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MULTI-TROPHIC INVASION RESISTANCE IN HAWAII: BIOACOUSTICS, FIELD SURVEYS, AND AIRBORNE REMOTE SENSING

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Abstract. We used airborne imaging spectroscopy and scanning light detection and ranging (LiDAR), along with bioacoustic recordings, to determine how a plant species invasion affects avian abundance and community composition across a range of Hawaiian submontane ecosystems. Total avian abundance and the ratio of native to exotic avifauna were highest in habitats with the highest canopy cover and height. Comparing biophysically equivalent sites, stands dominated by native *Metrosideros polymorpha* trees hosted larger native avian communities than did mixed stands of *Metrosideros* and the invasive tree *Morella faya*. A multi-trophic analysis strongly suggests that native avifauna provide biotic resistance against the invasion of *Morella* trees and exotic birds, thus slowing invasion “meltdowns” that disrupt the functioning of native Hawaiian ecosystems.

Key words: avifauna; AVIRIS; bioacoustics; Hawaiian submontane ecosystems; invasive species; landscape ecology; LiDAR, light detection and ranging; *Metrosideros polymorpha*; *Morella faya*; visible and infrared imaging spectroscopy.

INTRODUCTION

Biological invasions are a leading cause of vegetation structural changes and altered biogeochemical cycles in ecosystems (Vitousek et al. 1997, Mooney et al. 2005). Some invasive species can facilitate the introduction and proliferation of other exotic plants (Gerrish and Mueller-Dombois 1980, Vitousek and Walker 1989, Hughes et al. 1991), leading to cascading changes in the form and function of ecosystems (e.g., Hughes and Denslow 2005). Invasive plants can even alter the distribution of species at higher trophic levels (Vitousek and Walker 1989), such as among insects, mammals, and avifauna.

When an invasive species alters the assemblage and relative proportion of native and exotic species, fundamental ecosystem changes may occur with or without a concomitant change in biodiversity (Simon and Townsend 2003, Olden et al. 2004, Lockwood 2006). For example, a recent meta-analysis of 63 studies revealed that native herbivores suppress the invasion of exotic plants, whereas exotic herbivores facilitate exotic plant invasions through a chain of positive ecological feed-

backs (Parker et al. 2006), triggering invasion “meltdowns” (sensu Simberloff and Von Holle 1999). The biotic resistance provided by plant-animal interactions among native species represents a unique ecosystem service that is essential to the preservation of native biota. It is therefore critical to identify native plant-animal interactions that facilitate biotic resistance to invasion, allowing targeted steps that are cost-effective, long-term conservation management solutions.

Ecosystems of remote oceanic islands are hotspots of ecological change caused by biological invasion (Moulton and Pimm 1983, Vitousek 1988). The Hawaiian Islands are particularly well known for their invasive species problems, so much so that they are considered models for identifying, understanding, and monitoring multi-trophic level impacts of invasions (Vitousek 2004, Lockwood 2006). In terms of plant-animal interactions, Hawaii offers a unique combination of opportunities for study. First, island topography, substrate age, and climate variability result in a wide range of ecosystem types, from lowland rain forests to arid shrublands, each dominated by relatively few native plant species (Stemmermann 1983). Second, unlike continental ecosystems where the species richness of native birds far exceeds that of exotics (Stohlgren et al. 2006), the richness of native and exotic bird communities in Hawaii is similar. This unique combination of environmental

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PLATE 1. An Apapane, the most abundant species of native Hawaiian honeycreeper, perched on blossoms of a native Ohia tree (*Metrosideros polymorpha*). Ohia blossom nectar is the Apapane's primary food source. Photo credit: © Jack Jeffrey Photography, used by permission.

and biotic characteristics provides a framework to understand how habitat structure, plant species composition and invasion, and avifauna composition interact. However, it is difficult to measure this multi-scale suite of vegetation and faunal characteristics across landscapes using ground-based surveys alone.

