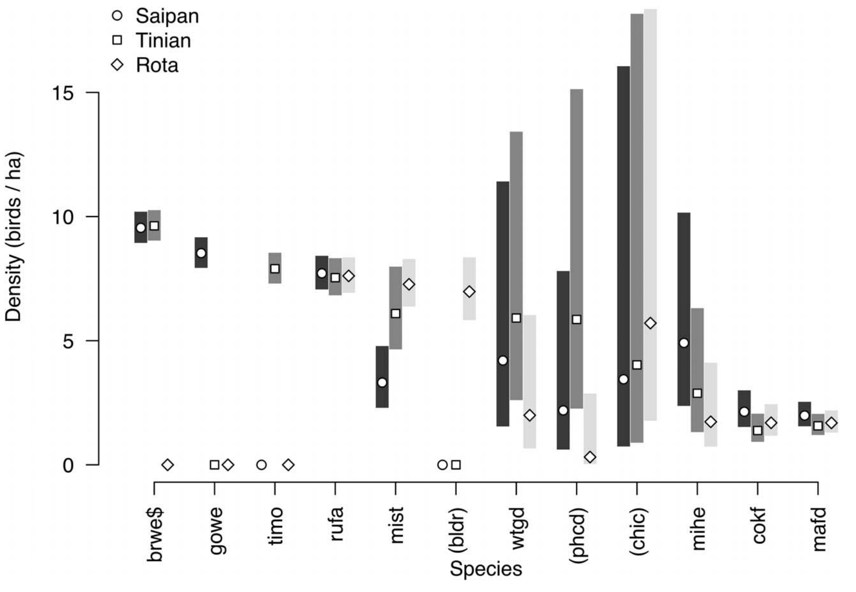

Figure 2. Detection-bias corrected estimates of limestone karst forest bird density compared across Saipan, Tinian, and Rota for species with sufficient observations. Species codes: brwe = Bridled / Rota white-eyes (*Zosterops conspicillatus / rotensis*); gowe = Golden White-eye (*Cleptornis marchei*); timo = Tinian Monarch (*Monarcha takatsukasae*); rufa = Rufous Fantail (*Rhipidura rufifrons*); mist = Micronesian Starling (*Aplonis opaca*); bldr = Black Drongo (*Dicrurus macrocercus*); wtgd = White-throated Ground Dove (*Alopecoenas xanthonura*); phcd = Philippine Collared-Dove (*Streptopelia dusumieri*); chic = Feral Chicken (*Gallus gallus*); mihe = Micronesian Myzomela (*Myzomela rubrata*); cokf = Collared Kingfisher (*Todiramphus chlori*); mafd = Mariana Fruit Dove (*Ptilinopus roseicapilla*). Species in parentheses are introduced species. The dollar sign ($) notes that we did not detect the Rota White-eye on Rota, although it does occur there.

