

Effect of forest fragmentation on bird species richness in Papua New Guinea

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ABSTRACT. Tropical forests worldwide are being fragmented at a rapid rate, causing a tremendous loss of biodiversity. Determining the impacts of forest disturbance and fragmentation on tropical biotas is therefore a central goal of conservation biology. We focused on bird communities in the interior (>100 m from forest edge) of forest fragments (300, 600, and 1200 ha) in the lowlands of Papua New Guinea and compared them with those in continuous forest. We surveyed bird communities using point counts, mist-netting, and random walks, and measured habitat and microclimate characteristics at each site. We also surveyed leaf-dwelling arthropods, butterflies, and ants, and obtained diet samples from birds to examine food availability and food preferences. We recorded significantly fewer bird species per point in the 300-ha forest fragment than in other study sites. Overall, we recorded 80, 84, and 88 species, respectively, in forest fragments, and 102 in continuous forest. Frugivores (especially large frugivores) and insectivores had lower species richness in forest fragments than continuous forest. Our results did not support the food scarcity hypothesis, that is, the decline of insectivorous birds in forest fragments is caused by an impoverished invertebrate prey base. We also found no significant differences among forest fragments and continuous forest in microclimates of forest interiors. Rather, we found that microhabitats preferred by sensitive birds (i.e., 30% of species with the strongest preferences for continuous forest) were less common in forest fragments (19%–31% of points) than in continuous forest (86% of points). Our results suggest that changes in microhabitats may make forest fragments unsuitable for sensitive species. However, limited dispersal capabilities could also make some species of birds less likely to disperse and occupy fragments. In addition, impoverished food resources, size of the forest fragment, or hunting pressure could contribute to the absence of large frugivorous birds in forest fragments. The forest fragments in our study, preserved as village-based protected areas, were not large enough to sustain the bird communities found in continuous forest. However, because these fragments still contained numerous bird species, preservation of such areas can be an important component of management strategies to conserve rainforests and birds in Papua New Guinea.

RESUMEN. El efecto de la fragmentación del bosque sobre la riqueza de especies de aves en Papúa Nueva Guinea

A nivel mundial los bosques tropicales están siendo fragmentados a una tasa rápida, causando una tremenda pérdida de biodiversidad. Por lo tanto determinar los impactos de los disturbios y la fragmentación sobre biotas tropicales es la meta central de la biología de la conservación. Nos concentramos en comunidades de aves en el interior (>100 m desde el borde del bosque) de fragmentos de bosque (300, 600, y 1200 ha) en las tierras bajas de Papúa Nueva Guinea y los comparamos con las de bosques continuos. Censamos las comunidades de aves usando puntos de conteo, redes de niebla y caminatas aleatorias, y medimos características del hábitat y microclima en cada uno de los sitios. También censamos artrópodos de hojarasca, mariposas y hormigas, y obtuvimos muestras de dieta de aves para examinar disponibilidad de alimento y preferencias de alimento. Detectamos significativamente menos especies de aves por punto en los fragmentos de bosque de 300-ha al compararlo con cualquiera de los otros lugares de estudio. En general, detectamos 80, 84 y 88 especies, respectivamente, en los fragmentos de bosques y 102 en bosques continuos. Frugívoros (especialmente frugívoros de gran tamaño corporal) e insectívoros tuvieron una menor riqueza de especies en los fragmentos de bosque en comparación a el bosque continuo. Nuestros resultados no apoyaron la hipótesis de escases de alimento, i.e., la disminución de las aves insectívoras en los fragmentos de bosques es causada por un empobrecimiento en las presas de invertebrados fundamentales. Tampoco encontramos diferencias significativas entre fragmentos de bosque y bosques continuos en el microclima al interior del bosque. Más bien, encontramos que los micro hábitats preferidos por las aves con alta sensibilidad (i.e., 30% de las especies con una fuerte preferencia por los bosques continuos) fueron menos comunes en los fragmentos de bosque (19–31% de los puntos) que en bosques continuos (86% de los puntos). Nuestros resultados sugieren que los cambios en micro hábitat pueden hacer que los fragmentos de bosque sean inadecuados para las especies sensibles. Sin embargo, la limitada capacidad de dispersión puede también hacer que algunas especies de aves tengan una más baja probabilidad

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de dispersarse y ocupar los fragmentos de bosque. Adicionalmente a el empobrecimiento de los recursos alimenticios, el tamaño del fragmento de bosque, o presiones de cacería pueden contribuir a la ausencia de los frugívoros de gran tamaño en los fragmentos de bosque. En nuestro estudio los fragmentos de bosques, conservados como áreas de protección basadas en aldeas, no son lo suficientemente grandes para sostener la comunidad de aves que se encuentra en los bosques continuos. Sin embargo, debido a que estos fragmentos todavía contienen una gran cantidad de especies, la conservación de estas áreas puede ser un importante componente en las estrategias de manejo para conservar bosques lluviosos y aves en Papúa Nueva Guinea.

Key words: conservation, food limitation, frugivorous birds, habitat selection, insectivorous birds, microhabitat, tropical forest

Lowland forests of the wet tropics support the most species-rich communities of terrestrial birds. Unfortunately, selective logging and conversion to plantations (Barlow et al. 2006) contribute to fragmentation of continuous forests in many areas. Such fragmentation typically results in a local loss of species (Turner 1996). Studies to date have focused mainly on the effects of forest conversion (Komar 2006) and fragmentation (Sekercioglu et al. 2002) on birds in the Neotropics. More information about the impacts of fragmentation on birds in other tropical forest systems is needed, particularly in Africa (Newmark 1991) and the Pacific Ocean islands (Marsden et al. 2006) where the rate of deforestation is increasing (Shearman et al. 2008).

Previous work in primary and secondary forests in Papua New Guinea (Tvardikova 2010) has demonstrated that lowland insectivorous birds and canopy frugivores are particularly sensitive to forest disturbance. Other investigators have also reported that large frugivorous and understory insectivorous birds are sensitive to habitat alteration (Stouffer and Bierregaard 1995, Sekercioglu 2002, Sekercioglu et al. 2002, Kattan et al. 2004, Lees and Peres 2010). Several hypotheses have been proposed to explain the disappearance of insectivorous bird species from forest habitats around the world (Canaday 1996, Ford et al. 2001). Four of these are particularly relevant to the decline of understory insectivores. The food scarcity hypothesis states that small fragments are impoverished in prey preferred by understory insectivores (Burke and Nol 1998, Zanette et al. 2000, Ford et al. 2001). The microclimate hypothesis proposes that these birds are particularly sensitive physiologically to changes in microclimate associated with forest fragmentation (Karr and Freemark 1983, Canaday 1996). The habitat specificity hypothesis states that the loss of some microhabitat elements from fragments (e.g., army ant swarms and dead trees)

may affect many understory insectivores (Canaday 1996, Ford et al. 2001). Finally, according to the limited dispersal hypothesis, understory insectivores, because of their relatively sedentary habits and possible avoidance of clearings and altered habitats (Stouffer and Bierregaard 1995, Báldi 1996, Sekercioglu 2002), may be less likely to disperse into more favorable habitats after forest fragmentation and may disappear from fragments as a result of stochastic events.