Airborne remote sensing offers a rapid, high-resolution, and nondestructive approach to quantifying biophysical structure across a range of spatial scales (Lefsky et al. 2002, Ustin et al. 2004). New airborne measurements of vegetation three-dimensional structure and composition are currently underutilized for studies of multi-trophic interactions, especially in the context of invasive species and interspecies facilitation. Similarly, digital bioacoustic measurements of avian community abundance and composition are evolving, and they offer an attractive alternative to traditional ornithological surveys (Haselmayer and Quinn 2000). The collection of bioacoustic recordings requires little skill and can be automated for frequent, long-term collection of biophony (e.g., bird calls, cricket chirps, frog vocalizations), which would be particularly valuable in studies of rapidly changing or remote ecosystems. Complex algorithms for automatically extracting detailed information on avian community composition (i.e., species

identification, species abundance, species richness) from digital recordings are currently in the developmental phase (Rempel et al. 2005). Therefore, we established a simple analytical technique that extracts relative abundance of avian community size from bioacoustic recordings, and that is ready to be automated. Our analysis technique offers no quantifiable information on species composition and it does not account for differences in detection probabilities among species, habitats, or sampling periods (Rosenstock et al. 2002). It may be suitable for detecting gross differences or changes in avian abundance when detection probabilities are constant. Like airborne remote sensing, the bioacoustic approaches have not been used to assess multi-trophic interactions in the context of invasive species. The combination of airborne observations and ground-based bioacoustics offers unique tools for rapid assessment of the potential floral and faunal changes taking place in ecosystems.

Using a combination of direct field surveys, bioacoustics, and airborne remote sensing, we assessed the effects of plant invasion and ecosystem structural variation on avian abundance and community composition in Hawaii. The study was conducted in Hawaii Volcanoes National Park (HAVO) along two structurally equivalent gradients of increasing canopy cover (Fig. 1) and vegetation height (Fig. 2a). The only significant difference between the two gradients was their vegetation composition. One gradient was dominated by the most common native tree species, *Metrosideros polymorpha* (see Plate 1) and is hereafter called the "native gradient." The second gradient, termed the "exotic gradient," contained *Metrosideros*, but was often dominated by the highly invasive, nitrogen-fixing tree *Morella faya* (formerly *Myrica faya*) (Fig. 1). Combining these biotic differences with a steep ~1000-mm mean annual rainfall gradient, the resultant canopy physiognomies across both gradients include: (1) closed-canopy forest, (2) open-canopy woodlands, (3) savannas, and (4) sparse shrublands. At the same time, these gradients span a distance of just 11 km, and are thus generally accessible by all avian species included in the study. These ecosystem gradients allowed us to control for the biophysical structure and composition of plant species in the context of *Morella* invasion. This, in turn, allowed us to separate the effects that ecosystem structure has on avian community characteristics relative to the presence and abundance of *Morella*. We first tested whether field-based bioacoustics and airborne remote sensing could be used to measure a range of vegetation and avian community properties across the landscapes. We then assessed whether *Metrosideros*-dominated ecosystems host different avifauna communities than those ecosystems containing the invasive *Morella* tree. We were particularly interested in understanding how the structure and abundance of native and exotic plants were related to the relative abundance of native and exotic bird species.

