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Long-term effects of fragmentation and fragment properties on bird species richness in Hawaiian forests

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ABSTRACT

Forest fragmentation is a common disturbance affecting biological diversity, yet the impacts of fragmentation on many forest processes remain poorly understood. Forest restoration is likely to be more successful when it proceeds with an understanding of how native and exotic vertebrates utilize forest patches of different size. We used a system of forest fragments isolated by volcanic activity 153 years ago in Hawaii to examine how long-term fragmentation, as well as fragment size and structural features affect the richness of native and exotic bird species. The total number of bird species increased rapidly with forest fragment size, with most of the native species pool found in patches <3 ha. Smaller fragments were dominated by native bird species with several exotic bird species found only in the largest fragments, suggesting that exotic bird species in this landscape show greater area-sensitivity than native species. We used airborne scanning light detection and ranging (LiDAR) to assess whether fragment area was correlated with estimates of fragment vegetation volume as well as measures of tree height. Fragment area was highly correlated with vegetation volume, maximum tree height, and canopy height heterogeneity, and these variables were strong predictors of bird richness, demonstrating that remote sensing can provide key insights into the relationship between fragment structural attributes and biodiversity indicators. Overall, this work demonstrates the value of conserving small remnant mid-elevation forest patches for native birds in Hawaii. This work also provides insight into how newly created forest patches might be used by native and exotic bird species in Hawaii.

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1. Introduction

One of the great challenges facing conservation science is to understand how fragmentation alters community structure and long-term population viability (Laurance and Peres, 2006; Broadbent et al., 2008). Although native Hawaiian species face numerous threats including introduced species and disease, a greater understanding of how native vs. exotic species respond to fragmentation could aid conservation by informing forest restoration. This challenge is particularly severe in Hawaii, where conversion of native forest to agriculture or pasture has restricted native flora and fauna to forests between 1000 and 2000 m elevation. These land-use changes along with invasive species and introduced diseases have

contributed to the endangerment and extinction of many endemic species in Hawaii (Scott et al., 2001). Of at least 113 endemic bird species including 59 honeycreepers (subfamily Drepanidinae; James, 2004), 71 species are considered extinct and 31 (29 species and two sub-species) are Federally endangered (Scott et al., 2001; Leonard, 2008). Many Hawaiian bird species are listed by the International Union for the Conservation of Nature (IUCN) as Endangered (EN), Critically Endangered (CR) or Vulnerable (VU) (Birdlife International, 2009).

Despite the pervasiveness of fragmentation in Hawaii and elsewhere, few simplified model systems exist for examining fragmentation effects on species (Ewers and Didham, 2006; Ferraz et al., 2007). Such simplified model systems facilitate understanding by providing a tractable, compact system for examining patterns and processes that occur at larger scales but where other confounding factors can complicate interpretation. As with all model

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systems, caution must be taken when extrapolating findings to more complex systems. Our model system may be particularly useful for understanding the influence of restored forest patch size on bird use, especially for species of conservation concern, which remains largely unknown. Such information would give predictive power to forest restoration plans and could allow planners to tailor the size and spatial arrangement of forest patches in ways that favor colonization and use by native communities.

Our kipuka model field system has relevance to tropical forests broadly, because much of the tropics have undergone extensive fragmentation as a result of land-use. Further, in limited situations, fragmented areas are undergoing the reverse process following restoration activities. The kipuka field system also has relevance to conservation efforts in Hawaii where avian malaria will likely move up slope – restricting native birds to elevations where forests are far more fragmented than the current habitat boundaries. The Hakalau National Wildlife Refuge and Mauna kea Forest Reserve are highly relevant examples of how restoration in Hawaii can facilitate recovery of highly fragmented forests with the goal of supporting re-colonization of a high elevation land-base by native birds (Scowcroft and Conrad, 1988; Scowcroft and Jeffrey, 1999).

Early fragmentation studies relied on island biogeography theory (IBGT; MacArthur and Wilson, 1967) to anticipate the potential effects of fragmentation on plants and animals. However, IBGT has proven to be overly simplistic for understanding fragmentation effects on biota (Ewers and Didham, 2006; Laurance, 2008). For example, IBGT assumes that fragments behave as true islands, but fragmentation studies have shown that fragmentation effects are highly dependent on the species of concern, meta-population dynamics, ecosystem type and matrix utilization (Lawler, 1986; Hanski, 1997; Brown and Lomolino, 1998; Fagan et al., 1999; Gascon et al., 1999; Schoener et al., 2001; Long et al., 2009).

Recent studies have incorporated landscape ecology and meta-population theory into studies of fragmentation to address such factors such as fragment shape complexity and matrix condition. However, understanding the influence of forest fragmentation on biota can be confounded by factors that are difficult to quantify (Laurance, 2008). The following factors reviewed in Ewers and Didham (2006) present important challenges for current and future fragmentation studies: (i) short period of study relative to the time lag prior to species loss; (ii) complex and dynamic matrix effects, which exert a sometimes over-riding influence on the isolation of fragments and which often vary by species; (iii) non-random process of human-mediated fragmentation across landscapes, because humans often convert one area from native condition to agricul-

ture for reasons that relate to soil fertility, access, ease of conversion, ownership, etc., and so residual native vegetation may have properties that differ fundamentally from what had been the surrounding native landscape; and (iv) fragmentation rarely occurs as an isolated human-mediated disturbance event, but rather following human fragmentation, fragments are exposed to continued land-use pressures, and so studies of such systems actually document the impacts of continuous disturbance in addition to the initial fragmentation event.