Although numerous studies have focused on the effects of forest fragmentation on bird diversity, few investigators (e.g., Stouffer and Bierregaard 1995, Sekercioglu 2002) have systematically tested alternative hypotheses explaining the loss of species in forest fragments. To our knowledge, these hypotheses have never been tested in Southeast Asia and the Pacific islands. Our objectives were therefore to (1) describe bird communities in lowland tropical forests in Papua New Guinea, and (2) determine which of the above hypotheses, if any, might best explain the loss of bird species in forest fragments. Papua New Guinea forests are continuous over large areas and represent one of the last three tropical wilderness areas along with Amazonian and Congo forests (Mittermeier et al. 1998). However, forests in New Guinea are under increasing threat from logging (Shearman et al. 2008).

METHODS

Field work was conducted in June 2010, October 2010, and January 2011 in continuous forest and forest fragments in the lowlands of Madang province, Papua New Guinea (PNG). Study sites included (1) continuous forest (5°13.5'S, 145°04.9'E, 120 m asl) located in the middle of >10,000 ha continuous lowland primary forest in Wanang Conservation Area, which itself is embedded within ~100,000 ha of selectively logged, but largely continuous, lowland rainforest, (2) a large fragment of primary

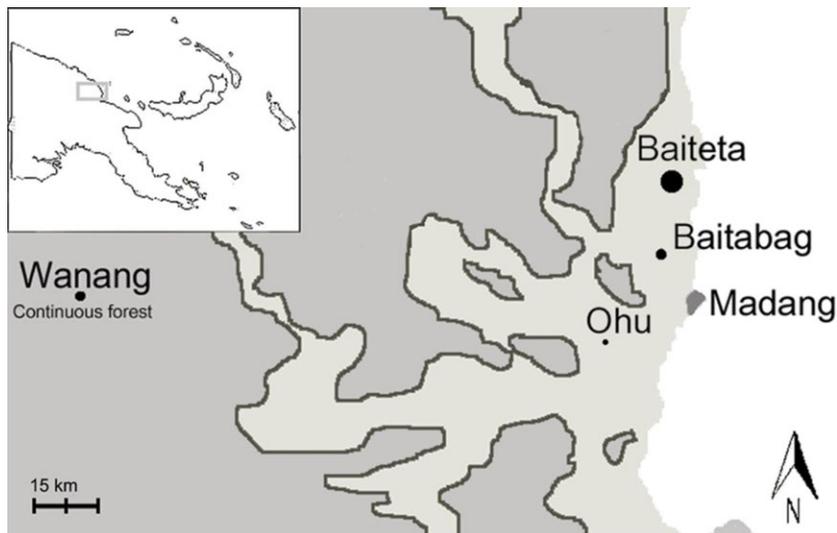


Fig. 1. Location of study sites in Papua New Guinea (inserted map) and in Madang Province. Baiteta = 1200-ha forest fragment, Baitabag = 600-ha forest fragment, Ohu = 300-ha forest fragment, and Wanang = continuous forest area >10,000 ha. Dark gray = undisturbed forest, and light gray = selectively logged or disturbed forest and forest plantations.

forest (1200 ha; $5^{\circ}01.73'S$, $145^{\circ}46.01'E$, 100 m asl) near the villages of Rempi and Baiteta, (3) a mid-sized fragment of primary forest (600 ha; $5^{\circ}07.99'S$, $145^{\circ}45.47'E$, 100-m asl) near the village of Baitabag, and (4) a small fragment (300 ha; $5^{\circ}16.2'S$, $145^{\circ}41.1'E$, 170 m asl) of primary forest near Ohu village. All three forest fragments were located in a relatively densely settled and intensely farmed landscape around the town of Madang, within 15–24 km of each other and 67–76 km from the continuous forest site (Fig. 1). The fragments have been increasingly isolated since the 1980s as the original mosaic of primary and secondary forests around villages has changed into a more intensely managed landscape with slash-and-burn food gardens, young secondary forest growing on abandoned gardens, deforested village settlements, and plantations. All fragments have been preserved as village-based protected areas where logging and hunting are forbidden. Village landowners supervise the forest preservation. Likewise, the continuous forest has been declared by village landowners as a conservation area with no logging and hunting (www.entu.cas.cz/png/wanang).

The location and size of the forest fragments in our study were representative of other landscapes in Madang province and lowland

PNG at large, where most of the inland area is still covered by continuous forest (although under increasing logging pressure). However, large areas along the coast are now a mosaic of food gardens, villages, secondary and selectively logged forests, and plantations. In Madang, people in many villages have an interest in conserving fragments of primary, undisturbed forests, similar to the ones where we conducted our research.

All study sites have a humid climate with a mild dry season from July to September; average annual rainfall is 3600 mm (McAlpine et al. 1983). Humidity, temperature, and dew point were recorded every 30 min for the duration of experiments (15 d) using data loggers (R3120, Comet System, Rožnov pod Radhoštěm, Czech Republic) placed in the forest interior (>100 m from forest edge) at each site. All study forests had closed, ~35-m-high canopies and relatively open understories without distinct stratification.

Bird surveys. Bird communities were surveyed using point counts, mist-netting, and random walks. During each month of the study (June 2010, October 2010, and January 2011), we conducted three point counts and 6 or 7 h of random walks (three afternoons). Mist-netting was conducted in two blocks of 3 d

that were split into 2 mo of study (continuous forest and 300-ha fragment in June and January, 600-ha fragment in June and October, and 1200-ha fragment in October and January). At each site, point counts were conducted at 16 points regularly spaced along a 2250-m transect (successive points were 150 ± 5 m apart to avoid double-counting). Transects at each site were directed through representative and diverse microhabitats (e.g., ridges, valleys, emergent trees, flat-land forest, and riparian areas ≥ 150 m from forest edge in forest fragments), and existing trails were used when possible. If existing trails were not available or did not lead through representative microhabitats, new transects were made so that we surveyed all available microhabitats at each site. All point-counts thus represented the heterogeneity of lowland forest habitats in a similar way. All birds seen or heard within 50 m of the point were recorded. Distances were measured with a laser tape measure and distances to conspicuous boundary trees or branches were memorized prior to the first point counts. During point counts, the location of birds close to the border of a point was measured by laser tape measure or estimated when views were obscured. We started censuses 15 min before sunrise at a randomly selected point and continued counts in a randomly selected direction. We counted birds for 15 min at each point so all 16 points were surveyed before 11:00. To minimize double-counting, we attempted to accurately track movements of birds, and recorded more individuals of the same species only when they called at the same time or from distinctively different directions. Each transect was surveyed nine times, resulting in 36 h of observation along each transect.