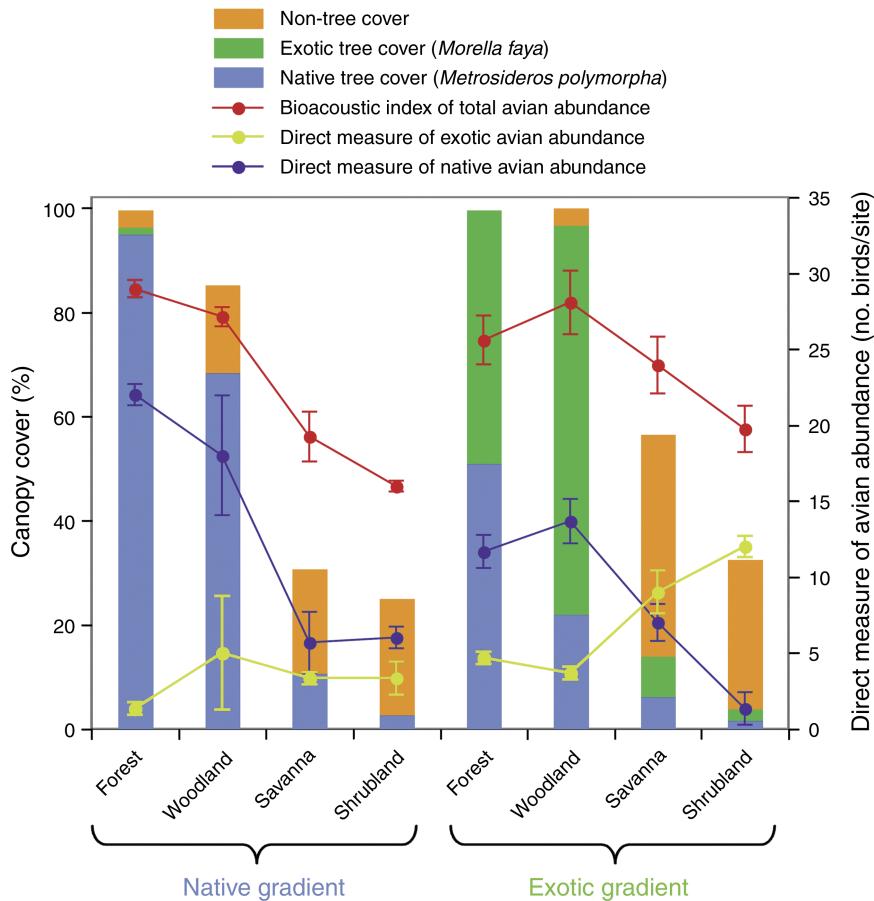


FIG. 1. Avian abundance in relation to canopy type and cover along native and exotic vegetation gradients. Histogram bars show remotely sensed estimates of percent canopy cover (total column height); ground-based measures of *Morella faya* percent cover (green), *Metrosideros polymorpha* percent cover (blue), and non-tree vegetation percent cover (orange). Symbols (mean \pm SE for three stations per site) and lines show field-based measures of native (blue) and exotic (green) avian abundance, and bioacoustic index (unitless) of total avian abundance (red). The bioacoustic index was calculated from the bioacoustic spectrum for each site (frequency [Hz] vs. sound level [dB], as shown in Appendix B: Fig. B1). The area under each bioacoustic spectrum included all frequency bands associated with the dB value that was greater than the minimum dB value for each spectrum. Area values are a function of both the sound level and the number of frequency bands used by the avifauna at each site. All bird species in HAVO are vocal in the spring. Avian abundance (no. birds/site) was measured directly using variable circular plot (VCP) counts: the number of birds heard at each of three stations (150 m apart) per site (four sites for each of two gradients).

MATERIALS AND METHODS

The recently upgraded JPL Visible and Infrared Imaging Spectrometer (AVIRIS; Jet Propulsion Laboratory, National Aeronautics and Space Administration [NASA], Pasadena, California, USA) and an Optech 2025 scanning discrete-return LiDAR (Optech, Vaughan, Ontario, Canada) were flown on separate aircraft at low altitude over the study gradients in 2005. The AVIRIS and LiDAR data were processed as described in Appendix A. During overflights, plot-level measurements of canopy fractional cover, height, and species dominance were also collected for the purposes of validating the remote-sensed data (Figs. 1 and 2a, b). Field-based bioacoustic recordings were then made in the early morning at each site using a digital audio recorder (722, Sound Devices, LLC, Reedsburg, Wisconsin, USA) and two microphones (MKH-30 and

