Bird Assemblage and Diversity along Different Habitat Types in a Karst Forest Area in Bulacan, Luzon Island, Philippines

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Little is known on the effects of degradation and disturbance on bird assemblage in lowland karst forests in the Philippines. In this study, we determined diversity patterns and distribution of birds along the vertical strata in two karst forest fragments adjacent to and one reforestation area within an active limestone quarry area in Bulacan province, Luzon island. Surveys were conducted using mist nets set in the understory (0–3 m) and sub-canopy (4–10 m) from November 2013 to October 2016. A total of 617 individuals belonging to 63 species and 13 feeding guilds were recorded from a mist-netting effort of 654,264.8 mist-net hours (m²·h); of these, 32 are Philippine endemics and six are threatened species. We recorded the highest number of species in the reforestation area, most of which are generalist and disturbance-tolerant species. Results from permutational multivariate analysis of variance (PERMANOVA) and non-metric multidimensional scaling (NMDS) indicate differences in bird assemblage between the three habitat types and between the two vertical strata within habitat types. Meanwhile, similarity percentage analyses and Mann-Whitney U tests showed that species and guilds that contributed to the observed dissimilarity in the two strata have higher capture rates in the understory. These observations provide insights into the effect of disturbance and habitat alteration in the vertical movement of birds, as evidenced by the shift of some arboreal species to the understory layer in more disturbed habitats. Understanding the behavior and habitat use of birds will, thus, help in identifying appropriate conservation measures to ensure proper resource partitioning among the different bird assemblages in fragmented habitats.

Keywords: birds, forest fragments, karst forest, limestone quarry, vertical stratification

INTRODUCTION

Karst forests occur in areas underlain by soluble rocks such as limestone (Ford and Williams 2007). It is one of the twelve forest formations present in the Philippines and covers almost 12% (35,000 km²) of the country’s total land area (Fernando et al. 2008; BMB-DENR 2019). This type of forest contains unique microhabitats and high environmental heterogeneity, which can support a wide range of flora and fauna – some of which are known to be highly restricted in such habitats (Brown et al. 2010; Tang et al. 2011; Rasalan et al. 2015). Moreover, the presence of unique features such as sinkholes and caves in these

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landscapes provide habitat and protection for many species (Clements et al. 2006).

Unfortunately, karst forests are largely understudied and considered one of the most threatened forest types in the Philippines due to mining and conversion of land to agriculture (Fernando et al. 2008; Tolentino et al. 2020). To date, only about 29% of the total karst forest in the country is protected (Restificar et al. 2006). The unique soil properties and environmental conditions of the karst forest are vulnerable to anthropogenic activities because recovery of its vegetation is very slow and often damages are irreversible (Tuyet 2010). Existing laws do not directly address the protection and conservation of this unique forest type at the landscape level, but focus more on the protection of its cave features and development of the area for ecotourism.

Birds are often used as bioindicator taxa in many studies because they are relatively easy to sample and identify and because they are sensitive to habitat disturbance (Furness 1993). Birds may be especially impacted by modification and destruction of karst forest since the landscape features of this habitat—including caves and limestone crags serve as refugia, breeding, and nesting grounds for many bird species (Lugo et al. 2001; Clements et al. 2006; IUCN 2020). For instance, Aerodramus fuciphagus—which have cultural and economic importance—are known to utilize caves as roosting, nesting, and feeding sites (IUCN 2020). Their nests—made of their saliva—are usually harvested and sold at a very expensive price (USD 2000–3000/kg) or made into a bird’s nest soup, which costs around USD 30 (Thorburn 2015). In addition, Napothera crispifrons is known to be restricted to karst forests in mainland Asia, while Pycnonotus hualon and Phylloscopus calciatilis were recently discovered from karst areas in Southeast Asia (Clements et al. 2006; Woxvold et al. 2009; Alström et al. 2010). In the Philippines, karst forests are important habitats for some highly threatened species of birds. For instance, protected karst forests such as Tabunan, Alcoy, and Nug-as on the island of Cebu have been the few remaining known habitats for the Endangered Kittacincla cebuensis and the Critically Endangered Dicaeum quadricolor (Paguntalan and Jakosalem 2008; BLI 2020; IUCN 2020).

