

Increase of an introduced bird competitor in old-growth forest associated with restoration

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Abstract

Many successful invasions involve long initial periods in which the invader exists at low densities followed by sudden population increases. The reasons for such time-lags remain poorly understood. Here we document a sudden increase in density of the introduced Japanese white-eye (*Zosterops japonicus*) in a restoration area contiguous with old-growth forest at Hakalau Forest National Wildlife Refuge on the Island of Hawaii. The refuge, with very high density of native birds, existed in a pocket of low white-eye density that persisted for at least 20 years since the late 1970s. The refuge began an extensive native trees restoration project in 1989 within a 1314 ha abandoned pasture above old-growth forest. This area was soon colonized by white-eyes and their population grew exponentially once the trees had grown tall enough to develop a canopy. This increase was in turn followed by significantly more white-eyes in the open and closed forests adjacent to the restoration area. Competition between white-eyes and native species was documented on study sites within these forests. Density data indicate that competition was more widespread, with loss of tens of thousands of native birds in the 5371 ha area surveyed. Our results are consistent with the view that ecological barriers may delay the population increase of invaders and that human-derived activities may help invaders cross these barriers by creating new ecological opportunities. Control of white-eye numbers may be essential for recovery of native species.

Keywords

Introduced bird, restoration, exponential population growth, propagule pressure, biotic resistance, competition, time-lag

Introduction

When introduced into novel environments, some invaders increase rapidly in the new location, while others experience time-lags of various lengths (Roughgarden 1986, Williamson 1996, Blackburn et al. 2009). The causes of the time-lags are not well understood (Crooks 2005), but some explanations have been advanced (summarized by Crooks and Soule 1999). Most explanations focus on demographic factors (e.g. Allee effects; Taylor and Hastings 2005, Tobin et al. 2007), and evolutionary factors (genetic changes for adapting to the novel environment or increased competitive ability; Sakai et al. 2001, Kolbe et al. 2004, Hufbauer and Torchin 2007). Nevertheless, it is also possible that some invaders remain at low numbers due to biotic or environmental factors, like diffuse competition or unfavorable climatic conditions. These cases can be detected when the factors limiting population growth no longer exist. The goal of this study is to document an avian invasion where the population exhibited a time-lag that lasted over 20 years and then suddenly increased in numbers when environmental conditions changed due to a native trees restoration project. That invasion eventually led to increased density off-site with strong negative impacts to native bird species.

Restoration is a human-derived environmental change that is known to provide ecological opportunities in habitat for plants and animals (D'Antonio and Meyerson 2002), similar to what happens during succession (Connell and Slayter 1977). Consequently, restoration can also attract invasive animals. While the existence of ecological opportunities should trigger the increase of the invader population, in restoration areas time-lags may arise associated with growth of plants, analogous to animals that become more abundant in later seral stages of succession. In addition, nearby mature habitat can be affected if the propagule pressure from the restoration area is strong enough to overwhelm biotic resistance (Hollebone and Hay 2005, Lockwood et al. 2005, von Holle and Simberloff 2005).

This paper focuses on the invasion of Hakalau Forest National Wildlife Refuge (Mauna Kea, Island of Hawaii) by the Japanese white-eye (*Zosterops japonicus*), a passerine bird native to Asia. The white-eye was intentionally introduced to the Island of Oahu in 1929 to control insects (Caum 1933). It was later introduced to the Island of Hawaii in 1937 (Foster 2009), where Baldwin (1953), Dunmire (1962), and Banko and Banko (1980) documented an explosive increase in numbers and range. During the Hawaii Forest Bird Survey conducted in the late 1970s, the white-eye was the most common bird in the state and was found in every forest (Scott et al. 1986). There was no documented lag time for its increase after the introduction.

Nevertheless, on Mauna Kea, in the land that eventually became Hakalau Forest National Wildlife Refuge in 1985, the white-eye remained at low densities documented in the late 1970s. The refuge has the highest density of native birds on the island (Scott et al. 1986), so it is possible that the low density was maintained by biotic resistance in the form of diffuse competition from the community of native birds (MacArthur 1972, Pianka 1974, Case 1990). The white-eye overlaps multiple foraging substrates with each native species (Freed et al. 2008a), as assumed by the theory

of diffuse competition (MacArthur 1972). In 1989 and following years, over 400,000 *Acacia koa* seedlings were planted in abandoned pasture above the old-growth forest. Seedlings were about 4 months old and 20 cm high, but by 5 years some trees had achieved heights of 8 m (Scowcroft and Jeffrey 1999), with a canopy that sustained arthropods and provided sufficient cover for thermal protection during cold nights at upper elevation.

Our goal is to describe how the refuge restoration area brought a sudden increase in white-eye density, and to ask whether this sudden increase may explain the recent increase of the invader in adjacent open and closed forests with native birds. Documenting the increased density of white-eyes throughout the refuge is particularly relevant given the diverse evidence that the species is negatively affecting native birds (Freed et al. 2008a, 2009; Freed and Cann 2009, 2012), and the possibility that the problems extend well beyond our study areas. We deal with this by also documenting changes in density of native species throughout the refuge.