Field systems containing long isolated fragments are of particular value as are new tools for quickly quantifying fragment characteristics. On the Island of Hawaii, active volcanoes periodically send meandering fingers of lava down their slopes into large blocks of continuous forest, leaving behind forest fragments of various sizes (Fig. 1), which are termed *kipuka* (in Hawaiian, “s” is not used to denote plural). Forests on Mauna Loa Volcano (4169 m) have experienced this type of disturbance for at least 400,000 years, and over 600 lava flows have been mapped and dated using ^{14}C and historical records (Lockwood et al., 1988; Carson and Clague, 1995). The resulting *kipuka* have been used to study the ecology of plants and insects (Aplet and Vitousek, 1994; Kitayama et al., 1995; Aplet et al., 1998; Morden and Loeffler, 1999; Vandergast and Gillespie, 2004), but they have not been used to examine fragmentation effects on birds.

We selected a subset of these forest *kipuka*, isolated in 1855 by a single large event, and two nearby continuous forests serving as unfragmented controls to use as a system for examining the sensitivity of a mixed native and exotic montane bird community to variation in forest fragment size and fragment structural features (Fig. 2). Across these *kipuka*, soils are uniform and all sufficiently old (3000–5000 years) to establish mature ohia (*Metrosideros polymorpha*) dominated montane wet forest (Vitousek, 2004). The combination of similarly aged soils within *kipuka* and a single-aged flow creating the matrix surrounding the *kipuka*, resulted in the long-term isolation of fragments characterized by a simple, species-poor tree and shrub flora. We used this landscape to test the hypothesis that native and exotic bird species richness increases as *kipuka* size increases. Because birds are generally good dispersers relative to other vertebrates, we expected that patterns of *kipuka* use would reflect primarily bird choice.

One additional weakness of previous fragmentation studies is reliance on fragment area as a measure of fragment capacity to support biodiversity. In the case of birds, two-dimensional fragment area provides a weak biological explanation for changes in



Fig. 1. Image of a Hawaiian forest fragment also known as a *kipuka* isolated in 1855 by lava flow on NE slope of Mauna Loa Volcano on the Big Island of Hawaii. This *kipuka* occurs within a field system of *kipuka* that range widely in size. Plant species composition, soil substrate age within *kipuka*, and matrix age surrounding *kipuka* are all similar across *kipuka*. (Photo: Colin Olito).

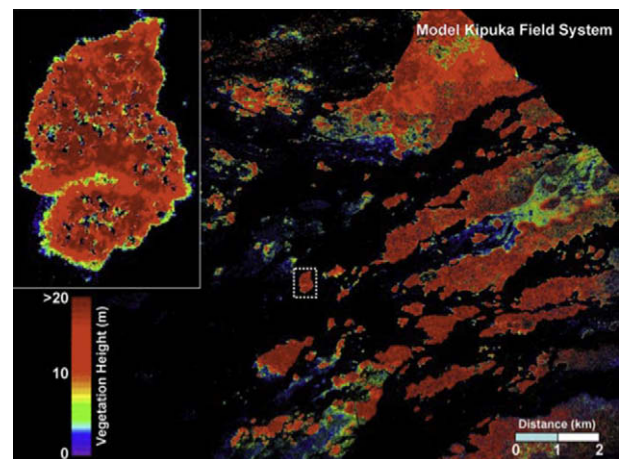


Fig. 2. Airborne CAO-LiDAR image from a January 2008 flight showing vegetation height for more than 100 *kipuka* in our *kipuka* field system on the Island of Hawaii. Inset shows one example *kipuka* of roughly 25 ha.

diversity because it is the three-dimensional features of a habitat that often influence avian composition and richness (Cody, 1985; Goetz et al., 2007). These features may include forest composition, vegetation density, and habitat architectural diversity, but such features are not easily sampled across landscapes and then related to avian habitat area (Power, 1976; Opdam et al., 1985; Kohn and Walsh, 1994). Habitat diversity remains difficult to define without making assumptions about how it is perceived by focal taxa (Simberloff, 1976). To partially address these issues, we used airborne Light Detection and Ranging (LiDAR) to estimate the three-dimensional structural features of forest canopies to identify those features most important to bird species richness.

LiDAR is a technology mostly flown on small aircraft that can penetrate vegetation layers using a laser (reviewed by Lefsky et al., 2002). LiDAR has now been used to measure the three-dimensional structure of forests for the particular purpose of avian habitat and diversity analysis (Clawges et al., 2007; Goetz et al., 2007; Vierling et al., 2008). Moreover, the utility of LiDAR for quantifying vegetation composition and structure in Hawaiian forests has recently been demonstrated (Boelman et al., 2007; Asner et al., 2008). We therefore used an airborne LiDAR to test hypotheses that *kipuka* volume and *kipuka* structural complexity are robust predictors of species richness, and so provide a mechanistic underpinning to species–area relationships. While area and complexity may be correlated, we predicted that complexity saturates relatively quickly with respect to changes in *kipuka* area. Our objective is to identify patterns of forest fragment use by an imperiled community of birds and to use newly developed remote sensing tools to compare classic species–area relationships with more fine grained vegetation characteristics.