In this study, we assessed patterns of diversity in the bird community (species and guild) of three highly modified habitat types present in an active quarry area in Bulacan Province, Luzon Island. We asked three main questions:

1. How do bird species richness, diversity, abundance, and composition differ between two forest fragments and a reforestation area in a karst landscape on central Luzon?

2. How do bird species richness, diversity, abundance, and composition differ between the understory and sub-canopy in these habitats?

3. How do bird feeding guild composition and abundance differ between these habitats?

The ecological services birds provide such as seed dispersal, pollination, and pest control make it important to understand how they use their habitat and their response to anthropogenic disturbances (Sekercioglu 2012). Furthermore, understanding these patterns can aid in the enhancement of forest restoration efforts and protection measures of mining companies operating in karst areas, as well as inform ecotourism management decisions for these unique areas.

**MATERIALS AND METHODS**

**Study Sites**

The study was carried out in a karst forest area in Bulacan Province, Luzon island with some sites located within an active quarry area operated by a private company (Figure 1). Original forest formation in our sites is forest over limestone or karst forest (Ong et al. 2016). Three different habitat types were identified based on the degree of disturbance for each site:

**Forest fragment 1 (FF1).** It is located near the edge of the contiguous karst forest at the foothills of the Southern Sierra Madre Mountain Range in Barangay Bayabas, Doña Remedios Trinidad, Bulacan (14.965° N, 121.100° E). We have established three sampling areas inside a ~160 ha forest fragment around a 1.2 km long Puning Cave (160 masl). Puning Cave is about 15 km south of Biak-na-Bato National Park, a protected karst area (Restificar et al. 2006), and about three kilometers away from the active quarry site in the mining area (Figure 1). Plants from families Malvaceae and Fabaceae are the most dominant and species-rich in the study sites. This includes species typical of karst forests such as Pterocymbium tinctorium (Malvaceae), Archidendron scutiferum (Fabaceae), and Kleinhovia hospita (Malvaceae), with canopy trees at least 10 m tall (DBH: 15–90 cm). Small-scale slash-and-burn (“kaingin”) and local limestone mining activity are present near the cave area. The site is also a local tourist destination because of the vast cave system and a birdwatching site.

**Forest fragment 2 (FF2).** One sampling area was established inside a 4.6-ha forest fragment (198 masl) (14.934° N, 121.092° E). The site is located in Sitio Turongisan, Barangay Bayabas, Doña Remedios Trinidad, Bulacan and adjacent (about 500 m north) to an active
quarry area. The area is characterized by rugged terrain with visible sharp-pointed limestone outcrops. Several small caves are also present within and near the forest patch. Dominant plant families in the site include Fabaceae, Malvaceae, and Moraceae. Canopy trees of at least 10 m tall (DBH: 20 to 136 cm) are present, with Pterocymbium tinctorium (“taluto”) and Garuga floribunda (“bogo”), tree species associated with karst forests dominating the upper canopy structure. The understory layer is mainly formed by dense clumps of Schizostachyum lumampao (Poaceae), along with herbs and shrubs such as Chromolaena odorata and Desmodium gangeticum.

Reforestation area (RA). It is composed of two sampling areas in a mining concession which covers less than 1 ha each (50 masl) (14.899° N, 121.081° E). The sites are located along a roadside and near a blasting site.
for quarry activities. The reforestation activities started between 1996–2000, with the monoculture of exotic tree species such as *Gmelina arborea* and *Mangifera indica*. *G. arborea* trees ranged in height from 5–20 m, with DBH from 10–54 cm; *M. indica* trees ranged in height from 5–20 m, with DBH from 12–111 cm. Native species such as *Pterocarpus indicus* were later inserted and through time, pioneer species such as *Melanolepis multiglandulosa* and *Macaranga tanarius* have established in the area. However, none of these have reached more than 10 m in height.