Methods

Hakalau Forest National Wildlife Refuge (Fig. 1) consists mainly of old-growth ohia-lehua/koa (*Metrosideros polymorpha*/*Acacia koa*) forest (Freed 2001). Bird surveys were conducted in the three main areas with transects indicated in Fig 2. The 3373 ha open forest area was formerly a cattle ranch so the understory is a matrix of patches of ferns and woody plants surrounded by expansive swatches of introduced pasture grasses. However, the old-growth forest remains in the form of many ohia-lehua trees, including large specimens, and large koa trees that provide nesting sites and foraging substrates for all species of native and introduced birds (Freed 2001, Freed et al. 2008a). Ohia-lehua comprise over 90% of the forest canopy (Freed et al. 2008a), and arthropods have been collected and analyzed from twigs and foliage (Freed et al. 2007). Below the open forest is the 1998 ha closed forest area with similar canopy trees and bird species, but with more native understory plants. Above part of the open forest area is the 1314 ha restoration area that had been extensively cleared for pasture more than 100 years ago (Tomonari-Tuggle 1996).

Estimates of white-eye density and variance from survey data were obtained from Camp et al. (2009) for years 1987–2007 in the restoration and open forest areas, and from 1999–2007 in the closed forest area, the initial time that area was included in surveys. We analyzed the data as follows. First, for all three areas, we tested for temporal autocorrelation using the “acf” function in S-Plus. This estimates the autocovariance function by summing the lagged products and dividing by the length of the series. For autocorrelation, all covariances are further divided by the geometric mean of the variances. The function produces 95% confidence limits for the different lags. No lags excluded 0 in any area. Then, for all areas, we compared exponential and linear trend models, because range expansion models frequently begin with exponential growth (Crooks and Soule 1999). We examined the distribution of residuals to determine the

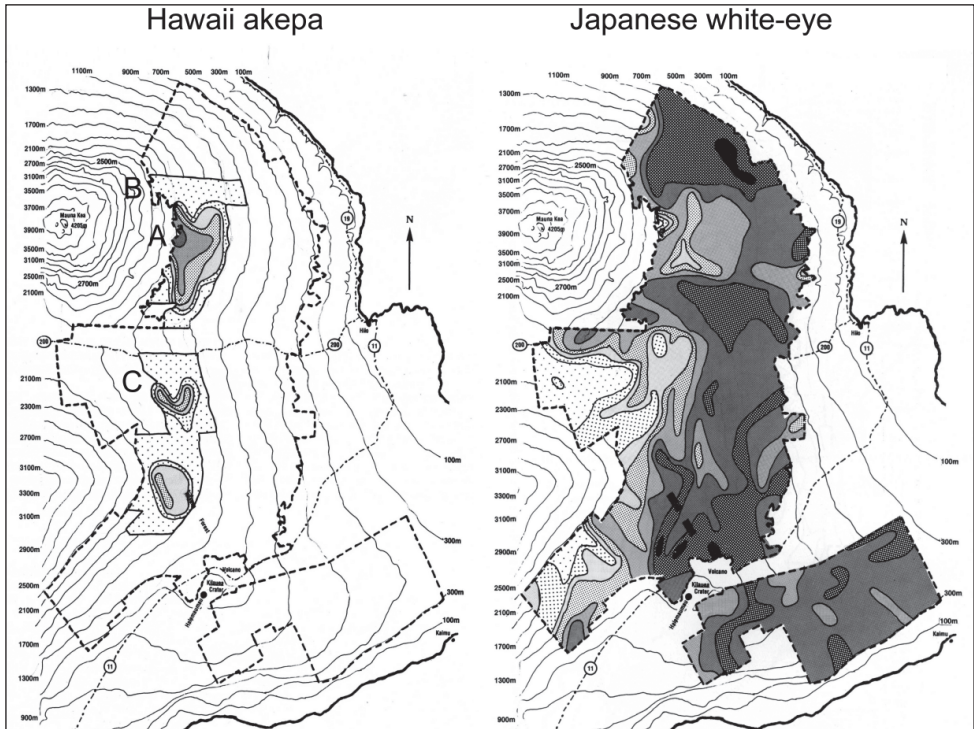


Figure 1. Maps of distribution and abundance of the endangered Hawaii akepa (*Loxops coccineus coccineus*) (left) and introduced Japanese white-eye (right) in the windward Hawaii study area from the Hawaii Forest Bird Survey conducted in the late 1970s (Scott et al. 1986). Darker colors indicate higher density. The pocket of low white-eye density contains the southern portion of Hakalau Forest National Wildlife Refuge. That pocket contains most of the Mauna Kea population of the akepa and other native birds. The small high density area of akepa **A** (401–800 birds/km²) almost perfectly matches a very low density of white-eyes 11–50 and 51–100 birds/km². The habitat around the area is identical old-growth forest, so habitat selection is not involved. The area to the north where the akepa is vanishingly rare **B** (1–10 birds/km²) corresponds to an area with very high white-eye density (400–800, 801–1600 birds/km²). The isolated akepa populations to the south **C** on Mauna Loa (101–200 birds/km²), are in areas with low density of white-eyes (11–50, 51–100 birds/km²). These data contrast with Mountainspring and Scott (1985), who documented a positive relationship between white-eye and akepa densities. The dark rectangular section of high white-eye density in the lower right contains Hawaii Volcanoes National Park, from which the akepa and many other native birds disappeared during the years 1940–1970 when the white-eye increased explosively (Dunmire 1962, Baldwin 1953, Banko and Banko 1980). Avian malaria may also have played a role (van Riper et al 1986). Modified from Scott et al. (1986), with permission from the Cooper Ornithological Society.