2. Materials and methods

2.1. Study area

Our study took place within a network of *kipuka* ranging from ~0.1 to 56 ha and nearby tracts (>1000 ha) of continuous forest located on Hawaii Island on the NE slope of Mauna Loa Volcano (Fig. 1; range of coordinates: 19°40′01″N and 155°20′56″; altitudinal range: 1470–1714 m). All *kipuka* were ≥0.5 km from continuous forest. The slope in this area is gentle, with a 214 m rise over a 4.3 km run. These *kipuka* are within the State of Hawaii Forest Reserve System, so they have remained largely undisturbed by people since isolation in 1855. Introduced bird, mammal, and arthropod species however are present within the *kipuka* and the surrounding matrix. The 1855 lava matrix surrounding the *kipuka* is a rough-textured patchwork of undulating mounds of pahoehoe lava and loose clinker-like rubble fields of a'a lava. This matrix is extremely porous with little standing water even after heavy rains. The plant community growing in the lava outside of the *kipuka* is much sparser, of a lower stature, and clearly distinguishable from the larger stature, closed-canopy of the *kipuka* forest (Figs. 1 and 2).

Because the *kipuka* were spared when lava flowed around them, the soils, vegetation, and microclimate within a *kipuka* differ dramatically from the surrounding lava matrix. *Kipuka* are cooler, moister, and contain dark brown histosol soils (Raich et al., 1997). Overall, canopy tree diversity is similar to other Big Island forests and is very low compared with other tropical regions. Consistent year-round trade winds from the NE generate orographic precipitation that supports relatively species poor mesic forests dominated by the native Hawaiian species ohia (Myrtaceae). With the exception of one *kipuka*, koa (*Acacia koa*; Fabaceae) was uncommon or absent. Across *kipuka*, the mid-canopy was dominated by olapa (*Cheirodendron trigynum*), pilo (*Coprosma montana*), kolea (*Myrsine lessertiana*), kawau (*Ilex anomala*) and the tree fern hapuu

(*Cibotium glaucum*) – all Hawaiian endemic species. Exotic plant species were almost entirely absent from all but the koa dominated *kipuka*, which had a moderate cover of exotic grasses in the understory. Rooting by pigs (*Sus scrofa*) and understory browse by mouflon-domestic sheep hybrids (*Ovis aries*), both exotic to Hawaii (Giffin, 1982), was apparent but low across *kipuka*, but heavier in continuous forest. Exceptions included a pair of smaller *kipuka* surrounded almost entirely by a'a type lava, which reduced access to the *kipuka* by ungulates. In addition to exotic bird species, discussed later, the non-native roof rat (*Rattus rattus*) was documented in nearly all *kipuka*. Hawaiian forests at this altitude are thought to be above the range of the mosquitoes that serve as vectors for avian malaria (*Plasmodium relictum*) (Scott et al., 2001) which has contributed to the extirpation of many endemic birds from lower elevations.

2.2. Vegetation sampling

Vegetation composition for each *kipuka* was sampled using belt transects (6 m × 75 m). For smaller *kipuka*, transect length equaled the long axis of the *kipuka*. For larger *kipuka*, the approximate center was identified, and a randomly selected bearing was used to orient transects out of the *kipuka*. All stems >2 cm were measured for diameter at breast height (DBH) and species recorded. Basal area was calculated by species on a per-hectare basis.

We used the Carnegie Airborne Observatory (CAO; Asner et al., 2007) to map the *kipuka* field system using LiDAR (Fig. 2). The CAO-LiDAR was operated at 50 kHz, with a maximum half-scan angle of 17 (after 2-degree cutoff) degree and 35–40% overlap between adjacent flightlines. The LiDAR point cloud data were analyzed using a physical model that was used to derive surface (top-of-canopy) and ground digital elevation models (DEM). Vegetation height was then estimated by differencing the surface and ground surface DEM (Lefsky et al., 2002). Vertical errors in ground heights and vegetation heights were previously estimated to be 0.12 m (s.e. = 0.14 m) and 0.7 m (s.e. = 0.2 m), respectively (Asner et al., 2007, 2008). *Kipuka* volume was estimated by multiplying the height of the vegetation by the area of each pixel (here, 1.2 × 1.2 m), and then summing across all pixels. *Kipuka* area was estimated using remote sensing from an airplane-based LiDAR flyover.

2.3. Bird species sampling

We surveyed birds by systematically searching forest habitat using a timed species count and recording all birds seen or heard (Bibby et al., 2000). All forests were visited during two seasonal periods (winter: December 2006–January 2007, December 2007; and summer: June 2007), and all forests were visited twice during each of the two seasonal periods for a total of four visits per *kipuka*. All bird surveys were conducted from 30 min after sunrise until 11:00 am, and were done under weather conditions of no rain to light mist. Surveys were done by a single observer (Flaspohler) walking along a compass bearing through the center of each *kipuka*, stopping frequently to look and listen for birds (>80% of all bird detections were confirmed by sight). Only birds that perched within the forest being surveyed were included (flyovers were noted but were not included in analyses). All *kipuka* were surveyed for approximately 30 min during each visit. The smaller *kipuka* could be surveyed completely in this time while the larger *kipuka* and continuous forests were partially searched at each visit. The timing of bird surveys alternated between early and late morning so that all *kipuka* were searched during both portions of the morning. Estimates of bird species richness should be viewed as indices, especially for larger *kipuka* and continuous forests for which the actual species pool was likely larger. Observations were made of