At each study site, we mist-netted birds along a 200-m-long line of nets (2.5 m high \times 12–18 m long, 16-mm mesh) for 6 d from 05:30 to 17:30, with checks every 20 min. During the first 3 d, nets were placed between the first three points of the point-count transect, and then transferred to the last three points of the point-count transect for the next 3 d. We identified all mist-netted birds, marked them with color bands, and released them within 10 min.

Finally, we walked along existing trails and along point-count transects, surveying the area of ~ 80 ha evenly, and noted all species identified during these random walks. Walks lasted 2–3 h per day (starting at 15:00, walking

distance = 3–4 km/d), and were standardized to 20 h per site. All surveys were conducted by K. S., B. K., and S. J., all of whom had previous experience with bird surveys in Papua New Guinea. We also recorded vocalizations at each survey point during surveys and any unrecognized bird vocalizations during our random walks (using a Marantz PMD 620 recorder and a Sennheiser ME67 microphone) to allow later identification.

Observed birds were categorized into four broad trophic guilds, including insectivores (invertebrates as main food), frugivores (fruit and seed eaters), omnivores (feed on plant material and invertebrates in similar ratios), and nectarivores, based on dietary information provided in several references (Peckover and Filewood 1976, Beehler et al. 1986, del Hoyo et al. 1992–2011) and our own observations. We considered birds with a body length (obtained from del Hoyo et al. 1992–2011) >40 cm to be large, 23–39 cm as medium, and <22 cm as small (www.whatbird.com). Raptors, swifts, and non-forest bird species passing through our study sites were excluded from analyses. See Table S1 for a list of observed species, species included in analyses, and their habitat and feeding preferences. We use the species-level International Ornithologists' Union taxonomy (Gill and Donsker 2013) in reporting our results.

Bird diets. We obtained diet samples from insectivorous and omnivorous birds captured in mist-nets using nonlethal 1.5% potassium antimony tartrate, based on established protocols (Poulin and Lefebvre 1995, Mestre et al. 2010). We did not detect any mortality or decreased number of recaptures (compared to nontreated birds), and all birds were able to fly away. K. S. examined each sample under a stereo-microscope, and counted and measured the length of prey items. The number of arthropod individuals per morphospecies was determined as the minimum number that was possible to assemble from body parts found in a sample. The length of individual arthropods was calculated from available measurements of body parts based on a reference collection and published order-specific regressions of mass on length (Tatner 1983, Ralph et al. 1985). Invertebrates were identified to order. Food analyses were based on examination of prey items in 120 regurgitated samples; five from each of six species captured at all four study sites, including

Ochre-collared Monarchs (*Arses insularis*), Little Shrikethrushes (*Colluricincla megarhyncha*), Mimic Honeyeaters (*Meliphaga analoga*), Long-billed Honeyeaters (*Melilestes megarhynchus*), Spot-winged Monarchs (*Symposiachrus guttula*), and Northern Variable Pitohuis (*Pitohui kirhoccephalus*). Other bird species either did not occur at all sites or we did not obtain the minimum of five samples thought to provide an adequate representation of the diet of a species in a given time period (Sekercioglu et al. 2002). We identified 18 prey categories, including 10 insect groups (Coleoptera, Diptera, Dermaptera, Neuroptera, Odonata, Orthoptera, Hemiptera, adult Lepidoptera, and Hymenoptera that were split into Formicidae and others), Chilopoda, Lepidoptera larvae, insect larvae, pupae, eggs, Araneae, Gastropoda, and vertebrates (small lizard and frog).

Habitat. At each point-count point, we measured (1 d before the first point count in June 2010) several variables within a circle of ~30-m-radius following methods described by Bibby et al. (1992), including canopy and shrub height (using heights of three randomly selected trees and shrubs, respectively, within the point-count circle and measured using a laser measuring device), shrub foliage density (five measurements at randomly selected places within each point-count circle, using scatter-plot estimates; Creagh et al. 2004), and percent ground cover of grass, bare ground, and litter (within $1 \times 1\text{-m}^2$ at 15 randomly selected places within each point-count circle). We also measured canopy openness (based on three photos taken where canopy height was also measured, and analyzed using Gap Light Analyzer; Frazer 1999, Frazer et al. 2001), and noted the presence or absence of fruiting trees within each point-count circle. Fruiting trees were recorded prior to each series of point counts, that is, in June 2010, October 2010, and January 2011. At each study site, we delineated three 150×2 m lines (between points 3–4, 6–7, and 12–13, respectively) where we counted all plant stems (DBH > 1 cm), and categorized them based on size (1–2 cm, >2–5 cm, and >5 cm DBH) and leaf size (small ≤ 100 cm², mid-size = 100–300 cm², and large ≥ 300 cm²). We counted the numbers of trees with and without epiphytes and termite nests within the lines. We also counted the number of dead logs and dead standing trees within the lines.

Prey availability. In January 2011, we sampled leaf-dwelling arthropod communities from tree saplings at all four study sites. At each site, crowns of 10 tree saplings (DBH ~5 cm; one sapling at 10 randomly selected point-count points) were lowered above a mosquito net, covered with a net, and sprayed with commercial insecticide. All arthropods were collected, placed in 70% alcohol, and identified into the same groups as invertebrates in food samples. All leaves from each sapling were collected, weighed, and their leaf area measured using digital images of leaves processed in Photoshop and ImageJ to obtain the area of individual leaves and total leaf area of whole trees.

A recent study of bird diets in Papua New Guinea showed that 61 of 98 bird species fed on ants, 47 species included ant eggs in their diet, 63 bird species fed on Lepidoptera larvae, and 39 bird species fed on adult Lepidoptera (Tvardikova 2013). Therefore, we identified butterflies and ants as important prey for birds (besides beetles and spiders). Ant abundance was determined in October 2010 using 30 tuna baits (one teaspoon of tuna meat (~5 gm in vegetable oil) placed on 5×5 -cm piece of gauze tied to trunks at breast height) per forest fragment and 25 baits in continuous forest placed on randomly selected tree samplings (~75 m apart). After 60 min of exposure, ants on or within 1 cm of each tuna bait were counted.

Finally, butterfly abundance was determined in July 2010 along three 300-m-long transects at each study site. Butterfly transects were set along bird point-count transects between the first two, middle (7–9), and last two points. Transects were walked slowly for 30 min, and walks were replicated 10 times (P. Vlasanek, unpubl. data). Abundance was determined as the mean number of butterflies observed along all three transects for each site.