fit of the model to the data. See Freed and Cann (2010) for an example where this procedure was mistakenly not followed for trend analysis of native Hawaiian birds. For the closed forest area we used non-linear regression, without transforming the dependent variable, so that Akaike information criterion (AIC) could be used to distinguish

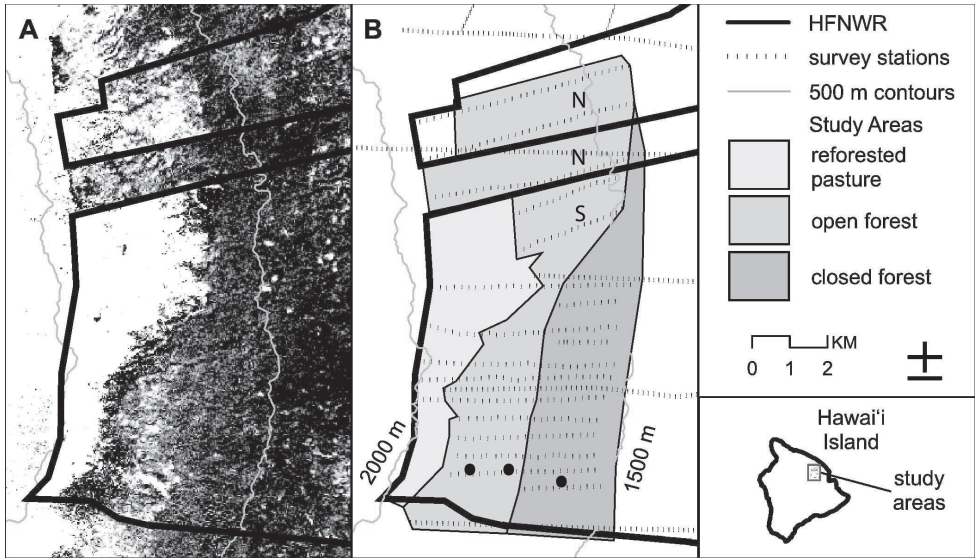


Figure 2. Portion of Hakalau Forest National Wildlife Refuge that was surveyed, relative to aerial photograph **A** and configuration of restoration, open forest, and closed forest areas **B** based on Camp et al. (2010). Black circles on (B) indicate study sites where birds were captured in mist-nets. Open forest sites are on Transect 1 which are numbered sequentially to the north. N and S indicate northern and southern sections of open forest area. The lower N is state-owned mixed native and introduced forest managed for pig-hunting. Light areas in (A) are pastures from former cattle ranching. The open forest area has large trees (Freed 2001) with mainly introduced grass understory. Modified from Camp et al. (2010), with permission from the University of California Press.

the models (Burnham and Anderson 2002). S-Plus 8.2 (TIBCO Software) was used for all statistical analyses.

For the open forest area, we also used a randomization test for a stepwise increase during 1988–1999 and 2000–2007. The time periods were based on mist-netting that indicated a stepwise increase beginning in 2000 (Freed et al. 2008a). For this test we eliminated the extreme outlier in 1987 (Fig. 3), justified because this was the first year that surveys were conducted on the refuge, and the outlier value was not corroborated by mist-netting in the open forest site (Freed et al. 2008a). We ran 10,000 permutations and used a two-sided test.

We determined the order of increase between areas in two ways. For the restoration area and the open forest area, we compared slopes of regressions of density on year for 1988–2000. This time period was selected because it occurred before the stepwise increase from mist-netting. A significant slope in the restoration area but not in the open forest area would establish order. For the open forest area and closed forest area, we compared sequential differences in density from 1999 to 2000 and to 2001 in relation to the standard errors of the estimates. We determined if the differences between years were greater than two standard errors of

those differences, indicating growth, or no growth if the differences were less than two standard errors.

We use functional data analysis (Ramsey and Silverman 1997, Murtaugh 2007) to document change in numbers of native birds between 2000 and 2007, using survey data from Camp et al. (2009). This type of analysis uses a function of the data, rather than all of the raw data, for statistical analysis that is readily interpretable. For example, growth of individuals can be analyzed through repeated measures analysis of variance, regression of size over time, or estimation of parameters of growth models like the von Bertalanffy. An even simpler function of growth data is the change between an early point and a later point in time. The change can be evaluated by the difference in values and variation associated with each value. We apply this simple function to survey data, using values from the beginning and end of a time interval, to determine if a significant change in numbers had occurred during that interval.