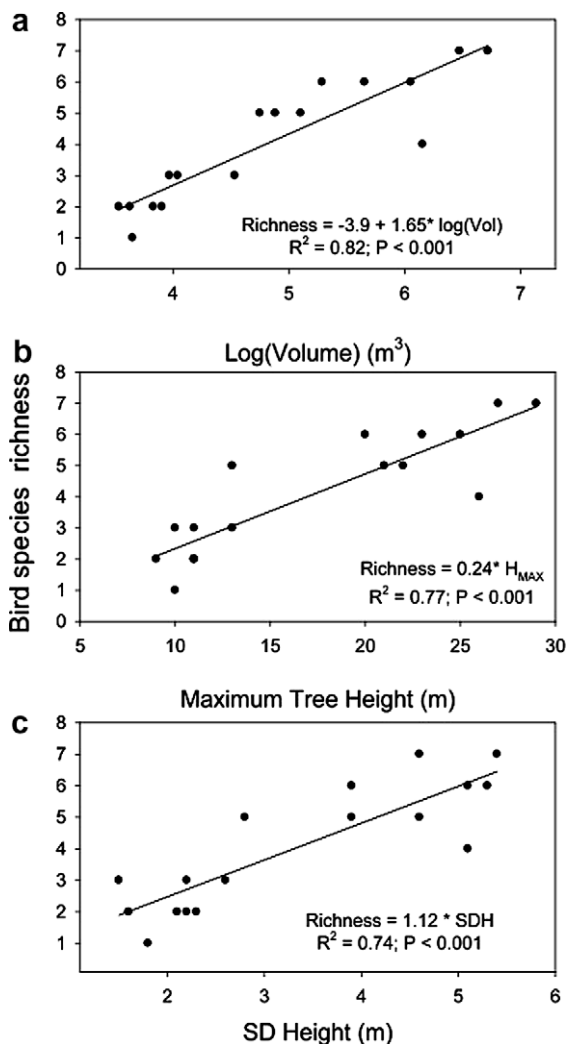


Fig. 3. Nonlinear regression relating LiDAR-based estimates of *kipuka* area with vegetation volume (a), maximum tree height within a *kipuka* (b), or standard deviation of maximum tree height per pixel within each *kipuka* (c).

perched or flying birds seen or heard in the lava matrix outside of the *kipuka* as the observer walked between *kipuka*.

Species–area relationships were expressed on a conventional log–log scale to allow comparison of slopes (Connor and McCoy, 1979; Sax and Gaines, 2006). We used simple nonlinear regression to compare vegetation characteristics from LiDAR to bird species

richness estimates. Logistic regression was used to test whether *kipuka* area was a significant predictor of the dichotomous presence-absence dependent variable of bird occurrence in a *kipuka*.

3. Results

3.1. Vegetation composition, basal area and volume

Ohia comprised >90% of the basal area in all transects except *kipuka* 16 where koa made up the majority of total basal area. In contrast to species composition, total basal area of transects was more variable across the *kipuka*. Ohia basal area in all of that non-koa *kipuka* ranged from just over 20 m²/ha to over 120 m²/ha, compared with 25 m²/ha for the intact forest. Remaining values for ohia basal area fell between 30 and 54 m²/ha. Other tree species included: olapa (0–1.5 m²/ha; 1.7 m²/ha in the intact forest); kolea (0–23 m²/ha; 1.4 m²/ha in the intact forest); pilo (0–2.0 m²/ha; 0.9 m²/ha in the intact forest); and kawau (0–1.6 m²/ha; 1.3 m²/ha in the intact forest). Few non-native woody species were encountered and none were present in any abundance in the shrub, sub-canopy, or canopy layer. Our transect approach sampled only a small portion of the larger *kipuka*, and so inevitably missed less common species. Our transect through *kipuka* 16 varied from the other *kipuka* and intact forest, with 25 m²/ha of koa basal area but just 8.7 m²/ha of ohia basal area.

Kipuka volume was strongly related to *kipuka* area (Volume = 10.5 × 10⁴ × area; r² = 0.86; p < 0.001), and ranged from just under 5000 to over 5,000,000 m³ (Fig. 3a). Maximum tree height was also related to *kipuka* area (H_{MAX} = 16.5 × area^{0.15}; r² = 0.75; p < 0.001), and ranged from 9 to 29 m (Fig 3b). There was a weaker relationship between standard deviation of maximum tree height per pixel and area (Fig 3c). While larger *kipuka* generally supported the largest trees, *kipuka* area was only weakly related to mean vegetation height (r² = 0.37), which ranged from 5 to 15 m.

3.2. Birds

The potential bird community composition on Hawaii Island is small (~14 species) relative to continental tropical ecosystems (see Table 1 for scientific names). The richest bird assemblage that we observed contained 10 species and was found in the continuous forest. Consistent with the species–area hypothesis, we observed a decline in bird species richness with declining *kipuka* area with as few as two species in the smaller *kipuka* (Table 2). We found little variation in seasonal patterns of species richness, with summer and winter surveys detecting almost identical bird communities.

Table 1

Common (from the American Ornithologists' Union [AOU]), scientific and code names for birds found using *kipuka* and continuous forests on NE slope of Mauna Loa, Big Island, Hawaii.