Statistical analysis. We used all three survey methods to determine local species richness and bird abundances. We examined microhabitat characteristics of all sites and eliminated those that did not differ among study sites, including canopy height ($F_{3,12} = 1.0$, $P = 0.42$), mean tree DBH ($H_{3,12} = 4.7$, $P = 0.19$), number of fruiting and flowering trees per point ($H_{3,12} = 3.1$, $P = 0.09$), number of trees with termite nests ($H_{3,12} = 4.0$, $P = 0.26$), and number of dead logs ($H_{3,12} = 1.3$, $P = 0.72$). Further, we used factor analysis of variables that differed

significantly among sites to identify suites (factors) of correlated (redundant) variables. We started with six factors (shrub foliage density, shrub height, three ground cover variables, and canopy openness) and reduced that number to three (explaining 86% of the variability) using the Kaiser–Guttman stopping rule (Jackson 1993). From each factor, we selected a single representative variable measured in the field (litter cover, shrub foliage density, and canopy openness) and used them in the following analyses.

Using Canonical correlation in R 2.11.1 (R Core Team 2012), we selected the species of birds showing the strongest preferences toward continuous forest (birds represented first axis scores > 0.3 ; CCA, first axis = continuous forest, resulting in selection of 19 insectivores, nine frugivores, and nine omnivores; i.e., $< 30\%$ of observed birds), and extracted values of representative variables (litter cover, shrub foliage density, and canopy openness) from all points where our focal species were observed foraging, without respect to whether the point was in a fragment or continuous forest. Thus, we obtained characteristics of preferred microhabitats and compared them with habitat characteristics of all points within individual study sites. See Figure S1 for a list of selected sensitive species and their habitat preferences.

RESULTS

We recorded a total of 116 bird species at all four sites, and exclusion of raptors and swifts resulted in 108 species used in our analyses (Table S1). Species richness was higher in the continuous forest (102) than in all forest fragments (1200 ha = 88, 600 ha = 84, and 300 ha = 80; Fig. 2). Daily mist-net capture rates (number captured per unit time) did not differ among sites ($H_{3,24} = 2.9, P = 0.42$). The mean number of bird species recorded at each point ($N = 16$ per study site) differed significantly among sites ($F_{3,60} = 9.1, P < 0.001$; Table 1). Similarity in species composition was relatively low between the smallest fragment and both larger fragments (Morisita–Horn index = 0.62) and continuous forest (Morisita–Horn index = 0.59). All other comparisons revealed higher similarity between bird communities (Morisita–Horn index = 0.77–0.89).

The total number of insectivorous bird species in the continuous forest (45 species) was higher than in all forest fragments (1200 ha = 39, 600 ha = 37, and 300 ha = 35; Fig. 2).

The mean number of insectivorous bird species recorded at each point ($N = 16$ per study site) differed significantly among sites ($F_{3,60} = 61.9, P < 0.001$; Table 1). Of 46 insectivorous species recorded across all sites, only one (Oriental Dollarbird, *Eurystomus orientalis*) was not recorded in continuous forest. Differences in numbers of insectivorous species among sites were significant mainly for sallying flycatchers and gleaners (e.g., Monarchidae, Rhipiduridae, and Acanthizidae) and forest ground-dwelling insectivores (e.g., Pittidae and Jewel-babblers, *Ptilorrhoa* spp.). In the family Monarchidae (7 species recorded across all sites), Black-winged Monarchs (*Monarcha frater*) were only observed in continuous forest, Rufous Monarchs (*M. rubiensis*) in the continuous forest and 1200-ha forest fragment, and four species were significantly more abundant ($F_{3,60} > 4.7, P < 0.001$; Tukey's *post hoc* test, $P < 0.04$) in continuous forest and the 1200-ha fragment than in the smaller fragments. The abundance of Golden Monarchs (*Carterornis chrysomela*) did not differ among sites ($F_{3,60} = 1.4, P = 0.24$). In the family Rhipiduridae (4 species), Rufous-backed Fantails (*Rhipidura rufidorsa*) were only observed continuous forest, Sooty Thicket Fantails (*R. threothorax*) were not recorded in the 300-ha fragment, and Northern Fantails (*R. rufiventris*) were significantly less abundant in the 600-ha fragment than at the other sites ($F_{3,48} = 5.5, P = 0.002$; Tukey's *post hoc* test, $P < 0.01$). Abundance of Willie Wagtails (*R. leucophrys*) did not differ among sites ($F_{3,48} = 1.1, P = 0.36$). In the family Acanthizidae (4 species), Rusty Mouse-warblers (*Crateroscelis murina*) and Pale-billed Scrubwrens (*Sericornis spilodera*) were only present in continuous forest, and Yellow-billed Gerygones (*Gerygone chrysogaster*) and Green-backed Gerygones (*G. chloronota*) were not recorded in the 300-ha fragment. All recorded insectivorous birds were either small (43 species) or medium-sized (3 species).

Total species richness of frugivores in continuous forest (24 species) was higher than in the forest fragments (1200 ha = 16, 600 ha = 16, and 300 ha = 14 species). The mean number of frugivorous species recorded at each point ($N = 16$ per study site) differed significantly

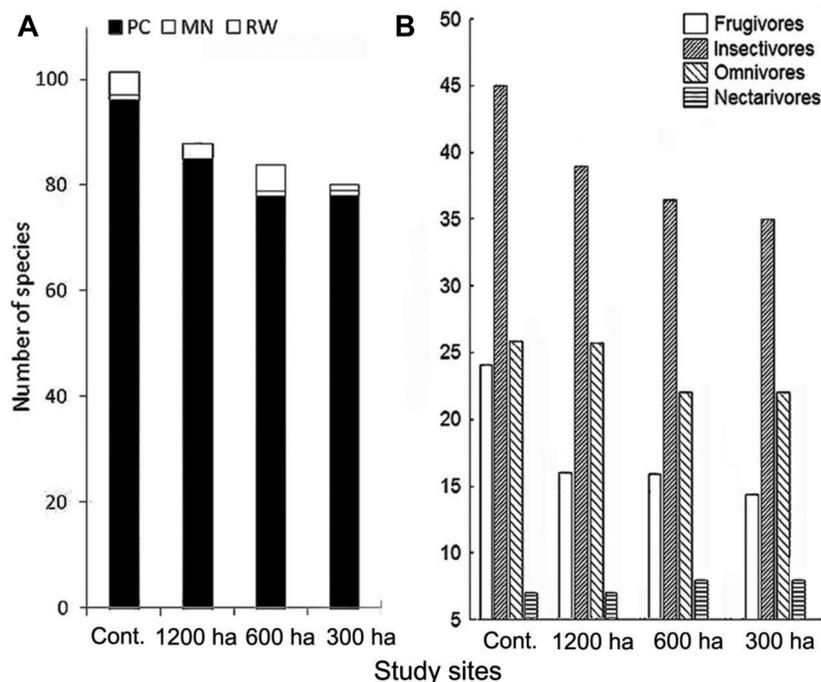


Fig. 2. (A) Number of species recorded by different survey techniques at each site (PC = point count, MN = species captured in mist-nets, but not recorded in point counts, and RW = species recorded only during random walks). (B) Number of species partitioned into feeding guilds in continuous forest (Cont.), 1200-ha fragment, 600-ha fragment, and 300-ha fragment.