This function tests the same hypothesis as regression, change over time, and it is particularly relevant for documenting the consequences of an environmental change. Unlike regression, the functional data analysis is not constrained by constant change per unit time, or by the location of the intercept relative to the data. There is no theory in population dynamics that predicts constant rate of change. The analysis can also estimate the magnitude of change using basic mathematical properties of mean and variance of sums and differences of random variables (DeGroot and Schervish 2002), and can calculate 95% confidence intervals of the differences in values at each end of the time interval. We use this approach to compare the number of species with significant changes compared with the two from piecewise regression (Freed and Cann 2010).

The two endpoints we compare are densities in 2000 and 2007. The year 2000 is the first year of an environmental change (Freed et al. 2008a; Freed and Cann 2009, 2012). The year 2007 is the last year of available data. To guard against anomalously large or small values at endpoints, we average the endpoints with values from surrounding years, using years 1999, 2000, and 2001 to calculate the mean density of the initial endpoint, years 2006 and 2007 for the mean density at the end of the series. Each density value has a variance, which integrates spatial variability, uncertainty of detection, detections at station center, and model fit from Program Distance (Buckland et al. 1993). Camp et al. (2009) reported the square root of that variance as standard error, which is really the standard deviation, so we square that value to calculate the variance of each point and then use properties of variance of sum of random variables to calculate the variance at each end of the time series. Then the difference in mean density was calculated along with variance of the difference. For each species, we calculated 95% confidence intervals from variance of the difference in density to assess significance of change in density.

We illustrate with this method the decline in the open forest area of the iiwi (*Vestiaria coccinea*), currently a species of concern in the process of being listed as endangered. The density in 2000 was 23.80 birds/ha, bracketed by 19.59 in 1999 and by 17.02 in 2001, for a mean density of 20.14. The density in 2007 was 7.77 birds/ha bracketed by 15.92 in 2006, for a mean density of 11.85. The standard deviations

were 0.0641, 0.890, and 0.722 for years 1999–2001 and 0.0766 and 0.0634 for years 2006–2007. Squaring these gives the variances. Then, the sum of variances for each set of years is calculated using the following property of variance of the sum of independent random variables: $\text{Var}(a_1X_1 + \dots + a_nX_n) = a_1^2\text{Var}(X_1) + \dots + a_n^2\text{Var}(X_n)$, where the a_i are coefficients. The mean is the sum of random variables with the a_i equal to $1/n$, where n is the sample size. For the iiwi, the means are the sum of independent random variables $X_1/3 + X_2/3 + X_3/3$ for 1999–2001 and $X_1/2 + X_2/2$ for 2006–2007. Therefore the variance of the mean random variables are $(0.0041 + 0.7921 + 0.5213)/9 = 0.1464$ for 2000 and $(0.0059 + 0.0040)/4 = 0.0002$ for 2007. Then, the difference between the means, $20.14 - 11.85 = 8.29$ becomes a new random variable representing the decline. The variance of the difference between independent random variables is the same as the variance of the sum. Thus the variance of the difference is $0.1464 + 0.0002 = 0.1466$. Taking the square root gives the standard error of the difference as 0.3829. Twice the standard error on either side of the 8.29 birds/ha difference between 2000 and 2007 gives the 95% confidence interval of (7.52, 9.06). Because the confidence interval does not include 0, we can conclude that a significant decline has occurred in the open forest area. The extent of the decline can be estimated by multiplying the 8.29 birds/ha change by the 3373 ha area.

We use this same methodology to document the white-eye increase in the closed forest area. For the open forest area, we use the difference in means established by the randomization test, and then calculate the variances associated with the standard deviations from all years during 1988–1999 and 2000–2007. Then the 95% confidence interval was calculated as specified for 2000 and 2007.

For community-wide changes in each survey area, we took covariance among species into account. We used the variance of densities of all 8 native species during 2000–2007 plus the covariance of densities from all pairs of native species those same years, according to the standard statistical formula $\text{Var}(X+Y) = \text{Var}(X) + \text{Var}(Y) + 2\text{Cov}(X,Y)$, extended to 8 species. From this total, the 95% confidence interval of variances of the difference in density in the community was calculated.

Results

Restoration area. White-eyes increased in the restoration area, especially from 1999 to 2007 (Fig. 3a). They had low or 0 density when seedlings were first planted in 1989, and were mainly present in the few remnant trees along predominantly dry streams following the mountain slope in the area. The linear growth model for the entire series was significant (slope = 0.27 ± 0.06 , $R^2 = 0.57$, $p = 0.0007$), but was dismissed because it had significant lack of fit. This was indicated by a run of 7 negative residuals (sign test, $p = 0.01$). The exponential growth model for the entire series was also significant (parameter = 0.14 ± 0.03 , $R^2 = 0.66$, $p = 0.0001$), with sufficient fit indicated by runs of no more than 4 positive or negative residuals. The increase did not really start until 1998 (Fig. 3a).