**Bird Sampling**
Mist netting was done from 2013–2016, covering both wet and dry seasons. Birds were captured using mist nets (12 x 2.6 m with 36 mm mesh); 20 mist nets were set near the ground level while five nets were placed at sub-canopy (4–10 m) to sample both strata. In the sub-canopy, two sets of three and two mist nets were vertically placed above each other, then raised to the sub-canopy using a pulley system described by Ingle (1993). The nets were opened for 12 h (6:00 AM–6:00 PM) for three consecutive days for each sampling site and were checked every 30 m to retrieve any captures.

All captures were identified following Kennedy et al. (2000). The birds were then measured and tagged with uniquely numbered aluminum bird rings prior to release. Furthermore, birds were classified into feeding guilds based on their dietary requirements (insectivore, frugivore, nectarivore, carnivore, or a combination of these) and their foraging layer (terrestrial, understory, arboreal). Published literature works (Gonzalez 1995; Posa and Sodhi 2006) and web sources such as BirdLife International (2020) and IUCN (2020) were used in categorizing the birds to their feeding guilds. Birds were classified into 13 feeding guilds.

Field sampling was covered by Wildlife Gratuitous Permit Nos. III-2013-06 and III-2016-01. We conducted bird capture and handling in accordance with guidelines to the use of wild birds in research published by the Ornithological Council (Fair et al. 2010).

**Data Analysis**
We compared the bird assemblage between habitat types and between vertical strata within each habitat (understory and sub-canopy) in terms of species richness, diversity, capture rates, and composition. To compare species richness between habitat types and strata, we calculated the estimated species richness as the mean of four non-parametric species richness estimators (Chao, Jack1, Jack2, and Bootstrap) using the Community Ecology package (“vegan” v. 2.4-1) (Oksanen et al. 2020) in the R statistical software (v. 3.5.0) (R Core Team 2015). Sampling completeness was then assessed by comparing the actual number of species sampled to the total estimated species richness, with greater than 90% considered sufficient (Mohd-Azlan et al. 2019). We also generated species accumulation curves with a 95% confidence interval based on expected species richness using the same package in R.

In this study, Shannon’s species diversity index (H’) was used as a measure of diversity, also calculated using the vegan package in R. Values were compared between habitat types and between strata using Kruskal-Wallis and Mann-Whitney U tests, respectively (α = 0.05). These tests were performed using IBM SPSS Statistics for Windows v 20.0.

As the total sampling effort varied between habitats, capture rates were expressed as the number of individuals captured per mist net hour (m²-h) of sampling effort. Kruskal-Wallis tests and Mann-Whitney U tests (α = 0.05) were also used to compare overall capture rates, as well as species and guild capture rates, between habitat types and strata.

We compared differences in species and guild composition between each habitat type and strata through PERMANOVA analysis using the “adonis” function of the “vegan” package in R (α = 0.05). We also performed two-dimensional NMDS based on Bray Curtis similarity matrices, with data log+1 transformed to reduce the contribution of the most abundant species. Moreover, Similarity Percentage (SIMPER) was also used to determine species or guilds that have contributed most to the dissimilarities observed. Both NMDS and SIMPER were performed using PRIMER (v 6.4.7) (Clarke and Gorley 2006).

**RESULTS**

**Bird Community**
After 654,264 mist-net hours (m²-h), we recorded a total of 617 bird individuals belonging to 63 species and 13 feeding guilds (Table 2). Species richness was highest in the RA with 41 species, while 30 species and 29 species were recorded in FF1 and FF2, respectively. A high proportion of bird species were recorded in only one of the three habitat types (Table 2). Twenty-three (23) species were caught exclusively in the RA, nine species exclusively in FF1, and six species exclusively in FF2. Only 12 species were recorded across all three habitats. Most of the species captured were insectivores – understory insectivores (UIs) (12 species), terrestrial insectivores (nine species), and arboreal insectivores (AIs) (eight species).
Of the 63 species recorded, 32 are Philippine endemics – four of which are endemic to Luzon island (Table 2). The number of endemics was highest in FF1 (21 species). We also recorded one species categorized as Vulnerable in the IUCN Red List (2020) and six species listed under different threatened categories in the Philippine Red List of Threatened Wild Fauna (BCSP 2020).