AOU code	Common name/HI name	Scientific name	Origin: N-native E-exotic	Vagility within lava matrix ^a	Primary/secondary diet
APAN	Apapane	<i>Himatione sanguinea</i>	N	High	Nectar
HAAM	Hawaii amakihi	<i>Hemignathus virens</i>	N	High	Arthropod
OMAO	Omao	<i>Myadestes obscurus</i>	N	Low	Fruit
IWI	liwi	<i>Vestiaria coccinea</i>	N	High	Nectar
ELEP	Elepaio	<i>Chasiempis sandwichensis</i>	N	Low	Arthropod
HAHW	Hawaiian hawk/lo	<i>Buteo solitarius</i>	N	High	Carnivore
JAWE	Japanese White-eye	<i>Zosterops japonicus</i>	E	High	Arthropod/nectar
HOFI	House finch	<i>Carpodacus mexicanus</i>	E	High	Seeds/arthropod
RBLE	Red-billed leiothrix	<i>Leiothrix lutea</i>	E	Low	Seeds/arthropod/fruit
MELT	Melodious laughing thrush/hwamei	<i>Garrulax canorus</i>	E	Unknown	Seeds/arthropod
KAPH	Kalij pheasant	<i>Lophura leucomelanos</i>	E	Unknown	Seeds/arthropod

^a Species with high vagility were seen frequently (>10 times during this study) outside the *kipuka* and flying between *kipuka*; species with low vagility never were seen flying outside of the *kipuka*; species with medium vagility were seen rarely (<10 times) flying or walking outside of the *kipuka*.

Table 2
Bird species detected in *kipuka* and continuous forests, with forest area. Bird codes in italics are not native to Hawaii. *Kipuka* are listed in ascending order including continuous forest.

<i>Kipuka</i>	Area (ha)	Total species	Bird species code											
			APAN	HAAM	OMAO	IIWI	JAWE	ELEP	HOFI	RBLE	MELT	KAPH	HWAH	
K4	0.07	2	X		X									
K1	0.07	3	X	X	X									
K11	0.09	2	X					X						
K13	0.13	3	X	X	X									
K2	0.13	4	X		X	X	X	X						
K17	0.17	2	X	X										
K12	0.19	3	X	X	X									
K9	0.57	5	X	X	X	X	X	X						
K14	0.59	3	X	X		X								
K6	1.22	5	X	X	X	X	X	X						
K10	1.7	5	X	X	X	X	X	X						
K3	2.18	6	X	X	X	X	X	X	X					
K15	3.18	6	X	X	X	X	X	X	X					
K5	9.28	5	X	X	X	X	X	X						
K7	18.54	6	X	X	X	X	X		X					
K8	35.55	7	X	X	X	X	X	X	X					
K16	38.64	8	X	X	X	X	X	X	X	X				
K18	55.7	9	X	X	X	X	X	X	X	X	X			X
Contig.	NA	10	X	X	X	X	X	X	X	X	X	X		X

3.3. Native and exotic species

Five of the six most frequently encountered bird species were native Hawaiian species, suggesting that the *kipuka* continue to support populations of native birds despite the loss of many native Hawaiian birds from these forests over the past 200 years. Although we did not quantify relative abundance, the nectar-feeding honeycreeper apapane was by far the most commonly encountered. The Hawaii amakihi and omao were both found in 16 of 19 surveyed forests including some of the smallest (<0.5 ha) *kipuka*. The apapane and Hawaii amakihi were frequently seen foraging in and flying over the lava matrix between *kipuka*. The o'mao, though common in many *kipuka*, was never detected outside of the *kipuka*. The i'iwi was detected in 13 of 19 forests but was detected only once in the smaller *kipuka*. Although i'iwi were occasionally seen flying across the lava matrix, it appears to do so less frequently than the apapane and Hawaii amakihi. The Hawaii elepaio was found in 6 of 19 forests – all of which were >2.2 ha. The only native non-passerine detected, the Hawaiian hawk, was found only in the largest *kipuka* and the continuous forest. Of the 11 species encountered during this study, five were non-native (Table 1). With the exception of the Japanese white-eye, a very abundant passerine, exotic birds were rare in all but the large *kipuka* (>18.5 ha) and intact forest. The white-eye was frequently seen flying within nearly all *kipuka*, as well as flying over the matrix between *kipuka*.

3.4. Species–vegetation relationships

As hypothesized, bird species richness (native plus exotic) was strongly correlated with *kipuka* area (Fig. 4a; $r^2 = 0.83$; slope = 0.18). The relationship between patch size and species richness was weaker though significant ($p < 0.05$) for both native (Fig. 4b; $r^2 = 0.06$; slope = 0.03) and exotic species ($r^2 = 0.11$; slope = 0.07). The slope of the species–area relationship was steeper for exotic bird species. As forest patch size increased, exotic bird species were added to the community more rapidly than native species, suggesting stronger area-sensitivity for exotic compared with native species. As a consequence, non-native bird species comprised a larger proportion of the bird community in large forest patches compared to small forest patches (Fig. 5). We note that *kipuka* 16 was the most isolated of our *kipuka*, but diver-

sity was identical to similarly sized but less isolated – and less degraded- *kipuka*. In fact, *kipuka* 16 was had more bird species than any other in this study.

A simple dichotomous logistic regression of area vs. species occurrence (based on Table 2) showed that *kipuka* area was a significant predictor of species occurrence for the Hawaii elepaio (log-likelihood = -6.47 , $n = 19$, $p = 0.052$). Area did not significantly predict the occurrence of the Hawaii amakihi (log-likelihood = -3.87 , $n = 19$, $p = 0.24$), o'mao (log-likelihood = -6.26 , $n = 19$, $p = 0.37$), i'iwi (log-likelihood = -2.93 , $n = 19$, $p = 0.27$), Japanese white-eye (log-likelihood = -5.85 , $n = 19$, $p = 0.16$), or house finch (log-likelihood = -7.68 , $n = 19$, $p = 0.26$). There was insufficient variation in the data to test for area effects on occurrence for the apapane, Kalij pheasant, Hawaiian hawk, red-billed leothrix and melodious laughing thrush. The logistic function for three native and two exotic bird species for which sufficient data and variation were available showed an abrupt rise in occurrence for the i'iwi, o'mao, and Japanese white-eye, the absence of the red-billed leothrix in all but the largest *kipuka*, and a more gradual increase in occurrence for the Hawaii elepaio.