Table 1. Mean number (\pm SD) of bird species recorded at each point ($N = 16$ per site, 15-min point counts) in our 300-ha, 600-ha, and 1200-ha forest fragments and the continuous forest in Madang Province, Papua New Guinea. Different letters indicate significant differences ($P < 0.05$, Tukey's *post hoc* test) between forest types.

| Forest type | All birds | | Insectivores | | Frugivores | |
|-------------|----------------|---|----------------|---|----------------|---|
| Continuous | 23.5 \pm 2.0 | A | 23.1 \pm 2.4 | A | 15.1 \pm 1.9 | A |
| 1200 ha | 22.1 \pm 2.5 | B | 20.8 \pm 2.6 | B | 11.2 \pm 1.0 | B |
| 600 ha | 21.3 \pm 2.7 | B | 19.8 \pm 2.4 | B | 10.9 \pm 1.8 | B |
| 300 ha | 18.7 \pm 3.3 | C | 11.4 \pm 2.9 | C | 10.8 \pm 1.8 | B |

among sites ($F_{3,60} = 23.4$, $P < 0.001$; Table 1). Of 25 frugivorous species recorded across all sites, seven were only present in the continuous forest, included Northern Cas-sowaries (*Casuarus unappendiculatus*), Purple-tailed Imperial Pigeons (*Ducula rufgaster*), Cin-namon Ground Doves (*Gallicolumba rufigula*), Victoria Crowned Pigeons (*Goura victoria*), Coronated Fruit Doves (*Ptilinopus coronulatus*), Dusky Lorries (*Pseudeos fuscata*), and Wompoo Fruit Doves (*Ptilinopus magnificus*). In addi-

tion, four species were not recorded in the smaller fragments (300 or 600 ha), including Pinon's Imperial Pigeon (*Ducula pinon*), Pink-spotted Fruit Dove (*Ptilinopus perlatus*), Zoe's Imperial Pigeon (*Ducula zoeae*), and Tawny-breasted Honeyeater (*Xantotis flaviventer*), and one was only recorded in forest fragments (Streak-headed Mannikin, *Lonchura tristissima*). Of 13 frugivorous species recorded at all sites, abundance did not differ among sites ($F_{3,60} > 0.2$, $P > 0.92$) for four species (Superb

Fruit Dove, *Ptilinopus superbus*; Red-flanked Lorikeet, *Charmosyna placensis*; Orange-bellied Fruit Dove, *Ptilinopus iozonus*; and Slender-billed Cuckoo-Dove, *Macropygia amboinensis*), three were significantly more abundant ($F_{3,60} > 4.1$, $P < 0.009$) in forest fragments than continuous forest (Eclectus Parrot, *Eclectus roratus*; Edwards's Fig Parrot, *Psittaculirostris edwardsii*; and Stephan's Emerald Dove, *Chalcophaps stephani*), and six were significantly ($F_{3,60} > 4.0$, $P < 0.01$) more abundant in continuous forest than in fragments (Beautiful Fruit Dove, *Ptilinopus pulchellus*; Palm Cockatoo, *Probosciger aterrimus*; Blyth's Hornbill, *Rhyticeros plicatus*; Great Cuckoo-Dove, *Reinwardtoena reinwardti*; Collared Brushturkey, *Talegalla jobiensis*; and Sulphur-crested Cockatoo, *Cacatua galerita*). Frugivorous species that were significantly less abundant in fragments ($U = 22.5$, $Z = 2.6$, $P = 0.008$) were larger ($N = 17$, mean length = 52.5 ± 31.2 [SD] cm) than species whose abundance was not influenced by forest size or species that were more abundant in forest fragments ($N = 8$, mean length = 23.6 ± 8.7 [SD] cm).

Total species richness of omnivores did not differ between the 1200-ha fragment and continuous forest (26 species) or between the 600-ha and 300-ha fragments (23 species, Fig. 2). The mean number of omnivorous bird species recorded at each point ($N = 16$ per study site) also did not differ significantly among sites ($F_{3,60} = 2.6$, $P = 0.052$). Total species richness of nectarivores was similar (7, 7, 8, and 8 species, respectively) among sites (Fig. 2), and the mean number of nectarivorous species recorded at each point did not differ among sites ($F_{3,60} = 1.7$, $P = 0.17$).

In diet samples, we found that Coleopterans, spiders (Araneae), Hymenopterans (other than ants), Lepidoptera larvae, and ants (Formicidae) were the most common prey, comprising 62%–71% of all food items (Fig. 3). The relative importance of individual arthropod groups generally corresponded with their relative abundance on tree saplings, with a few exceptions, for example, ants and cockroaches were more abundant on tree saplings than in food samples (Fig. 3). More importantly, composition of prey items in diet samples from the continuous forest and fragments did not differ for any bird species ($\chi^2 < 7.2$, $P > 0.21$; Fig. 3). With one exception, that is, the number of items per

sample decreased with fragment size for Ochre-collared Monarchs, the average number of prey items/diet sample did not differ among sites (Fig. 4).

The number of arthropods per centimeter square of leaf area ($F_{3,36} = 1.2$, $P = 0.33$) and average body length of arthropods (e.g., Araneae, $F_{3,360} = 1.2$, $P = 0.31$; Lepidoptera larvae, $F_{3,111} = 0.2$, $P = 0.81$; Coleoptera, $F_{3,452} = 1.0$, $P = 0.37$) did not vary among sites. Similarly, we found no difference among sites in either the number of butterflies observed along transects ($\chi^2_3 = 6.7$, $P = 0.083$) or ant abundance ($F_{3,19} = 1.0$, $P = 0.40$).

We found no differences in microclimates of the forest interiors among study sites. None of the measured variables (average daily temperature, $F_{3,29} = 0.8$, $P = 0.53$; average daily humidity, $F_{3,29} = 1.2$, $P = 0.32$; and daily temperature fluctuation, $H_{3,29} = 2.1$, $P = 0.34$) differed among sites.

In general, microhabitats in forest fragments differed from those in continuous forest (canopy openness, $H_{3,64} = 23.1$, $P < 0.001$; litter cover, $H_{3,64} = 17.6$, $P < 0.001$; shrub density, $H_{3,64} = 12.3$, $P = 0.006$; Fig. 5). Canopy openness in forest fragments was higher than in continuous forest (multiple comparisons of mean ranks, $P < 0.025$), resulting in a higher proportion of ground covered by grass (and ferns), less litter ($P < 0.022$; Fig. 5), and lower shrub densities ($P < 0.016$; Fig. 5). Canopy openness, litter cover, and shrub density were also more variable across individual point-count circles in the forest fragments (variance of canopy openness: 57.7–800.5; litter cover: 235.4–1229.8; shrub density: 85.2–231.9) than in continuous forest (variance of canopy openness: 18.6; litter cover: 57.2; shrub density: 48.9; Fig. 5). Along transects, the proportion of small (1–2 cm DBH) to larger (>2 cm DBH) stems was higher in the smallest fragment (33%) than in the larger fragments or continuous forest (16%–23%). Also, small stems tended to be species with larger leaves (7% small leaves, 51% mid-size leaves, and 55% large leaves within 1–2 cm DBH category in the 300-ha fragment; 22%, 28%, and 29%, respectively, in continuous forest). Leaf-size composition of larger plants did not differ among study sites.