MKH-40, Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany). From these digital recordings, we calculated a bioacoustic index of relative avian abundance for each site (Figs. 1, 2c, and 3a), and compared frequency–amplitude spectra to detect or infer differences in avian community composition among sites (see Appendix B: Fig. B1). These bioacoustic measurements were validated by traditional ornithological surveys that directly measured avian abundance (Fig. 2c) and species composition (see Appendix B: Fig. B2). See Appendix A for details on the methodology of field-based vegetation and traditional ornithological surveys, and the collection, post-processing, and analysis of bioacoustic recordings. For each of the eight study sites along the two gradients, bioacoustic and direct field measures were made at three stations spaced at 150-m

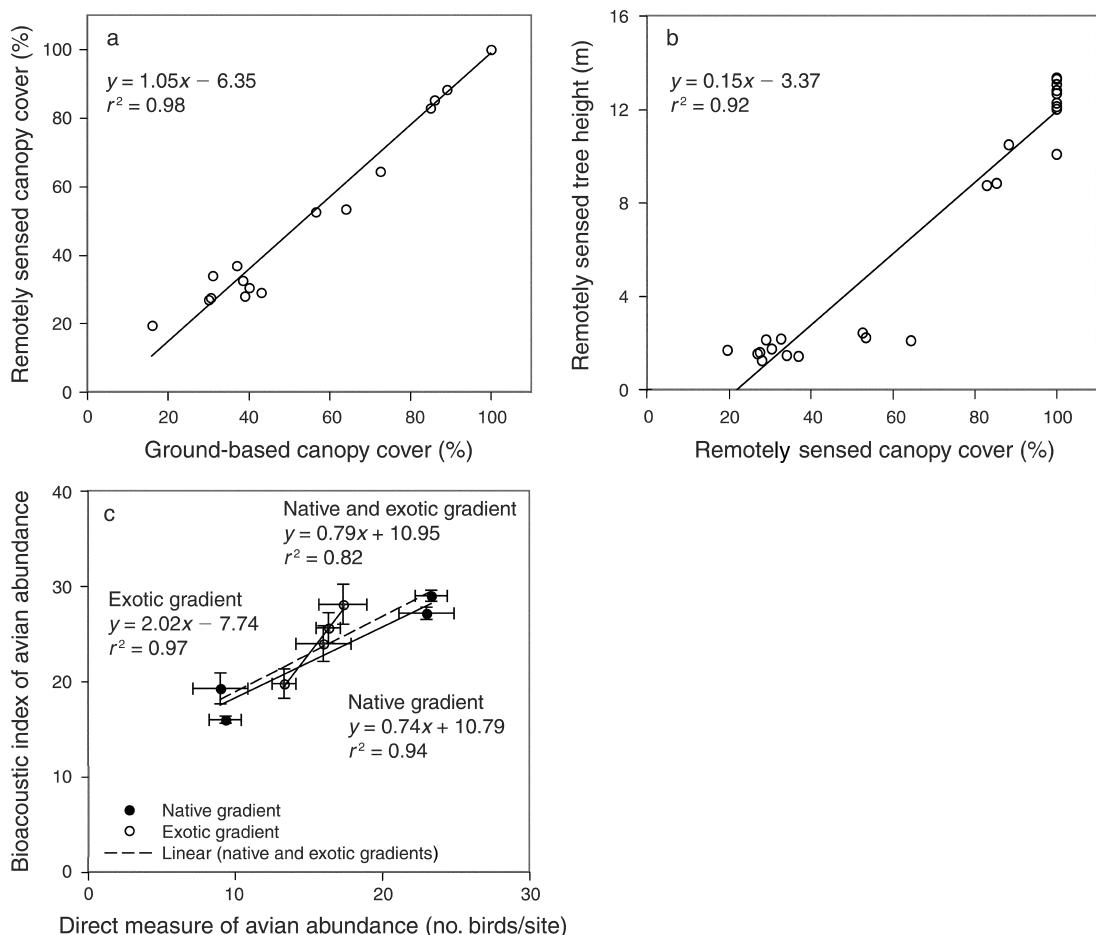


FIG. 2. (a) Relationship between remotely sensed and field-based canopy cover at 24 stations on both ecosystem gradients (native and exotic); (b) relationship between remotely sensed vegetation heights and remotely sensed canopy cover at 24 stations on both ecosystem gradients; (c) relationships between bioacoustic index of avian abundance and direct ornithological survey counts across all sites (dashed line), and along each of the native (solid circles) and exotic (open circles) gradients. Each data point represents one site, and is the mean (\pm SE) of three station values. See Fig. 1 for calculation of the bioacoustic index and the direct measure of avian abundance.

intervals along a straight-line transect. Remote-sensing measurements covered the entire 150-km² study region.

RESULTS