The strongest vegetation-based predictors of bird species richness were *kipuka* vegetation volume (Fig. 6a; $r^2 = 0.78$), *kipuka* maximum tree height (Fig. 6b; $r^2 = 0.77$), and heterogeneity of tree height within a *kipuka* (Fig. 6c; $r^2 = 0.78$). In contrast, mean tree height was a weak ($r^2 = 0.33$) predictor of bird species richness. As with *kipuka* area, bird species richness increased rapidly as vegetation volume increased, then quickly slowed as forest patch sized increased and the pool of available species was exhausted. In contrast, the relationship between maximum tree height and bird richness was strongly linear.

4. Discussion

Many ecological processes are altered when contiguous habitat is fragmented into smaller patches. Our study advances understanding of fragmentation effects by addressing four critical and potentially interacting limitations of previous studies: (i) fragmentation occurred 153 years before initiation of the study – previous studies have focused on short-term (decadal) responses (e.g., Keller and Largiader, 2003; Ferraz et al., 2007), with studies longer than several decades considered to be “long-term” (Ewers and Didham,

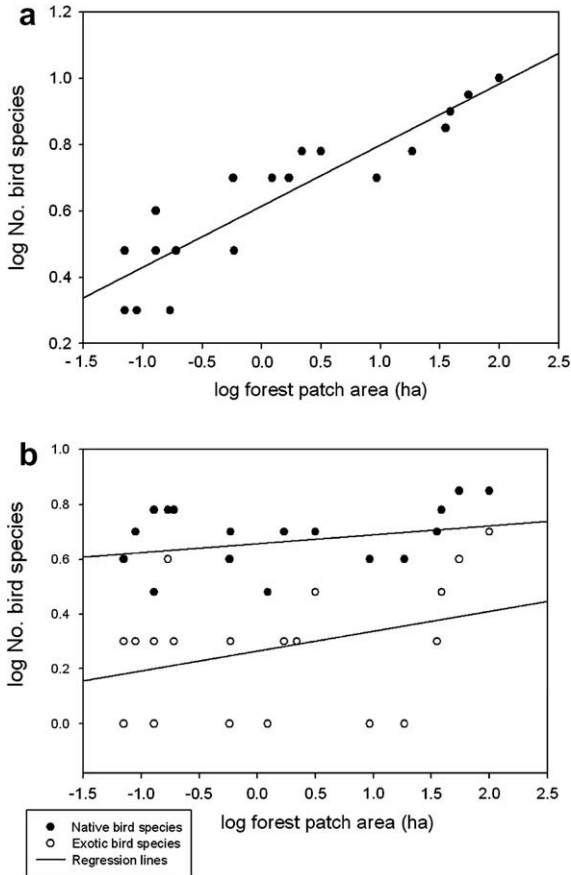


Fig. 4. Log–log plots of species–area relationship for: (a) all bird species detected in *kipuka* and continuous forest, and (b) native and exotic bird species detected in *kipuka* and continuous forest, NW slope of Mauna Loa, HI. Note steeper slope for exotic bird richness and occurrence of apparent area-sensitive native and exotic species within larger forest patches (upward jump in scatter-plots on right side of graph).

2006); (ii) fragmentation occurred as a single event through homogenous forest contained within a single life zone; (iii) primary succession is exceedingly slow in these high elevation lava fields, and so the matrix surrounding forest fragments is relatively

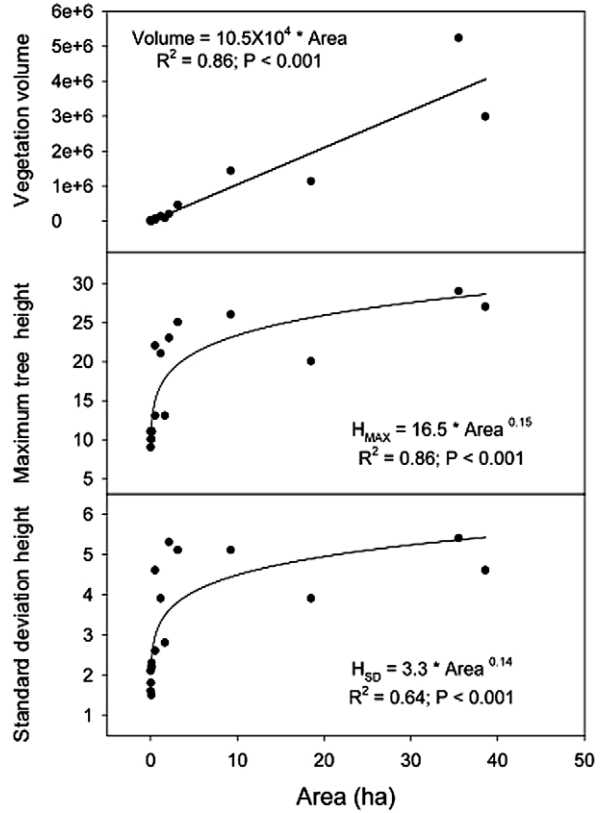


Fig. 6. Proportion of native vs. exotic birds found in three *kipuka* size classes. Pooled bird species found in *kipuka* of <10 ha were 83% native and 17% exotic. For *kipuka* >10 ha, 63% of the bird species were native, while 37% were exotic. In continuous forest, 60% were native, while 40% exotic.

stable through time; and (iv) fragments are difficult to access, have been protected within a State of Hawaii Forest Reserve, and so while several exotic species are present, people have had a minimal direct impact on forests since fragmentation. Further, this study used LiDAR-based remote sensing to move beyond two-dimensional fragment area and consider the three-dimensional features of forests that can influence plant and animal biodiversity (Goetz et al., 2007; Vierling et al., 2008).