Most bird species showed the strongest preferences for continuous forest at points with low canopy openness (~10%) and relatively high

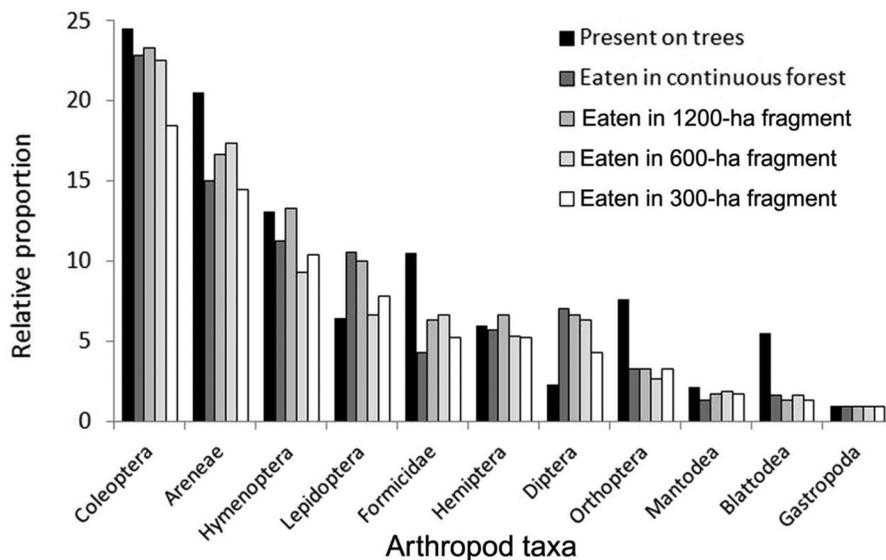


Fig. 3. Mean relative importance of main arthropod taxa present on tree saplings across study sites (we found no significant difference in number of individuals per leaf area among study sites) and in food samples collected from birds captured in mist-nets in forest fragments and continuous forest. Differences among study sites were not significant.

litter cover (~78%) and shrub densities (~25%; Fig. 5). We recorded such conditions at 87.5% of points in continuous forest. All selected species showed little tolerance for changes in canopy openness (low variance), but were found at points with variable shrub densities (Fig. 5). Although some points (18.8%–31.3% of points) in forest fragments provided such conditions, canopy openness in fragments was higher, and shrub density and the proportion of ground covered by litter were generally lower than at points where those birds were found (Fig. 5).

DISCUSSION

We found fewer bird species in forest fragments than in continuous forest, with the number of insectivorous species lowest in the 300-ha fragment, higher in both larger forest fragments (600 and 1200 ha), and highest in continuous forest. In addition, species richness of frugivores was higher in continuous forest than in all three forest fragments.

Food did not seem to limit insectivorous birds in the forest fragments in our study. Arthropod richness per leaf area was similar at all four study sites, and our examination of bird diets revealed

no significant differences among sites in either food composition or number of insects taken. Only one species (Ochre-collared Monarch) had fewer arthropods in food samples of individuals captured in smaller fragments. Although we may have underestimated more subtle specificity in food preferences because we only identified prey items to order, the lack of support for the food scarcity hypothesis in our study was in agreement with a study conducted in Costa Rica (Sekercioglu et al. 2002). In contrast, a study conducted in New South Wales (Australia) revealed that food (mainly arthropods) was significantly more abundant in larger (>400 ha) than in smaller (~55 ha) forest fragments, and this difference corresponded with differences in the abundance and reproductive performance of two insectivorous bird species (Zanette et al. 2000).

In contrast to our results and those of Sekercioglu et al. (2002), other investigators have documented both changes in community composition and differences in the abundance of invertebrates (focusing on Coleopterans, Hymenopterans, and Lepidopterans) as a result of tropical forest fragmentation (Klein 1989, Turner 1996, Didham et al. 1996). In a review

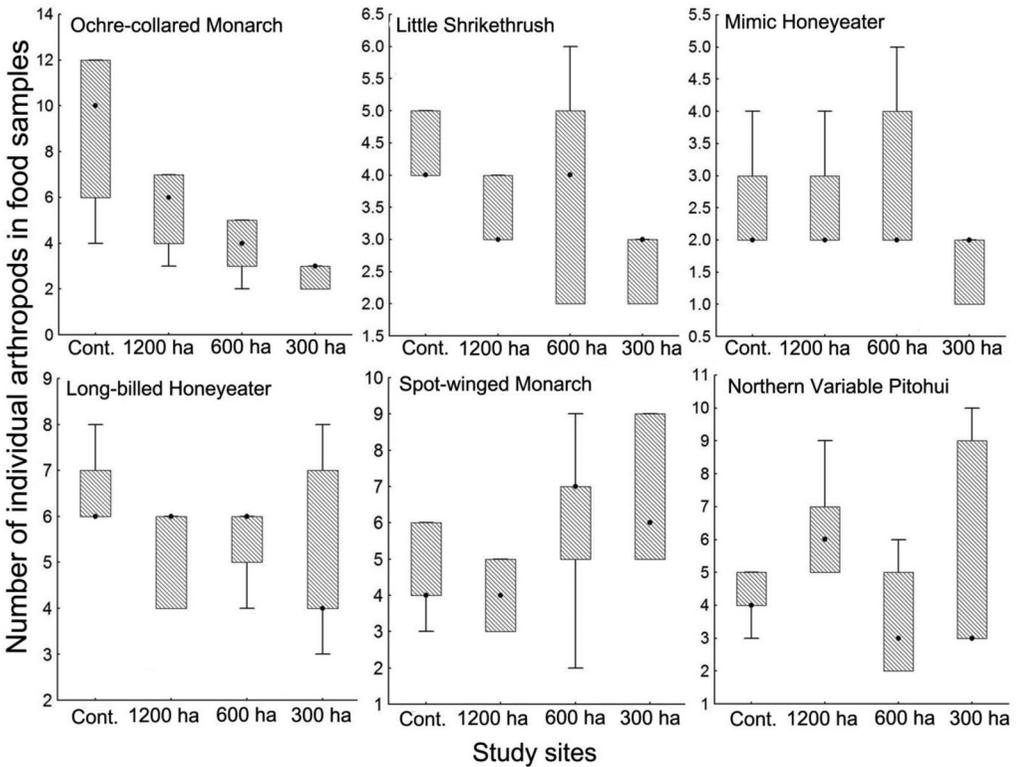


Fig. 4. Number of individual arthropods in food samples collected from six bird species in continuous forest (Cont.), 1200-ha fragment, 600-ha fragment, and 300-ha fragment. Differences among study sites in the number of arthropods in food samples were significant only for Ochre-collared Monarchs (Kruskal–Wallis; $H_{3,20} = 11.6, P = 0.008$).