Species Richness, Diversity, and Abundance
Species richness was highest in the RA, although sampling effort was different for each habitat type (Table 1). Moreover, species accumulation curves for the three habitat types and both vertical strata did not reach an asymptote, and it is likely that additional species will be captured with additional sampling effort (Figure 2). This is also supported by the calculated sampling completeness, which ranged from 50–70% (Table 1).

Mean estimated species richness was 70 for RA, 42 for FF1, and 38 for FF2 (Table 1), although Kruskal-Wallis test found no significant difference in the estimated species richness between habitat types ($H = 2.747$, $p = 0.253$). Shannon index values and mean capture rates also did not differ significantly between habitat types ($H = 1.965$, $p = 0.374$; $H = 3.741$, $p = 0.152$, respectively).

Species Assemblage and Composition
Bird species assemblages differed significantly between the three habitat types based on PERMANOVA ($F = 3.50$, $p = 0.001$). Pairwise comparisons revealed significant differences in assemblage between FF2 and the RA ($F = 2.52$, $p = 0.002$), and between FF1 and the RA ($F = 3.78$, $p = 0.001$), but not between the two forest fragments ($F = 1.52$, $p = 0.126$). These results are also evident in the

**Table 2.** Species list of birds recorded including their assigned feeding guilds, residence status, endemicity, conservation status based on IUCN (2020) and BCSP (2020), and the number of individuals mist-netted in each habitat type.

<table>
<thead>
<tr>
<th>Species</th>
<th>Guild</th>
<th>Residence status</th>
<th>Endemicity</th>
<th>IUCN (2020)</th>
<th>BCSP (2020)</th>
<th>FF1</th>
<th>FF2</th>
<th>RA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acrocephalus stentoreus</td>
<td>FGI</td>
<td>R</td>
<td>LC</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Actenoides lindsayi</td>
<td>UI</td>
<td>E</td>
<td>Philippines</td>
<td>14</td>
<td>8</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aerodramus amelis</td>
<td>AI</td>
<td>E</td>
<td>Philippines</td>
<td>0</td>
<td>11</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alcedo atthis</td>
<td>UC</td>
<td>M</td>
<td>LC</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthus gustavi</td>
<td>TI</td>
<td>M</td>
<td>LC</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthus rufulus</td>
<td>TI</td>
<td>R</td>
<td>LC</td>
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<td>0</td>
<td>2</td>
<td></td>
<td></td>
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<tr>
<td>Bolbopsittacus lunulatus</td>
<td>AF</td>
<td>E</td>
<td>Philippines</td>
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<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cacomantis sepulcralis</td>
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<td>R</td>
<td>LC</td>
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<td></td>
<td></td>
</tr>
<tr>
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<td>TI</td>
<td>M</td>
<td>LC</td>
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<td>1</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caprimulgus manillensis</td>
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<td>E</td>
<td>Philippines</td>
<td>2</td>
<td>1</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceyx cyanopeckty</td>
<td>UIC</td>
<td>E</td>
<td>Philippines</td>
<td>CR</td>
<td>0</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chalcophaps indica</td>
<td>TF</td>
<td>R</td>
<td>LC</td>
<td>10</td>
<td>1</td>
<td>10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cinnyris jugularis</td>
<td>UIN</td>
<td>R</td>
<td>LC</td>
<td>1</td>
<td>1</td>
<td>0</td>
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<tr>
<td>Collocalia marginata</td>
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<td>E</td>
<td>Philippines</td>
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<td>6</td>
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<tr>
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<td>AI</td>
<td>E</td>
<td>Philippines</td>
<td>7</td>
<td>2</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copychus luzoniensis</td>
<td>TI</td>
<td>E</td>
<td>Philippines</td>
<td>VU</td>
<td>10</td>
<td>11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copychus mindanensis</td>
<td>TI</td>
<td>E</td>
<td>Philippines</td>
<td>1</td>
<td>2</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dasylophus cumingi</td>
<td>AFI</td>
<td>E</td>
<td>Luzon (greater)</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dasylophus superciliosus</td>
<td>AFI</td>
<td>E</td>
<td>Luzon (greater)</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
generated NMDS plot showing clustering between FF1 and FF2 samples, separated from the RA (Figure 5).