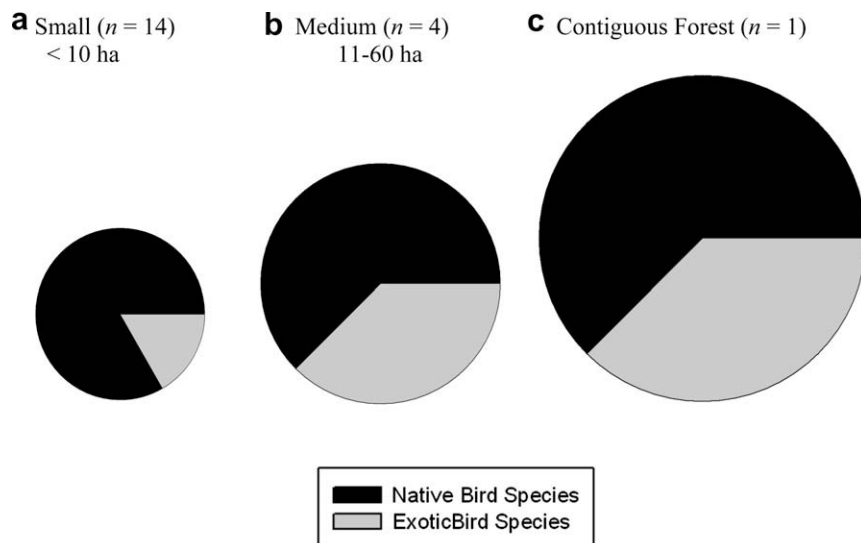


Fig. 5. Nonlinear regression relating bird species richness to LiDAR-based estimates of *kipuka* volume (a), maximum tree height within a *kipuka* (b), or standard deviation of per pixel tree height within each *kipuka* (c).

4.1. Native vs. exotic species–area curves

The slope and intercept of the log–log species–area relationship integrates several key traits of the Hawaiian bird community including: species distribution and richness, the role of dispersal limitation, and the importance of area-sensitivity (Sax and Gaines, 2006). The different species–area slopes for native and exotic birds suggest that the two groups respond to changes in forest patch size in different ways. Several studies looking across broad geographic areas including Europe have found that native species show a different relationship with area compared with exotics (Crawley, 1987; Pysek, 1998), with some exotic species showing little relationship with area (Sax and Gaines, 2006). Explanations for such deviations from classic species–area patterns include dispersal limitation of natives in a fragmented landscape and/or enhanced dispersal of exotics as a result of human activity. The autecology of each bird species clearly shapes patterns of occurrence in the landscape. Bird species known to forage over a wide range such as Apapane, Hawaii amakihi, and Japanese white-eye are inherently more likely to be found in isolated *kipuka* because their home range is large relative to more sedentary species such as the Omao, Hawaii Elepaio, and Red-billed leiothrix. Re-colonization after local extinction within a *kipuka* may take longer for more isolated *kipuka*.

For birds at the spatial scale of our study, where communities have had decades to equilibrate following forest isolation in 1855, dispersal limitations are likely minimal. However, several native Hawaiian bird species formerly known to use these mid-elevation forests are now extinct (e.g., 'o'o [*Moho nobilis*], Hawaii mamo [*Drepanis pacifica*], greater 'amakihi (*Hemignathus sagittirostris*), lesser akialoa (*Hemignathus obscurus*), Hawaiian rail [*Porzana sandwicensis*]), functionally extinct (Hawaiian crow [*Corvus hawaiiensis*], o'u [*Psittirostra psittacea*]), or are endangered and very rare (e.g., akiapolaau [*Hemignathus munroi*], Hawaii creeper [*Oreomystis mana*], Akepa [*Loxops coccineus*]). Therefore, the pre-human species–area relationship would undoubtedly shifted upward for native species alone, but nothing is known about how the extinct, pre-malaria avifauna of Hawaii would have responded to *kipuka* size.

4.2. Bird richness and structural attributes of vegetation

Habitat measures such as vegetative structural complexity are often good predictors of bird species richness, but are time consuming to gather, even as subsamples of larger habitat patches. Forest characteristics that can now be quantified across large spatial scales using LiDAR-based remote sensing may offer a superior approach to understanding structure-dependent controls in ecology and conservation biology. Increasing habitat diversity is the most straightforward and common explanation for the species–area relationships, and using LiDAR we were able to evaluate structure-based indexes of habitat complexity. In line with this hypothesis, bird species richness increased rapidly and non-linearly with both *kipuka* area and remotely-sensed vegetation volume while bird species richness increased linearly with maximum tree height. We also found a strong linear relationship between bird species richness and the standard deviation of maximum tree height per pixel within each *kipuka* (Richness = $0.63 * \text{Height} - \text{SD} + 0.79$; $r^2 = 0.74$; $p < 0.001$). These findings highlight the value of whole stand indices of fragment spatial complexity because the bird community was composed of either generalists (e.g., Hawaii amakihi, Japanese white-eye) or diet specialists (e.g., apapane, iwi) for which the key resource (flowering ohia) was common.