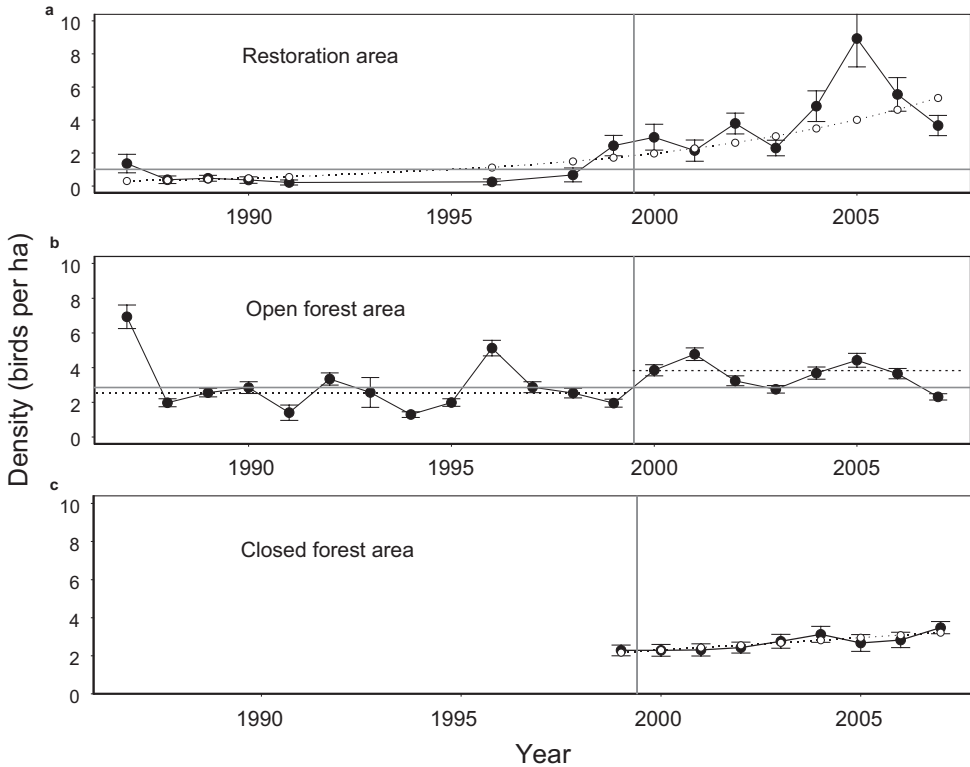


Figure 3. Long-term patterns of Japanese white-eye density with standard error in: **a** restoration area **b** open forest area, and **c** closed forest area. Fitted values from the best model (deviation) are shown in a) and c). Median of the entire series is shown in a) and b). For b), medians for 1987–1999 and for 2000–2007 are shown in dotted lines.

Open forest area. White-eyes also increased in the open forest area where they previously existed at lower density (Fig. 3b). Linear regression did not reveal the increase (slope = 0.01 ± 0.05 , $R^2 = 0.004$, $p = 0.78$). However, residuals had significant lack of fit, indicated by 2/13 positive residuals during 1987–1999 and 6/8 positive residuals during 2000–2007 (test of proportions, $p = 0.023$). The exponential regression model had adequate fit (runs of maximum length 3) but was not significant (parameter = 0.01 ± 0.02 , $R^2 = 0.035$, $p = 0.49$). Nevertheless, the randomization test clearly indicated a higher mean density during years 2000–2007 (critical value for 0.975 quantile = 0.97, observed difference = 1.05), consistent with a stepwise increase that could not be modeled with linear or exponential regression.

Closed forest area. White-eye density also increased in the closed forest area, where the birds had previously existed at low density (Fig. 3c). Both linear and exponential models were supported (linear: slope = 0.13 ± 0.03 , $R^2 = 0.74$, $p = 0.003$; exponential: parameter = 0.05 ± 0.01 , $R^2 = 0.77$, $p = 0.002$), had adequate fit by runs of signed residuals, and were indistinguishable ($\Delta AICc$ exponential = 0, linear = 0.16).

Order of increase among areas. During years 1988–2000, density increased in the restoration area (slope = 0.6, se = 0.06, p = 0.04), but not the open forest area (slope = 0.08, se = 0.08, p = 0.33). Thus the increase began in the restoration area before the open forest area. Changes in density during the years 1999–2001 were significant in the open forest area (1.90 ± 0.79 , 2.82 ± 0.85), but not in the closed forest area (0.01 ± 0.42 , 0.03 ± 0.85). The overall order of increase was from the restoration to the open forest to the closed forest area (Fig. 3).