of 22 studies conducted in forest fragments (range = 10–2000 ha) and continuous forest, and focusing on various groups of arthropods (Coleoptera, Lepidoptera, and termites) and birds, Turner (1996) suggested that a change in community structure and decreased abundance of invertebrates may ultimately lead to second- and higher-order effects. However, we found no differences between forest fragments and continuous forest in the number of arthropods per unit of leaf area, number of ants per tuna bait, or number of butterflies per transect. One possible explanation for our results is that our fragments were relatively large and we focused mainly on the forest interior in each fragment.

The microclimate hypothesis states that sedentary understory insectivorous birds react more unfavorably to microclimate fluctuations in forest fragments than more mobile species

frequently exposed to different microclimates. However, we found no significant differences in the microclimates of continuous forest and forest fragment interiors, as measured by data loggers placed at least 100 m from forest edges. Other studies in tropical forest fragments have revealed significant effects on microclimates up to ~100 m from edges in Manaus in central Brazil (Didham and Lawton 1999) or up to 50 m from edges in a tropical forest in New Zealand (Davies-Coley et al. 2000). Our results and those of other studies suggest that the microclimate hypothesis would likely only explain changes in bird communities in small forest fragments with a significant proportion of their area located within 100 m of forest edge.

Although most measured forest characteristics did not differ among sites in our study, 26 species of birds (i.e., 25% of species recorded only in

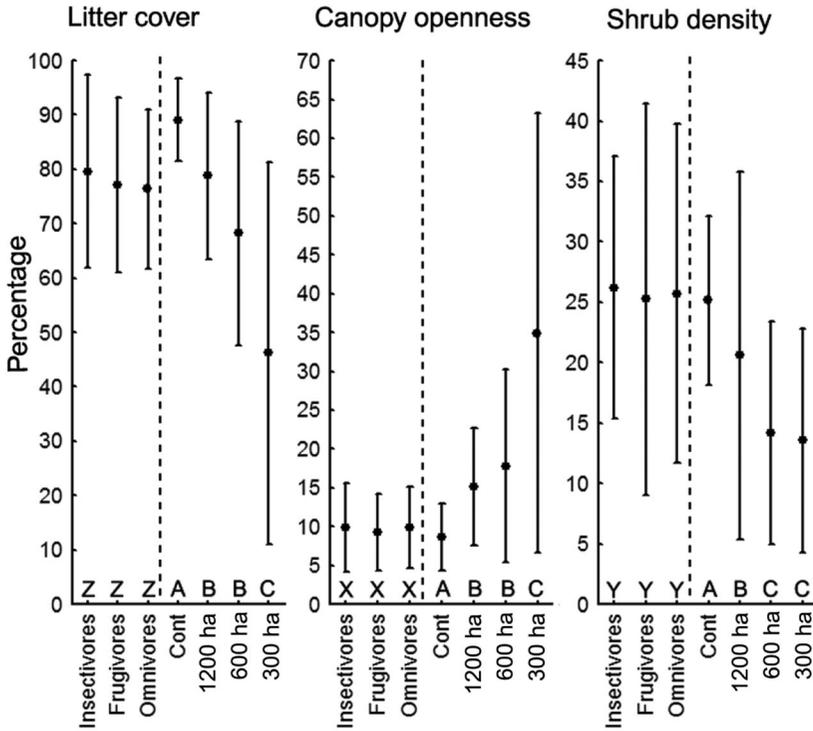


Fig. 5. Microhabitat characteristics (mean \pm SD; in percentages) at points where 19 insectivorous, nine frugivorous, and nine omnivorous birds were observed, and the mean (\pm SD) values for these variables in continuous forest (Cont), 1200-ha fragment, 600-ha fragment, and 300-ha fragment (separated by dashed line). Significant differences ($P < 0.05$; multiple comparisons of mean ranks) between microhabitats at points where a species was observed and those available in forest fragments (X, Y, and Z) are indicated as: Z = significantly different from 300-ha fragment, Y = significantly different from 300-ha and 600-ha fragments, and X = significantly different from 300-ha, 600-ha, and 1200-ha fragments. Among forest types, different letters indicate significant differences ($P < 0.05$; multiple comparisons of mean ranks).

forest fragments) in forest fragments were recorded more often at points with microhabitats similar to those in continuous forest, including a higher percentage of ground covered by litter rather than dense grass and fern cover, and low canopy openness with little light transmitted to the understory. Measured habitat variables (canopy openness, litter cover, and shrub density) were more variable in forest fragments than in continuous forest. Compared to continuous forest, the understory in the smallest forest fragment in our study also had more plant species with large leaves. Large leaves (e.g., *Pandanus* spp., *Musa* spp., and *Ficus dammaropsis*) have been found to be less attractive as foraging substrates for most (~70%) insectivorous birds in New Guinea (Bell 1969).

Species in the families *Monarchidae*, *Rhipiduridae*, and *Acanthizidae* were among those either not recorded or found in reduced numbers in forest fragments in our study. These species are sallying flycatchers and gleaners that search for prey in the low or midstory sections of forests (Storr 1958, del Hoyo et al. 1992–2011) and were found to be influenced by decreased shrub density (Sedgwick and Knopf 1992, Creagh et al. 2004, Clawges et al. 2008, Stratford and Stouffer 2013). Other insectivorous species, for example, Pittidae (*Ptilorrhoa* spp.) and Papuan Babblers (*Pomatostomus isidorei*), are dependent on forest litter (where they search for arthropods; del Hoyo et al. 1992–2011) that we found was significantly less

available in forest fragments than continuous forest.

All surveys and measurements in our study were conducted at least 100 m from forest edges, a distance believed by some investigators to control for direct edge effects (Laurance 1991, Didham 1997). Abiotic conditions (air moisture, temperature, light, and soil moisture) appear to stabilize 50–60 m (Murcia 1995) from forest edges, whereas canopy cover may be impacted at least 150 m from the edges of forest fragments (Laurance 1991). In Ontario, Burke and Nol (2000) found that a 225-ha forest fragment actually represented only 23 ha of core area (i.e., the area with abiotic conditions comparable to those of a continuous forest), and a study in northeast Queensland revealed increased canopy openness up to 500 m inside fragment margins, although the most striking changes occurred within 200 m of edges (Laurance 1991). We observed higher canopy openness and higher variance in canopy openness at points located at least 100 m from edges of forest fragments, confirming that the edge effect could influence birds deep in forest fragments and supporting previous recommendations for a 250-m distance from forest edge as buffer zones for bird point-counts (Buckland and Handel 2006).