Remote-sensing estimates of canopy cover were highly correlated with ground-based measurements across all 24 stations, which included individual station values across both the native and exotic gradients (Fig. 2; $r^2 = 0.98$). Similarly, the bioacoustic index of avian abundance was strongly correlated with avifauna counts from direct ornithological survey methods along both gradients (Fig. 2c; $r^2 = 0.82$), and was highly correlated across the four site averages along the native (Fig. 2c; $r^2 = 0.94$) and the exotic (Fig. 2c; $r^2 = 0.97$) gradients independently. Canopy cover and tree height covaried across both gradients (Fig. 2b; $r^2 = 0.92$). Although it was not quantified, *Metrosideros* bloom was observed to be at intermediate densities throughout our study area during

the time that avian community characteristics were measured (March/April).

Along both the native and exotic gradients, total avian abundance was significantly higher in forest and woodland sites containing high canopy cover and tall trees than in savanna and shrubland sites with lower cover and shorter trees (Figs. 1 and 3a). In addition, the ratio of the abundance of native to exotic avifauna ($A_n:A_e$) was higher in the woodlands and forests than in the savanna and shrubland ecosystems of both gradients (Fig. 4).

Although vegetation structure was the primary correlate with avian community size and composition, the relationship between habitat structure and avifauna community characteristics differed between the two contrasting gradients. The native gradient had a wider range in avian community size (direct measure = 14, bioacoustic index = 6.5) than did the exotic gradient (direct = 4, bioacoustic = 4.1; see Fig. 2c). Consequently, sites along the native gradient had more distinctive