Changes in native birds in the forested areas. Figure 4 shows significant declines in native birds the same years that the white-eye was increasing in both the open and closed forest areas. The declines in the closed forest area were smaller than those estimated in the open forest area (Fig. 4, paired t = 2.15, df = 7, p = 0.034). However, the high correlation between changes in density in the two forest areas (cor = 0.93, p = 0.0003), including white-eyes, indicates that the pattern of changes among native species and white-eyes was similar in the open and closed forest areas. Table 1 shows that tens of thousands of native birds perished even under the most optimistic scenario. Based on mean 2000 densities times 3373 ha, there were approximately 166,927 native birds in the open forest area. The loss of 61,289 birds represents a 37% decline, ranging from 51 to 22%. The closed forest area had 86,653 birds with a loss of 9091, representing a 10% decline. The white-eye was the only bird that significantly increased in each area (Fig. 4, Table 1).

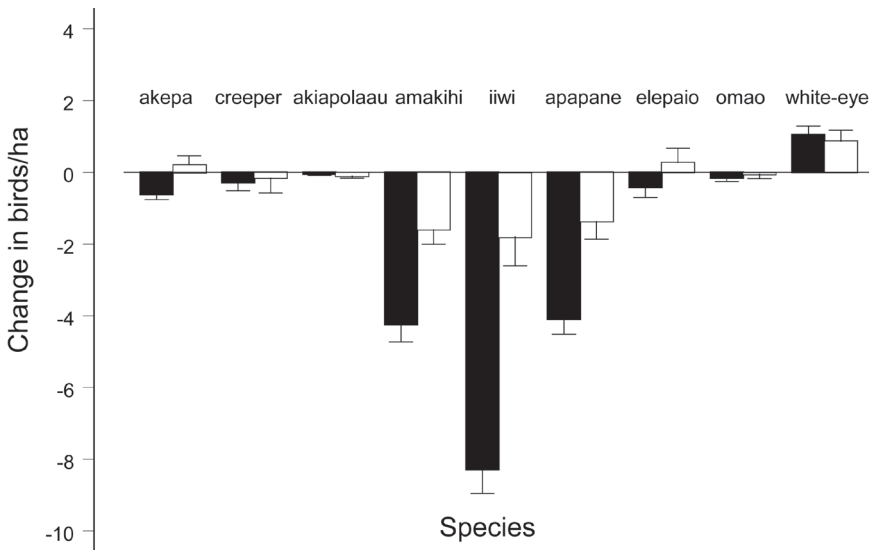


Figure 4. Change in densities with standard error of native birds and Japanese white-eyes in the open forest area (black bars) and closed forest area (white bars), between 2000 and 2007. Native passerine species present throughout the closed forest area and the southern section of the open forest area were Hawaiian honeycreepers: Hawaii akepa (*Loxops coccineus coccineus*), Hawaii creeper (*Oreomystis mana*), akiapolaau (*Hemignathus munroi*), Hawaii amakihi (*Hemignathus virens virens*), iiwi (*Vestiaria coccinea*), and apapane (*Himatione sanguinea*); Monarchine flycatcher: Hawaii elepaio (*Chasiempis sandwichensis ridgwayi*); and Thrush: omoa (*Myadestes obscurus*).

Table 1. Changes in numbers between 1999–2001 and 2006–2007 in open and closed forest (Fig. 1), based on changes in density multiplied by area (ha). Endangered species (E), species of concern (SOC). Confidence intervals for species are based on two standard errors of changes in density. Confidence intervals for community change are based on two standard errors of the sum of variances and twice the sum of covariances of all native species densities from 2000 through 2007.

Species	Change in Numbers	Lower 95% CI	Upper 95% CI
Open Forest			
Hawaii akepa (E)	-2,081	-3,080	-1,083
Hawaii creeper (E)	-968	-2,506	570
Akiapolaau (E)	-169	-405	69
Hawaii amakihi	-14,329	-17,587	-11,070
Iiwi (SOC)	-27,969	-32,442	-23,496
Apapane	-13,823	-16,602	-11,043
Hawaii elepaio	-1,400	-3,329	530
Omao	-550	-1,191	91
Community change:	-61,289	-85,892	-36,686
Japanese white-eye	3,542	5,083	2,001
Closed Forest			
Hawaii akepa (E)	440	-515	1,395
Hawaii creeper (E)	-320	-1,990	1,351
Akiapolaau (E)	-180	-432	72
Hawaii amakihi	-3,177	-10,557	-7,305
Iiwi (SOC)	-3,576	-6,833	-320
Apapane	-2,737	-4,707	-767
Hawaii elepaio	539	-1,083	2,162
Omao	-80	-615	456
Community change:	-9,091	-12,778	-5,404
Japanese white-eye	1,738	2,829	647

Discussion

Land that became Hakalau Forest National Wildlife Refuge existed for years in a pocket of low white-eye density, especially in the southern end with the intact bird community (Scott et al. 1986). There are several reasons why the invader remained at such low densities. Because white-eyes exhibit substantial overlap in the foraging niche with all native species, invader numbers may have remained low due to biotic resistance. Alternatively, conditions in the forested areas may have been sub-optimal for the invader. Calculation of the deterministic rate of population growth was 0.97 with an assumption of breeding success of 0.6 (Freed et al. 2008a), indicating that limited immigration might have been necessary to maintain numbers. Nevertheless, when the pasture land above the forest became a restoration area, the white-eye colonized that area and eventually grew exponentially in it. The bird then increased in density in the contiguous open forest area followed by the more distant closed forest area. Substantial

decline in native birds in the open forest area and lesser declines in the closed forest area followed. There are many issues concerning numbers and impacts.