A comparison of the two largest *kipuka* also highlights the role of forest structure as a regulator of bird species richness. *Kipuka* 16 and *kipuka* 8 were nearly identical in area but differed with respect

to canopy and mid-story plant species, land-use history and matrix condition. *Kipuka* 16 was dominated by koa, had been heavily disturbed by grazing, was relatively isolated, had few mid-story species found in the other *kipuka*, and was surrounded by grass dominated pasture. In contrast, *Kipuka* 8, as with the other *kipuka*, was dominated by ohia, supported a diverse mid-story, was surrounded by a sparsely vegetated lava matrix, and had undergone little human disturbance. Despite the many differences, *kipuka* 8 and 16 both had similar values for maximum tree height and bird species richness (8 and 7 species respectively).

The strong correlation between bird richness and maximum vegetation height suggests that managers may be able to use remotely-sensed LiDAR data as a rapid indicator of bird diversity although we recognize that multiple features of forest structure and composition govern patterns of bird species richness. Further, the largest *kipuka* and continuous forest contain very tall trees that are not found in small and even some medium-sized *kipuka* and these influence utilization and occupancy. At least one bird species, the Hawaiian hawk, was found only in the largest forests, and is known to prefer closed-canopy forests with tall ohia trees (Clarkson and Laniawe, 2000).

Notably, biotic features apparently can over-ride structural features for certain bird species. For example, the federally endangered akiapolaau was seen in *kipuka* 16 during vegetation surveys, and strongly favors koa as a foraging substrate (Pratt et al., 2001). Similarly, oma'o, an understory fruit eating bird and a key native seed disperser for fruiting plants (Foster and Robinson, 2007), appeared to be largely insensitive to fragment structural properties or size, and was found in nearly all *kipuka*. While extirpated from much of its former low elevation range as well as from all other Hawaiian islands, this species may serve a unique role in fostering colonization of lava flows by some fruit bearing plants. The lack of area-sensitivity for oma'o may explain why *kipuka* shared similar fruit bearing native species.

4.3. Implications for forest restoration and species conservation

Tropical forest restoration has the potential to mitigate the loss of biodiversity that accompanies widespread habitat conversion. Restoration projects are nearly always constrained by resources. A clearer understanding of the benefits from projects of different size will allow planners to more accurately predict which species are likely to utilize restored habitat patches of different size, and allocate scarce resources more efficiently. Results from this study can be used to test hypotheses related to bird use of forest patch restoration. Worldwide, many areas with high rates of endemism (e.g., New Zealand, many Pacific islands, mainland parts of southern California, USA) have experienced similar rates of habitat conversion during the last 200 years and the long-term persistence of a number of endemic bird species may depend on the restoration of degraded habitat and growth in species populations. Understanding how habitat patch area influences community characteristics (e.g., species richness) is an important first step in such restoration efforts.

With climate change, it is anticipated that avian malaria will extend into higher elevations, thereby reducing critical habitat at mid-elevations (Benning et al., 2002). Therefore, restoration of potentially critical but currently degraded high elevation habitat is important for meeting conservation objectives for an entire community of rare and endemic birds, but also plants, insects and other taxa. Ecosystem processes may be restored when new patches of forest are created, including abiotic conditions such as temperature and moisture, and biotic characteristics such as species abundance, community structure, species interactions, and demographic traits such as survival and reproductive success (Murcia, 1995; Fagan et al., 1999; Flaspohler et al., 2001), but effective restoration of na-

tive forests in Hawaii will require a better understanding of how isolated forest patches function within a matrix of contrasting habitat. Certainly forest stature including canopy layering and the presence of tall mature trees is an important element that contributes to greater habitat complexity in some of the larger *kipuka*. In this restoration context, forest *kipuka* may provide information on size thresholds for afforestation projects that seek to create usable habitat for native birds.

Within a matrix of relatively young lava, even very small mid-elevation forest remnants of 3 ha or less are used by all but one native bird species, the Hawaiian hawk. These smaller forest patches also contained a larger proportion of native species than did the larger *kipuka* and the continuous forests that also attracted non-native species. Overall, the dominance of small *kipuka* by native bird species support the findings of Boelman et al. (2007) that native birds are capable of excluding or inhibiting invasion by non-native birds.

Occupancy of any restored forest by native Hawaiian birds will depend on forest altitude and may also depend on landscape considerations such as forest patch density and percent of landscape in native forest. Because we do not yet know how forest patch size influences key demographic traits such as breeding density, reproductive success, and adult and juvenile survival, we caution against extrapolating the value of tiny forest patches. However, it is possible that evolution in a dynamic volcanic landscape has given at least some species the capacity and/or proclivity to thrive in a patchwork forest landscape. Further, findings of high native bird richness for *kipuka* 16, despite relative isolation and a strong history of disturbance, indicates that recently restored patches of forest in a pasture matrix may provide adequate habitat for many native species. These patterns of habitat use, if confirmed, would be good news for restoration projects in Hawaii. Worldwide, few native bird communities have experienced more disruption and still fewer persist under such severe threats (Leonard, 2008). If the remaining native avifauna of Hawaii is to persist into the next century, mitigation of proximate threats such as introduced disease needs to be increasingly coupled with restoration of native ecosystems, especially at higher elevations.

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