SIMPER analysis revealed species that contributed most to the difference in bird assemblage between the three habitat types. For instance, *Pycnonotus goiavier* contributed most to the dissimilarity observed between the habitat types, being more abundant in the RA (Figure 6). Moreover, *Geopelia striata* and *Todiramphus chloris* were caught exclusively in the RA, adding to the observed dissimilarity in bird assemblages between habitat types.

Meanwhile, the endemic birds *Actenoides lindsayi* and *Pycnonotus urostictus* also contributed to the differences in bird assemblage observed, being more abundant in FF1 and FF2, respectively.

### Guild Structure

Thirteen (13) feeding guilds were identified during the study. However, four guilds represented by only one representative species and/or one or two individuals were excluded from the analysis to avoid skewing the results.
due to these low sample sizes. The UI guild had the most representative species (12 species), while arboreal frugivore-insectivores (AFI) comprised 39% (n = 238) of the total number of individuals captured.

Guild assemblage was found to be significantly different between habitat types ($F = 3.71, p = 0.001$). Species richness of three guilds – AI, TF (terrestrial frugivore), and UIC (understory insectivore-carnivore) – showed a significant difference between habitat types (Figure 3): AI was more species-rich in FF2 while TF and UIC are significantly more species-rich in the RA. These three guilds also showed a significant difference in their capture rates between habitat types. Pairwise analyses showed that AI was significantly more abundant in FF2 than either FF1 or RA while TF was more abundant in the RA than in FF2 (Figure 4). UIC, meanwhile, was exclusively captured in the RA.

**Vertical Stratification**

PERMANOVA showed a significant difference in bird assemblage between vertical strata within each habitat type (FF1: $F = 2.70, p = 0.006$; FF2: $F = 2.66, p = 0.017$; RA: $F = 2.90, p = 0.001$). These results are also evident from the NMDS ordinations, showing a clear separation between understory and sub-canopy assemblages (Figure 7).

Additionally, more species were captured and Shannon index showed species diversity to be higher in the understory than in the sub-canopy for all habitat types.
Mann-Whitney U-tests showed that mean capture rate was higher in the understory than the sub-canopy in the RA (U = 4.00, p = 0.001). On the other hand, capture rates between the two strata did not differ significantly between the two forest fragments (FF1: U = 42.00, p = 0.920; FF2: U = 10.00, p = 0.691) (Figure 8).

**DISCUSSION**

Our mist-netting record of 63 bird species is 9% of the total number of bird species recorded in the Philippines (WBCP 2019). Moreover, we recorded 32 Philippine endemic species, which accounts for about 13% of the total number of endemic birds in the country (n = 241). Of these, four are Luzon endemics – about 33% of the total number (n = 12).
of endemic bird species in Greater Luzon. We recorded the highest number of endemic species in FF1, six of which were not recorded in the other habitat types surveyed. Our species accumulation curves did not reach an asymptote, indicating that additional sampling is needed to fully represent the bird community in the sites. This is supported by our species records from transects conducted concurrently with our mist net sampling. From a combined total of 134 species recorded from transects and mist-netting, 70 were sampled exclusively in transects. These species include additional bird species in the area, which could further enrich the biodiversity of this karst forest area.