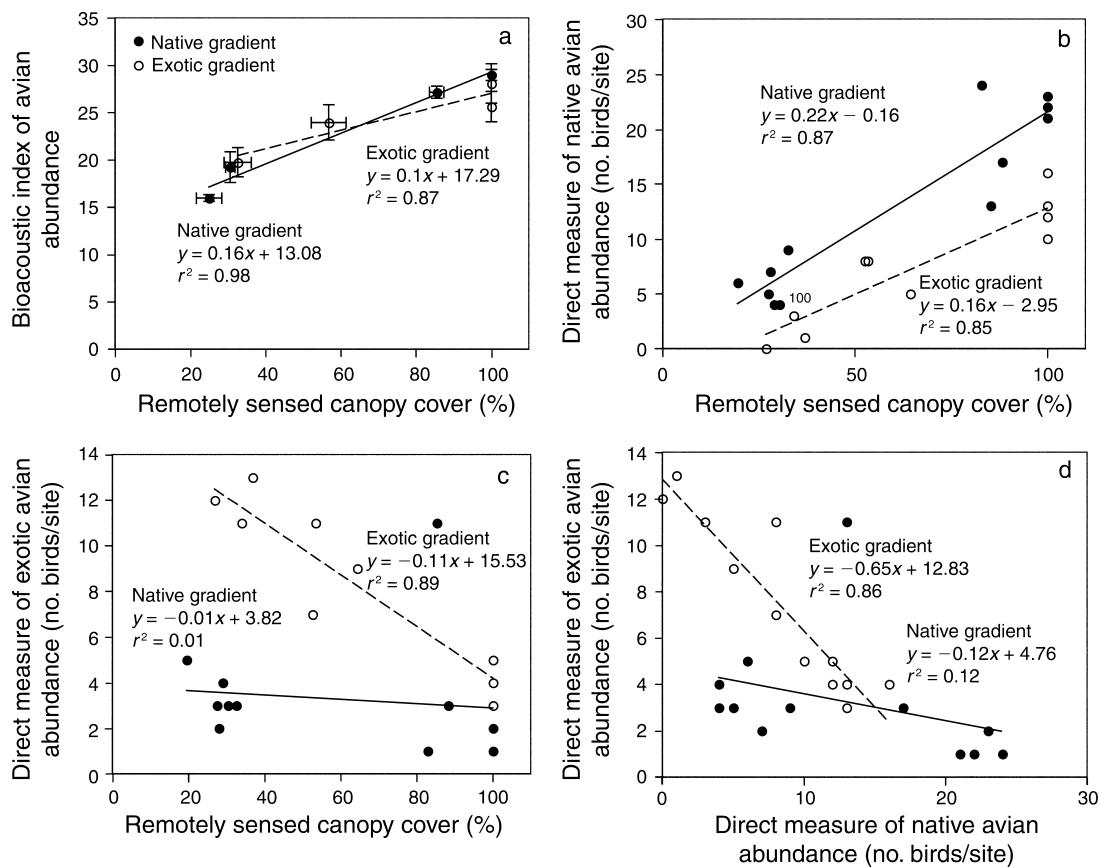


FIG. 3. Avian abundance in relation to native (solid circles) and exotic (open circles) ecosystem gradients. (a) Relationships between bioacoustic index of avian abundance and remotely sensed canopy cover across sites along each of the native and exotic gradients. Each data point represents one site and is the mean (\pm SE) of three station values. (b and c) Relationships between remotely sensed canopy cover and field-based measures of (b) native and (c) exotic avian abundance as measured by direct ornithological survey counts across 12 stations along the native and exotic gradients. (d) Relationships between direct measures of avian abundance measured by ornithological survey counts across 12 stations along the native and exotic gradients.

bioacoustic spectra than those along the exotic gradient (see Appendix B: Fig. B1). In addition, while native bird communities increased in size with increasing canopy cover and height along both gradients (Fig. 3b), exotic bird community size did not change significantly along the native gradient, and decreased with increasing canopy cover and height along the exotic gradient (Fig. 3c, d). Ecosystems along the native gradient had significantly higher $A_n:A_e$ values than structurally equivalent ecosystems along the exotic gradient (Fig. 4). As a result, the native gradient had a wider range in $A_n:A_e$ among ecosystems (range in $A_n:A_e = 16$) than did the exotic gradient (range in $A_n:A_e = 3$) (Fig. 4).

DISCUSSION

Because the three native bird species present at our study sites (see Appendix B: Fig. B2) evolved in native forest, it is not surprising that $A_n:A_e$ and native bird abundance were higher at sites with higher canopy cover and height. Sites with higher canopy cover provide increased habitat, nutritional, and other resources required by the native avifauna (Willson 1974, Holmes