Sekercioglu (2002) tentatively rejected the microhabitat hypothesis, and concluded that limited dispersal capabilities of insectivorous birds may be the most important factor in their sensitivity to fragmentation. However, Sekercioglu (2002) studied dispersal across cleared areas, whereas our study sites were surrounded by secondary growth or plantations and not by cleared areas. New Guinean birds can generally be considered sedentary with limited dispersal abilities (Diamond 1973), but we were not able to test the limited dispersal hypothesis. Our observations in surrounding secondary forests (3 km from fragments) suggest that at least 36 bird species observed in forest fragments and continuous forest were using (e.g., foraging) less suitable habitats, confirming that those bird species are able to use and move through highly fragmented landscapes (Tvardikova, unpubl. data).

We found that species richness of frugivorous birds was higher in continuous forest than in forest fragments. Relative to insectivores, frugivores generally are more mobile (Levey and Stiles 1992), sometimes making daily flights > 10 km

(Holbrook et al. 2002) following food resources across large areas. Large frugivores (>40 cm) in our study, that is, Northern Cassowaries, Victoria Crowned Pigeons, Blyth's Hornbills, and Collared Brush turkeys, depend on spatially and temporally patchy keystone fruits (Kattan et al. 1994) and may have been missing from our forest fragments due to regular seasonal movements (Loiselle and Blake 1990, Levey and Stiles 1992). In contrast to large frugivores, small canopy frugivores (<22 cm, i.e., many *Ptilinopus* spp. in our study) tend to be habitat generalists and depend on small, carbohydrate-rich fruits abundant in gaps and along edges (Kattan et al. 1994). Thus, small frugivores are less likely to be influenced by forest fragmentation than large frugivores (Kattan et al. 1994).

Human hunting of medium- (23–39 cm body length) and large- (>40 cm body length) bodied birds cannot be excluded as another possible explanation for their absence in forest fragments in our study because some villagers hunt them on the borders of protected areas or even circumvent the ban (K. Sam, pers. observ.). For example, Victoria Crowned Pigeons, Northern Cassowaries, *Ducula* spp., *Talegalla* spp. (large-bodied birds), and *Ptilinopus* spp. (medium-bodied birds) are known to be hunted in Madang lowlands as a source of protein (K. Sam, pers. observ.).

The size of the forest fragments in our study may also explain the absence of large frugivores. The mean home range of adult cassowaries is ~206–213 ha (Moore 2007), male megapodes have home ranges of ~100 ha (Booth 1987), and large, canopy frugivores, such as hornbills and fruit pigeons (*Ducula* spp. and *Ptilinopus* pp.), are known or suspected (based on radio-telemetry and banding data) to have home ranges of >100 ha (Corlett 2009). These species of large frugivores can incorporate both primary and secondary forests within their ranges (Corlett 2009), but ranges are limited by the presence of suitable nest sites (e.g., nest cavities in old trees) and by food availability, which is usually higher in primary forest (Asia, Kitamura et al. 1994; South America, Parry et al. 2007). Declines in populations of large-bodied frugivores in forest fragments have been reported in New Zealand (Wotton and Kelly 2012) and Colombia (Kattan et al. 1994), whereas other investigators reported no significant changes in this guild in forest fragments on the Pacific coast

of Mexico (MacGregor-Fors and Schondube 2011). These conflicting results could be due to the fact that many fragments studied by MacGregor-Fors and Schondube (2011) were in areas formerly covered by semideciduous forest, a highly endangered habitat at the regional level and important for many wildlife species during the dry season when water and other resources are limited (Renton 2001).

Papua New Guinea is one of the few countries where customary ownership of land (85%) is recognized by legislation (Sekhran 1997, West 2006, Shearman et al. 2008). Fragmented tribal ownership of land makes conservation of large areas of rainforest difficult, and the current national protected-area system consists of 34 wildlife management areas (2.8% of total land area). Thirty-two of these officially protected areas have experienced a 23% decline in forest cover; only two relatively inaccessible management areas have experienced little forest loss (2%–3% from 1972 to 2011, Shearman et al. 2008). This loss of rainforest illustrates that management of officially protected areas has not been taken seriously by the government of Papua New Guinea (Shearman et al. 2008). However, many communities preserve smaller forest fragments, typically from 100 to 1000 ha, as sources of medicine or other forest products (e.g., our 600-ha and 1200-ha fragments) or possible commercial use, such as ecotourism (e.g., our 300-ha fragment; Novotny 2010). These forest fragments (~300–1000 ha) can be maintained for long periods of time even when not financially profitable, particularly if they represent a small percentage of the land owned by a community (Ancrenaz et al. 2007, Novotny 2010). As such, these forest fragments can be an important component of management strategies to conserve rainforests in Papua New Guinea. Our results suggest that forests fragments larger than 300 ha can support relatively large numbers of birds. However, forest fragments larger than the largest fragment in our study (1200 ha) would be needed to maintain a larger proportion of native forest birds. For community-based conservation efforts to succeed in perpetuity, NGOs or governments should provide incentives for communities to conserve forest fragments, for example, assistance in launching new businesses, such as ecotourism lodges, that would allow villagers to generate profits. Another alternative would be to provide a combination of service

delivery (e.g., education, medical help, and roads), conservation-linked employment (e.g., forest guides and research assistants), and direct cash payments for conservation. The latter is somewhat controversial with many NGOs, but emulates royalty payments given to forest owners by logging companies often competing for the same forest (Novotny 2010).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. List of bird species recorded at all sites during all surveys, their scientific and English names, authority, and information on habitat requirements, trophic strategies, and feeding guild (Ca, carnivores; Omn, omnivores; Fr, frugivores; In, insectivores; and Ne, nectarivores). Raptors, swifts, and nonforest bird species passing through sites were excluded from analyses and are marked with an asterisk.

Fig. S1. Microhabitat characteristics (mean \pm SD; in percentages) of points where 19 insectivorous, nine frugivorous, and nine omnivorous birds were observed, and the mean (\pm SD) values for these variables in continuous forest (Cont.), 1200-ha fragment, 600-ha fragment, and 300-ha fragment (separated by interrupted line). Significant differences ($P < 0.05$; multiple comparisons of mean ranks) between microhabitats at points where

a species was observed and those available in forest fragments (X, Y, and Z) are shown as: Z = significantly different from 300-ha fragment, Y = significantly different from 300-ha and 600-ha fragments, and X = significantly different from 300-ha, 600-ha, and 1200-ha

fragments. Significant differences ($P < 0.05$; multiple comparisons of mean ranks) between forest types are marked by letters a, b, and c. Bird codes are formed by first four letters of genus and first four letters of species name (see Table S1 for list of names).