**Figure 4.** Box-and-whisker plots of differences in mean capture rates of feeding guilds based on mist-netting of birds between two forest fragments and a reforestation area in a limestone quarry area on central Luzon island, Philippines. Asterisks denote significant pairwise differences. Filled points are outliers. FF1 – forest fragment 1, FF2 – forest fragment 2, RA – reforestation area; AF – arboreal frugivore, AFI – arboreal frugivore-insectivore, AI – arboreal insectivore, TF – terrestrial frugivore, TFI – terrestrial frugivore-insectivore, TI – terrestrial insectivore, UC – understory carnivore, UI – understory insectivore, UIC – understory insectivore-carnivore.
included several species that are more active in the higher canopy and open-air, such as raptors and aerial foraging birds. These species are difficult to sample using mist nets, especially since our sampling of the canopy layer was limited to just five nets per site. Our mist nets also likely undersampled owls, egrets, and sunbirds – several species of which have also been recorded in our transects. Ground birds such as waterhens and buttonquails were also observed in transects but not captured in mist nets, as these species are known to be elusive and are usually able to avoid mist nets. Moreover, the lower shelf of our mist nets does not touch the ground and is usually elevated when set up and thus are not ideal for capturing ground birds (MacArthur and MacArthur 1974). Additional
Figure 7. NMDS ordination plots of the understory and sub-canopy bird captures based on mist-netting of birds between two forest fragments and a reforestation area in a limestone quarry area on central Luzon island, Philippines.

Figure 8. Comparison of estimated species richness, mean capture rate (individuals/m²·h), and diversity (Shannon index) between understory and sub-canopy captures based on mist-netting of birds between two forest fragments and a reforestation area in a limestone quarry area on central Luzon island, Philippines. Error bars indicate a 95% confidence interval.
sampling effort may result in the sampling of these species. Such undersampling may also be attributed to the inherent limitations of mist netting as a bird sampling technique. These include net avoidance after increased netting in the same site and comparatively low efficiency in terms of detection rate per unit effort, among others (Ralph et al. 2004). Thus, the combination of mist netting and transects will likely lead to more complete documentation of the bird community in any particular area. Nonetheless, evaluation studies have shown that bird abundances derived from mist-netting showed good correspondence with independently derived data, such as point counts and transects at the same locations (Dunn and Ralph 2004).

**Bird Assemblage and Distribution across Habitat Types**

Bird assemblages differed significantly between habitat types, which may be attributed to differences in their floristic composition, vegetation structure, and levels of disturbance in these habitats. A recent study done in our sites by Galindon et al. (2018) found a significant difference in the tree and herbaceous species composition between forest fragments and exotic species-based reforested areas. Based on our results, our two forest fragment sites did not vary in terms of bird species composition, sharing most of the species present in these two habitat types. Their similar floristic composition and vegetation structure may have resulted in a higher resemblance in bird assemblage. These similarities include the presence of at least 10-m high canopy trees, emergent layer dominated by families Malvaceae and Euphorbiaceae, understory formed mostly by Schizostachyum lumampao (Poaceae), and presence of climbing bamboos.

The differences in resource availability and environmental conditions between forest fragments and RAs may have influenced the composition of the bird community that could thrive in them (Azman et al. 2011). For example, P. goiavier was found to be more abundant in RAs because this species has a high tolerance for disturbance and occupies a wide range of habitats, but is rarely seen in good quality forests (Kennedy et al. 2000). In addition, G. striata and T. chloris – both of which are known to be disturbance-tolerant and common in urban areas – were caught exclusively in the RA. Meanwhile, endemic species such as P. urostictus and Aerodramus amelis characterized FF2, although the abundance of the latter may be due to proximity to caves in the area, which serves as their nesting sites. Moreover, Copsychus luzoniensis and Actenoides lindsayi were abundant in both FF1 and FF2 but never captured in the RA. These species are more commonly found in the understory and edge of lowland forests and are more sensitive to anthropogenic disturbance (Kennedy et al. 2000; Posa and Sodhi 2006). The distribution of these species within the study area provides additional support for the degree of tolerance and habitat preference of some of the abundant species occurring in karst forests in Luzon.

**Bird Assemblage and Distribution across Vertical Strata**

Within each habitat type, we observed a significant difference between the two vertical strata in terms of species richness, diversity, capture rate, and species composition. Our results revealed that the understory had more species and higher capture rates and diversity index values compared to the sub-canopy.