Increase of white-eye numbers. The restoration is a clear example of a human activity that increases ecological opportunities for an introduced species that otherwise should have remained at low numbers. The restoration also offered opportunities for three native species (Camp et al. 2010). The Hawaii amakihi (*Hemignathus virens virens*), the most generalized native bird, was growing exponentially at comparable densities with the white-eye. The iiwi and apapane (*Himatione sanguinea*) populations were growing linearly and had much lower densities than the white-eye and amakihi during 2004–2007 (Camp et al. 2010). But unlike the white-eye, these three native species were significantly declining throughout the old-growth forest after 2000 (Fig. 4).

The increase of white-eyes in the open forest area seems to be due more to immigration from the restoration area than to *in situ* reproduction. This is because juvenile survival dropped from 0.27 to 0 for all years during the increase (Freed et al. 2008a). The order of increase excludes the closed forest area as the source of necessary propagules. Given no other land use change near the refuge, it is most likely that white-eyes came from the restoration area. The exponentially growing population may have exceeded carrying capacity each year after 1999, set in part by native species whose populations were also increasing in the restoration area. The excess white-eyes over carrying capacity may have immigrated into the old-growth forest below.

However, the 0 juvenile survival of white-eyes was not associated with lower mass (Freed et al. 2008a), and is thus contrary to the general pattern in birds of lower mass resulting in lower juvenile survival (Medeiros and Freed 2009). Juveniles produced in the open forest area may have dispersed along a path of least resistance toward the lower density closed forest area. The increase in that area otherwise contradicts the assumption that the white-eye prefers open habitats in Hawaii (Scott et al. 1986) and in the Bonin Islands (Kawagami and Higuchi 2003), although preference for one habitat does not preclude preference for other habitats. The exponential increase in the closed forest at Hakalau either confirms the renowned ability of the entire family Zosteropidae for range and niche expansion (Scott et al 2003, Moyle et al. 2009), or simply resulted from dispersal of juveniles from the open forest or restoration areas.

The relatively small magnitude of the increase in white-eye density in the open forest area may have been severely underestimated. The area is very large (3373 ha) and includes introduced forest and forest with more open structure in the northern sections (Fretz 2002) (Fig. 2). Endangered species have their highest density in the southern section (Scott et al. 1986, Hart 2001). The closed forest area, where endangered species also have high density, is contiguous only with the southern section. There was a discrepancy between the white-eye densities in the two areas during 2004–2005 estimated from survey and mist-netting data. The survey data from the two areas indicated a density in the open forest area 1.4 times that in the closed forest area. However, capture rates in mist-nets were five-fold greater in the open forest study sites than in the closed forest site (Freed and Cann 2009), all in the southern portion of the refuge (Fig. 2). In addition, preliminary trend analysis indicated that the white-eye was increasing

while the endangered Hawaii akepa was declining in the southern-most transects 1–4 (Fig. 2), where akepa density was highest (Fig. 1), but this pattern disappeared when densities of the two species from the entire open forest area were analyzed (Freed et al. 2008a). These diverse data imply that most of the white-eye increase was in the southern portion of the open forest area, with an extent of increase much higher than the overall 1.05 bird/ha. It is critically important that future analysis of survey data treat the southern portion of the open forest area separately.

Impacts of white-eyes on native species. Competition between species is indicated by change in condition, survival, and/or numbers of one species as the other increases or decreases in numbers (Keddy 2001). There is some evidence that changes in native species were caused by competition with white-eyes. Mountainspring and Scott (1985) documented competition between white-eyes and several species of native birds from survey data collected during the late 1970s from the Hawaiian Forest Bird Survey (Scott et al. 1986). They detected negative correlation in density between white-eyes and native species, with adjustment for differences in habitat between study areas. Freed et al. (2008a) showed that the white-eye was replacing the akepa in the open forest study sites, but not in the closed forest site with lower white-eye captures in mist-nets (Freed and Cann 2009). Figure 1 shows more spatial evidence of negative correlation between akepa and white-eye densities.

The piecewise regression used by Freed and Cann (2010) showed declines in all native species in the open forest area during 2000–2007, two of which were significant (akepa and iiwi). Here we add two more species (amakihi, apapane) with significant declines during the white-eye increase (Fig. 4). White-eyes spend as much time in ohia-lehua foliage as the amakihi and apapane (Freed et al. 2008a).