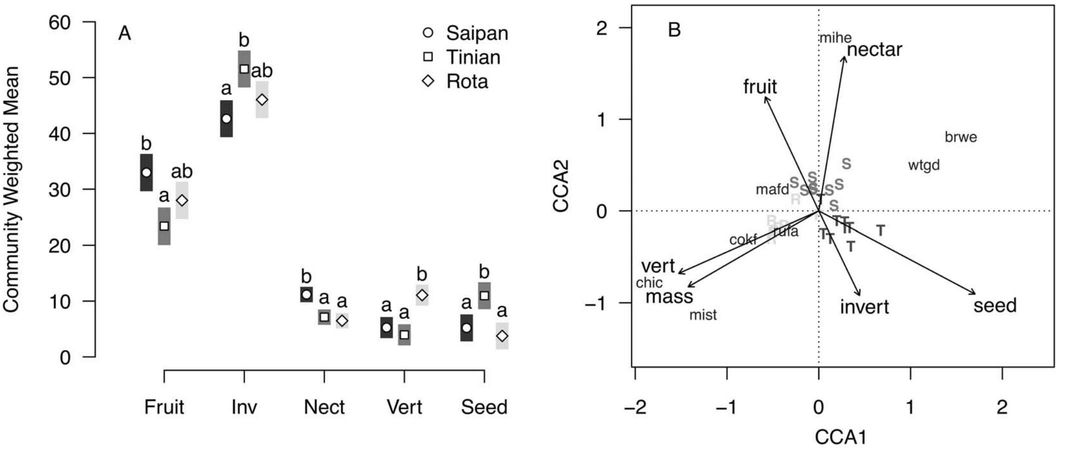

Figure 3. (A) Community-weighted means for rounded percentage of diet compared across islands, with points representing model estimates and bars representing 95% confidence intervals. Letters above bars indicate statistically significant inter-island differences within each diet category. (B) Constrained canonical analysis of the influence of abundance and foraging guilds on functional differences across islands. Arrows show loadings for diet and mass traits. Bird species codes represent the location of each species in multivariate space. Island names (R, Rota; T, Tinian; S, Saipan) indicate the location in multivariate space of individual observation sessions conducted on each island.

and Saipan (Wiewel et al. 2009, Zarones et al. 2015), and anthropogenic habitat disturbance is unlikely to explain the lower overall bird densities on Rota, as Rota contains significantly more primary forest than either Saipan or Tinian (Falanruw et al. 1989). Alternatively, bird populations in nonnative forest on Saipan and Tinian might boost densities in adjacent native forest fragments above levels naturally occurring in Rota's much more expansive karst forest habitat. However, evidence of declines in specific species on Rota suggest this possibility is unlikely (Fancy et al. 1999, Fancy and Snetsinger 2001). Continued research on the threats to forest birds on Rota is needed to determine why species or congeners common to all islands are found in lower abundance on Rota.

Our study revealed that island is a significant predictor of functional diversity, a metric that reflects the range and values of organismal traits that influence ecosystem functioning (Petchey and Gaston 2002). Functional diversity may be influenced by the effect of abiotic factors on niche space, biogeographic history, and biotic factors such as competitive interactions. Our community-weighted mean and canonical correlation analyses pointed to biogeographic history and recent introductions as drivers of functional differences across the 3 islands, which are nearly identical in climate. Specifically, we believe differences in functional diversity between islands primarily reflects (1) the abundance of the large, nonnative Black Drongo on Rota, one of two species with vertebrates as a substantial part of their diet in the Micronesian avifauna; (2) the abundance of smaller frugivores such as Golden and Bridled white-eyes on Saipan, potentially as a result of widespread anthropogenic landscapes featuring gardens and fleshy fruited exotics; and (3) the abundance of insectivores on Tinian, reflecting the presence of the endemic Tinian Monarch. Our results reveal that the native forest avifauna across each island plays differing functional roles within the broader native forest ecosystem, and this may impact ecological processes occurring within these ecosystems directly (e.g., differing seed dispersal for plants, predation of insects) or indirectly (e.g., plants impacted by differing bird–insect–plant trophic links). Future research may clarify these processes by focusing on mechanistic links between specific bird taxa and ecological processes.

Both these results and finer-scale species occurrence data raise concerns about the long-term health of the avifauna and ecosystems of the Mariana Islands. Despite surveying in the expected range of both the Rota White-eye and the Tinian population of the Micronesian Megapode, we detected neither. While this may support prior evidence of declining populations in these species (Craig and Taisacan 1994, Daniel and Krueger 1999, Fancy and Snetsinger 2001, Camp et al. 2015), it may also be an artifact of our failure to survey within both species' patchy distributions. On Saipan and Rota, respectively, we detected too few Micronesian Megapodes and Mariana Crows (*Corvus kubaryi*) to include them in our analysis, consistent with low numbers reported in prior studies (Fancy et al. 1999, Camp et al. 2009).

If patterns in our data are due to previously reported temporal population trends, changing bird communities are likely to have impacts that reverberate through the ecosystem. Recent studies have shown that bird loss on Guam has caused a severe decline in plant recruitment as a result of disrupting the fruit–frugivore mutualism (Rogers et al. 2017) and a dramatic increase in spider densities (Rogers et al. 2012). Our results support the importance of incorporating assessments of the functional composition of bird communities in assessments of ecosystem health. With lower community-weighted mean values for frugivores and insectivores on Rota than on either Saipan or Tinian, Rota's forest may be experiencing reduced dispersal and top-down control of arthropods, similar to the situation on Guam, but prior to the wholesale loss of forest birds. We encourage future studies to monitor bird populations on Rota, and if declines continue to be detected, to provide specific recommendations for conservation managers focused on preserving species diversity and ecosystem function.

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