We found that some arboreal species (mostly bulbuls) exhibit a downward shift from the higher forest strata to the understory in both RA and FF2. For instance, P. goiavier and Hypsipetes philippinus, which contributed 38% to the observed dissimilarity between strata in the RA, have significantly higher capture rates in the understory. In FF2, P. goiavier and P. urostictus also have significantly higher capture rates in the lower strata. In FF1 meanwhile, our species-level analysis showed that birds were generally found in the strata we expected them to prefer based on their designated feeding guilds.

The vertical shift towards the understory we observed in these bird species may be related to the availability of resources and complexity of the habitat. In the RA, for example, the understory is mostly dominated by the invasive shrub Lantana camara – the fruits of which are commonly consumed by generalist frugivores such as bulbuls, flowerpeckers, babblers (Ramaswami et al. 2017). The abundance of this shrub may have drawn these arboreal species to the lower stratum, along with the availability of other understory plants such as Oplismenus compositus, Piper sp., and grasses (Poaceae) – which birds may utilize as food or materials to build a nest. Moreover, the simplification in the vertical vegetation structure of the RA caused by the planting of exotic tree species may have favored the increase of specific trophic guilds and generalist species. A study by Munro et al. (2011) has shown that reforested areas maintained to have complex vegetation structures could still harbor high numbers of forest-dependent species and support other trophic guilds. Thus, management practices that aim to increase habitat and vegetation structure variability by planting native understory and canopy plant species should be considered when implementing reforestation plans in an area. Such practices may facilitate recolonization by birds, as well as other native wildlife such as fruit bats, amphibians, and reptiles.

Similarly, the reduced canopy cover and denser understory vegetation in FF2 may have apparent edge effects on some of the bird species. The modification of the habitat may
have influenced the movement of some species to shift downwards during midday to avoid the heat while the dense foliage in the understory layer could have provided the substrate for some insectivore guilds to glean their prey and use to perch for aerial sallying (Pearson 1971; Wunderle et al. 2005).

No shifts in stratification were observed in FF1. This may be due to the relatively lower degree of disturbance experienced by the site, owing to local policies to protect the cave and its vicinity for ecotourism activities. Moreover, large trees – which are required by some avian groups such as parrots and large-bodied frugivores for foraging, perching, and nesting – are relatively more abundant in the area.

**Feeding Guild Structure**

Bird assemblage and diversity patterns among the three habitat types were further assessed by considering the dietary niche of the identified bird species. Frugivores and insectivores, considered to be the two major dietary groups in birds, are well-represented in all three habitat types in our study areas and may provide essential ecological services to these degraded habitats (Sekercioglu 2012). Insectivores (AI, TI, UI) were the dominant guild within each habitat type and in our study area, with 29 insectivores out of the 63 species sampled. Although insectivores are commonly observed to dominate tropical forests in terms of species richness and abundance, they are very sensitive to habitat modification (Sekercioglu et al. 2002). This is especially the case for those insectivores situated in the understory, which usually become the first groups to disappear when a disturbance occurs within their habitat.

UI and TI were least represented in the RA (10 species) and made up mostly of migratory (Lanius cristatus, Ficedula narcissina) and generalist species (Copsychus mindanensis), whereas resident Philippine endemic forest-dependent species such as Actenoides lindsayi and Copsychus luzoniensis represent the insectivores in the FF1 (11 species) and FF2 (15 species).