In previous studies, we identified changes in condition of native birds in our open forest sites that could be produced only by a factor that influenced foraging substrates used by each native species. Changes included lower mass, lower fat, shorter legs, and shorter bills (Freed et al. 2008a,b; Freed and Cann 2009), which generated lower juvenile and adult survival. In addition, we identified changes in timing, duration, and symmetry of molt of all native species, with increasingly lower survival during the winter months of 2000–2004 (Freed and Cann 2012). These changes in molt have been experimentally induced by severe food limitation in other birds (Murphy et al. 1988, Swaddle and Witter 1994). It is difficult to imagine an alternative factor that reduced arthropods from the foliage and branches of ohia-lehua trees, and hidden in lichen-covered branches of koa trees, all foraging substrates used by white-eyes (Freed et al. 2008a).

None of the skeletal changes in native birds in the open forest sites were observed in the closed forest site during 2004–2005, where white-eye capture rates were only 20% of open forest rates (Freed and Cann 2009). During 2005, prevalence of non-normal molt was lowest in the closed forest site, but became highest in 2006 (Freed and Cann 2012). This reversal was associated with increased density of white-eyes in the closed forest area and decreased density in the open forest area between 2005 and 2006 (Fig. 3).

The impact of direct competition in the decline of native species cannot be ascertained without experimental evidence, but alternative explanations are unconvincing.

Avian malaria kills native birds, but it is too cool at upper elevations for avian malaria to be endemic (Freed et al. 2005). Introduced yellow-jacket wasps (*Paravespula pennsylvanica*) compete for food with native birds (Gambino et al. 1987), but these were controlled after 2000 (Freed and Cann 2009). Parasitoid wasps, escaped from biological control, could reduce native arthropods, but these were more prevalent at lower than at upper elevations (Peck et al. 2008). We documented an explosive increase in chewing lice (from a different introduced bird), which can increase food requirements to replace heat lost from degraded plumage (Freed et al. 2008b). However, signs of food limitation began in 2000 and worsened in 2002 (Freed et al. 2008a, Freed and Cann 2012), before lice became widespread in the community in 2003 (Freed et al. 2008b). Mean monthly air temperatures did not change between 1993–1999 and 2000–2006, indicating that climate change was not responsible for reduced productivity of arthropods (Freed and Cann 2012). If any of these alternatives had caused food limitation and lower survival in all native species, then they should have caused comparable food limitation and declines in white-eyes given the similarity in foraging substrates. In particular, the dynamic of molt and white-eyes between study sites and areas during 2005 and 2006 suggests that a third factor was not involved. Such factors, that favor one species over another to resemble competition, are frequent alternatives to competition (Keddy 2001).

Our data also presage connections between biotic resistance, diffuse competition, and a reversal of diffuse competition through propagule pressure. Biotic resistance relevant to this system is diffuse competition, which arises when multiple native species overlap different parts of the niche of a potential invader (MacArthur 1972). For an invader at low density, such competition in a tightly interacting native community can prevent increases in density (Case 1990). The overlap of multiple foraging substrates with each native species likely provided the diffuse competition that kept the white-eye at low density in the old-growth forest. However, when the population increased, based on the opportunities offered in the restoration area, this competition was overwhelmed by propagule pressure, as documented for other systems (von Holle and Simberloff 2005, Hollebone and Hay 2005, Colautti et al. 2006, Lockwood et al. 2005, Simberloff 2009). A removal experiment that reduces the density of white-eyes may help determine if limiting propagule pressure enables diffuse competition to be restored.

Conclusion

The pocket of low white-eye density that persisted for decades is now filling up with white-eyes from the restoration area. That area is a complete counterexample to restoration areas constraining invasion (Bakker and Wilson 2004). The entire bird community was at the threshold of food-limitation before the increase (Hart 2001). A moderate but sustained increase in white-eyes could then create major food limitation, although that increase may have been much higher in the southern portion of the refuge. Competitive superiority combined with propagule pressure was involved in

the increase in old-growth forest, while ecological opportunism was the basis for the increase in the restoration area. These are usually considered as alternatives for invasion success (Sax et al. 2007, Sol et al. 2012).

The U.S. Fish and Wildlife Service, in formulating its final comprehensive conservation plan in late 2010 (<http://www.fws.gov/hakalauforest/planning.html>), emphasized habitat restoration efforts on the refuge. Evidence presented here indicates that this plan will provide more ecological opportunities for white-eyes, and this will likely further increase the negative impacts on native birds in the forest below. The plan assumes that avian malaria is the greatest long-term problem for the birds (Benning et al. 2002, Atkinson and LaPointe 2009), and we have shown that epizootics occur in the open forest area (Freed et al. 2005). However, white-eye competition could be a more serious and immediate problem for Hawaiian forest birds, especially if the impacts are in the most intact native communities, as found by Herbold and Moyle (1986) for introduced fish.

A white-eye removal experiment must be performed to determine conclusively if competition is the cause of current food limitation in native birds and extensive declines. An experiment in New Zealand identified positive responses from multiple native species when an introduced bird was controlled (Tindall et al. 2007). Native Hawaiian birds have become so food-limited that they can neither breed successfully nor molt efficiently, and will certainly not be able to mount the expected energetically expensive immune response to malaria (Freed et al. 2005). The outcome of the experiment should serve to inform the future of management of Hawaiian forest birds at Hakalau and perhaps at other forested locations in Hawaii with native birds.

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