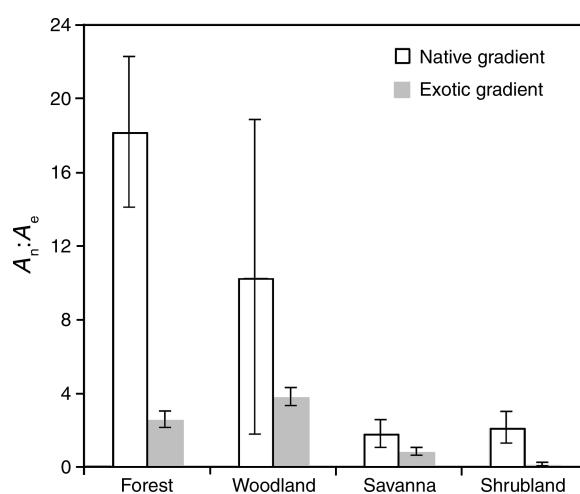


FIG. 4. The ratio of the abundance of native to exotic birds ($A_n:A_e$) at each site along the native (open) and exotic (light gray) gradients. Each site value represents the mean (\pm SE) of three station values. Avian abundance was measured directly as the number of birds per site.

et al. 1979, Scott et al. 1986) that are present at our study sites (see Appendix B: Fig. B2). Although the native Amakihi (*Hemignathus virens*) is suited to a variety of habitat types, the native Apapane (*Himatione sanguinea*; see Plate 1) is an upper-canopy specialist (Fancy and Ralph 1997), feeding primarily on *Metrosideros* flower nectar and foliage insects (Baldwin 1953). Similarly, the native Omao (*Myadestes obscurus*) prefers dense forest to open shrub or savanna habitats, feeding primarily on native fruits, and often selecting protected branches for perching (van Riper and Scott 1979, Scott et al. 1986, Wakelee and Fancy 1999).

In contrast, the invasive Japanese White-eye (*Zosterops japonicus*), the most abundant land bird in the Hawaiian Islands and the most abundant exotic bird species in HAVO, is a habitat generalist (Scott et al. 1986). This species occurs in high densities across a range of habitat types (Scott et al. 1986) and feeds on a variety of resources, including fruit, nectar, and insects (Guest 1973, Conant 1975, van Riper 2000). Similarly, the Melodious Laughing-thrush (*Garrulax canorus*) also commonly occurs across a wide range of biophysical habitats (Scott et al. 1986). Our results demonstrate this lack of habitat specificity among exotic birds (Figs. 1 and 3c). The difference in biophysical habitat selectivity between native and exotic avifauna is strongly associated with the higher total avian community abundance, and higher $A_n:A_e$ found in the forest and woodland than in the savanna and shrubland sites (Figs. 1 and 4).

The wider range in avian community size along the native as compared to the exotic gradient indicates that avian communities are more closely tied to changes in the canopy structure of native ecosystems than in systems dominated by the invasive *Morella* tree/shrub. This greater sensitivity is explained by the inherent dependence of native birds on the resources provided by native vegetation, which results in consistently higher $A_n:A_e$ values, as well as a wider range in $A_n:A_e$, along the native gradient sites than in equivalent exotic gradient sites (Fig. 4).

The lack of change in exotic bird abundance along the native gradient reflects the fact that exotics birds are habitat generalists, yet there was a dramatic change in their abundance along the exotic gradient (Figs. 1 and 3c) that mirrored the response of native birds (Figs. 1 and 3d). This caused $A_n:A_e$ to be lower (≤ 1 ; Fig. 4), and avian community size greater (Fig. 1), at savanna and shrubland sites on the exotic gradient compared to biophysically equivalent sites on the native gradient. This suggests that exotic birds may have a nutritional preference for *Morella* fruit over *Metrosideros* products (Vitousek and Walker 1989, Woodward et al. 1990). However, if the presence or absence of *Morella* was the sole determinant of exotic bird abundance, the forest and shrubland sites on the exotic gradient would host significantly more exotic birds than biophysically equivalent sites on the native gradient. Instead, our results indicate that the abundance of exotic birds may

be determined by the level of resource competition that they encounter with native birds, which is strongest at sites that provide particularly suitable native habitat resources. Past work has shown strong native–exotic competitive interactions across a range of Hawaiian ecosystems (Mountainspring and Scott 1985). We contend that, in this relatively simple Hawaiian avian community, a small number of competitive interactions between resident native and exotic bird species may provide a form of biotic resistance against exotic avifauna invasions, but only when the native vegetation is sufficient to support a substantial native bird community. In this sense, we suggest that the effects of an invasive tree can ripple throughout a food web by changing avian community characteristics and facilitating the invasion of nonnative birds.