More frugivorous birds were recorded in the RA (eight species) than either FF1 (five species) or FF2 (one species). The diversity and distribution of frugivorous guilds could be largely affected by both abundance and richness of their food and the vegetation structure of habitat types (Moegenburg and Levey 2003). For instance, most of the frugivorous birds encountered in the RA are disturbance-tolerant species (G. striata, Lonchura atricapilla, Lonchura leucogastra, and Lonchura punctulata) that commonly feed near the ground on grains from plant sources such as rice and grasses. Meanwhile, all the frugivore species present in FF1 are forest-dependent – four of which (Bolbopsittacus lunulatus, Loriculus philippensis, Phapitreron amethystinus, and Treron axillaris) are Philippine endemic arboreal feeders. The availability of fruits from tall trees may explain the abundance of these arboreal frugivores (AFs) in FF1. On the other hand, frugivore guilds were represented in FF2 by just a single species, Chalcophaps indica. This is surprising, as we expected the same AFs captured in FF1 to also be present in FF2. Indeed, we observed the same species in FF2 from our transects on the site. It is possible that in FF2, these species forage in even higher strata than the sub-canopy covered by our netting and, thus, may have eluded capture. Hunting pressure has also been observed to cause the decline of frugivores in forests on Luzon island (Posa and Sodhi 2006; Española et al. 2013). However, it is unlikely that hunting had a significant influence in the reduced number of frugivores in FF2 as the area was managed by a mining company, and security personnel is present at the site. Thus, we saw that – in general – TFs were more abundant in the RA while AFs were more abundant in the forest fragments, likely due to differences in the kinds of plant resources they consume (i.e. seeds and grains vs. fruits from trees).

We identified 18 species belonging to several omnivore guilds (AFI, FGI, TFI, TIG, UIC, UIN). Omnivores are particularly dominant in the RA with 14 species recorded while seven and six species each were recorded for FF1 and FF2, respectively. The abundance of generalist species with wide dietary breadths in more disturbed habitats is a common trend in fragmented landscapes of tropical forests (Devictor et al. 2008). These omnivorous guilds are dominated by bulbuls (Pycnonotidae), which are habitat and dietary generalists, and are known for their importance in forest restoration in lowland forests (Corlett 2017). We also recorded seven Philippine endemic species that belong to these omnivorous guilds in the reforestation sites. The presence of these groups in the area underlines the value of reforestation in mined-out areas, particularly for endemic species. The RAs in the mining site were first established in 1996 and 2000 and were initially planted with Gmelina arborea, a fast-growing exotic tree species (Galindon et al. 2018). Native species were inserted later and other pioneer and naturally occurring species re-established through time. Studies suggest that bird species richness and abundance in areas dominated by exotic plant species are significantly lower compared with sites with native vegetation (Braithwaite et al. 1989; Fleishman et al. 2003; Isaac et al. 2005; Flanders et al. 2006). However, a study by Thompson and Thompson (2004) showed that bird composition changes with the reforestation age and biodiversity recovery in the RAs planted with exotic species is still possible by re-establishing the floral component using native species. Thus, it is also important to monitor reforestation sites’ recovery and evaluate the re-colonization of the original wildlife and native plant species in the area.
CONSERVATION IMPLICATIONS

Although we recorded the highest number of species in the RA, the simplification in the vertical vegetation structure and high level of disturbance in these exotic species-based reforestation sites resulted in the dominance of generalist and disturbance-tolerant species of lower conservation value. Thus, priority should be given to protect existing forests and increase the habitat and vertical complexity of these sites to attract forest-dependent and sensitive bird species of high conservation priority. Planting of native and indigenous tree species are also recommended for reforestation projects since studies suggest that reforestation sites composed of native trees and maintained to have complex vegetation structure facilitates colonization of original wildlife in the area (Thompson and Thompson 2004; Munro et al. 2011). RAs should also be established near remaining forest fragments to increase habitat availability and maintain habitat diversity in fragmented landscapes. Green belts or forest corridors should also be established to maintain landscape connectivity between fragmented habitats and reduce the impacts of fragmentation in wildlife (Mullu 2016). This will allow greater mobility of sensitive species, such as UIs, between fragments. Furthermore, long-term programs on reforestation maintenance and protection are also needed to allow natural forest regeneration.

The abundance of endemic and forest-dependent birds, as well as the presence of threatened species in FF1 highlight the conservation value of karst habitats. In the Philippines, existing policies and laws do not directly address the protection of karst areas but instead focused mainly on the protection of caves and cave features to boost tourism (Tolentino et al. 2020). However, the high level of endemism and presence of threatened species in karst habitats underlines the importance of protecting the forests surrounding the caves for these species to continually thrive in the area. Local management policies should consider reducing further development near caves and forested areas, as well as the strict enforcement of slash-and-burn activities for agricultural purposes, to maintain the diversity of birds on the site.

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