Because native birds have evolved in *Metrosideros* forests, they may be superior to introduced avifauna as competitors for *Metrosideros* resources. For example, although the generalist Japanese White-eyes consume *Metrosideros* nectar (Carpenter 1976), the Apapane and other Honeycreeper species such as ‘Amakihi that dominate native avian communities at forest–woodland sites (see Appendix B: Fig. B2) have specialized bill and tongue morphologies that may make them more efficient than White-eyes at extracting nectar from *Metrosideros* flowers (Carothers 1982, Pratt 2005). In addition, it is likely that White-eye abundance is low where native avian abundance is high, in part because White-eyes have been observed to visit *Metrosideros* flowers infrequently where behaviorally dominant Apapane are abundant (Pimm and Pimm 1982). Through these nutritionally and behaviorally based competitive advantages, the native avifauna may provide strong biotic resistance in *Metrosideros*-dominated stands, preventing exotic avian communities from expanding at sites along the native gradient, even at savanna–shrubland sites that are biophysically less attractive to native avifauna (Fig. 1).

Expanding on our results, we hypothesize that the biotic resistance provided by native avifauna in the vegetation habitats most structurally and compositionally suitable to them not only acts to suppress invasions by exotic birds, but also, in turn, probably buffers these prime habitats against rapid invasion by *Morella faya* and other exotic plant species. For example, the Japanese White-eye is the primary disperser of *Morella* seeds throughout our study area and the national park (Vitousek and Walker 1989, Woodward et al. 1990). In addition, Vitousek and Walker (1989) suggest that the invasion of nitrogen-fixing *Morella* probably facilitates further plant invasions (Gerrish and Mueller-Dombois 1980), such as the exotic strawberry guava tree (*Psidium cattleianum*), which has been most successful in soils located under *Morella* canopies.

CONCLUSIONS

Our results demonstrate that the submontane native avian community of Hawaii Volcanoes National Park

(HAVO) is primarily sensitive to biophysical habitat characteristics and secondarily sensitive to the presence of an invasive exotic tree species, *Morella faya*. In contrast, biophysical structure plays no apparent role in determining exotic bird abundance. Instead, the abundance of exotic birds is probably determined by the level of competition that they encounter with native birds.

Although Parker et al. (2006) show that native faunal species provide biotic resistance to exotic plant invasions, "meltdowns" (sensu Simberloff and Von Holle 1999) are common and widespread, resulting from positive feedbacks among exotic floral and faunal species that often facilitate the success of each species. Combined with the findings of previous studies, our results highlight the importance of protecting the remaining native *Metrosideros*-dominated ecosystems in Hawaii Volcanoes National Park as a means to protect native bird populations and to slow the multi-trophic cascade of biological invasions currently underway.

Our findings were facilitated by the unique measurements and insight provided by advanced remote-sensing technologies (hyperspectral and LiDAR), brought together to monitor landscapes and invasive species in Hawaii. Although these technologies are not yet widely available, they are growing in popularity in the remote-sensing literature. Here we showed that these technologies have a tangible role to play in understanding the ecology of a landscape or region. Furthermore, we demonstrated that airborne remote sensing and bioacoustics offer a landscape ecological approach for identifying and monitoring the key interactions of species, both within and across trophic levels, that maintains the form and function of ecosystems.

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APPENDIX A

Detailed methods of airborne imaging spectroscopy, LiDAR, bioacoustic recordings, and bird surveys (*Ecological Archives* A017-086-A1).

APPENDIX B

Supplementary figures showing bioacoustic spectra of avian vocalizations and abundance of native and exotic birds by habitat (*Ecological Archives* A017-086-A2).