BIODIVERSITY RESEARCH

WILEY **Diversity** and **Distributions**

Predicting effects of large-scale reforestation on native and exotic birds

Liba Pejchar[1] 🄳 | Travis Gallo[2] | Mevin B. Hooten[3,1,4] | Gretchen C. Daily[5]

[1]Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO, USA

[2]Urban Wildlife Institute, Department of Conservation and Science, Lincoln Park Zoo, Chicago, IL, USA

[3]Colorado Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, Fort Collins, CO, USA

[4]Department of Statistics, Colorado State University, Fort Collins, CO, USA

[5]Department of Biology, Center for Conservation Biology and Woods Institute, Stanford University, Stanford, CA, USA

Correspondence
Liba Pejchar, Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO, USA.
Email: liba.pejchar@colostate.edu

Abstract

Aim: Ecological restoration is critical for recovering biodiversity and ecosystem services, yet designing interventions to achieve particular outcomes remains fraught with challenges. In the extensive regions where non-native species are firmly established, it is unlikely that historical conditions can be fully reinstated. To what degree, and how rapidly, can human-dominated areas be shifted via restoration into regimes that benefit target species, communities or processes?

Location: We explore this question in a >20-year-old reforestation effort underway at Hakalau Forest National Wildlife Refuge in montane Hawaii. This large-scale planting of *Acacia koa* trees is designed to secure populations of globally threatened bird species by transitioning the site rapidly from pasture to native forest.

Methods: We surveyed all forest birds in multiple corridors of young planted trees, remnant corridors of mature trees along gulches and at sites within mature forest. Using a Bayesian hierarchical approach, we identified which factors (distance from forest, habitat type and surrounding tree cover) had the most important influence on native and exotic bird abundance in the reforestation area.

Results: We found that 90% of native and exotic bird species responded quickly, occupying corridors of native trees approximately a decade after planting. However, native and exotic forest birds responded to markedly different characteristics of the reforested area. Native bird abundance was strongly predicted by proximity to mature forest and remnant corridors; conversely, exotic bird abundance was best predicted by overall tree cover throughout the area reforested.

Main conclusions: Our results demonstrate that large-scale tree planting in corridors adjacent to mature forest can catalyse rapid recovery (both increased abundance and expanded distribution) of forest birds and that it is possible to design reforestation to benefit native species in novel ecosystems.

KEYWORDS
Acacia koa, avian community composition, Bayesian hierarchical model, ecological restoration, habitat corridors, Hakalau Forest National Wildlife Refuge, Hawaiian forest birds, non-native species, reforestation

1 | INTRODUCTION

Large-scale ecological restoration is widely recognized as critical for recovering biodiversity and ecosystem function (Chazdon, 2008; Montoya, Rogers, & Memmott, 2012; Ouyang et al., 2016). Yet, these ecological experiments remain relatively young and few, with outcomes awaiting rigorous documentation, evaluation and use to improve the design of future projects (Allan et al., 2013; Lamers et al., 2015; Wortley, Hero, & Howes, 2013). Of special scientific interest and conservation urgency, is the outcome of restoration in the presence of non-native species. Across the large portion of the planet dominated by human land use (Ellis, Goldewijk, Siebert, Lightman, & Ramankutty, 2010), outcomes are likely to be novel, differing substantially from historical assemblages (Hobbs, Higgs, & Harris, 2009; Perring et al., 2015).

Perhaps the most challenging question facing large-scale restoration is how to restore human-dominated areas to provide benefits to target species, communities or processes. Eradication of non-native species is often unfeasible or undesirable, particularly where they are firmly established and the costs of eradication are prohibitive (Davis et al., 2011) or where they now play important ecological roles (Ewel & Putz, 2004). Under these conditions, in particular, the ability to predict restoration outcomes remains very poor (Block, Franklin, Ward, Ganey, & White, 2001; Miller & Hobbs, 2007).

We consider this challenge in the Hawaiian archipelago, a hotbed of endemism, extinction and invasion (Lockwood, 2006). Although Hawaii has 34 federally endangered bird species—more than all other U.S. states combined (USFWS, 2013)—it receives comparatively little funding for conservation (Leonard, 2008), making return on investment of restoration especially critical. Hawaii's birds are under siege from extensive habitat loss and fragmentation, and the compounding effects of novel herbivores, predators and parasites introduced on a naïve flora and fauna (Reed, Desrochers, Vanderwerf, & Scott, 2012; van Riper & Scott, 2001). Avian malaria has restricted the rarest species to high elevations at the edges of their historical ranges (van Riper, van Riper, Goff, & Laird, 1986). These refugia are relatively intact native forest patches in a mosaic of exotic-dominated shrubland and pastureland, but they are projected to shrink with climate change (Benning, LaPointe, Atkinson, & Vitousek, 2002). In the face of these challenges in Hawaii and elsewhere, large-scale restoration within the current and future critical range of species or communities at risk may offer the best prospect for recovery.

In Hawaii, and globally, plants and mammalian predators are most often the focus of control and eradication efforts, with non-native birds generally left unmanaged and their impacts unexamined (Case, 1996; Duncan, Blackburn, & Sol, 2003; but see Hughes, Martin, & Reynolds, 2017). Early studies focused on non-native birds as reservoirs of disease (van Riper et al., 1986), as competitors with native birds for food and nesting sites (Moulton & Pimm, 1983) and as catalysts for the promotion of other non-native species (Simberloff & Von Holle, 1999). At the same time, introduced birds may fill the same ecological roles (e.g., seed dispersal; Foster & Robinson, 2007) as missing native birds, with cascading effects on plant and animal communities. Understanding how restoration impacts the distribution and abundance of the entire bird community is, therefore, critical (Norton, 2009).

Native reforestation efforts in Hawaii are generally focused on the removal of a small number of highly invasive plants and animals and the restoration of native canopy and understorey plants to improve habitat for native species (USFWS, 2006). Eradication of the many additional well-established exotic birds (Lockwood, 2006) and invertebrates (Peck, Banko, Schwarzfeld, Euaparadorn, & Brinck, 2008) in these forests is impractical and not of immediate conservation priority. Areas undergoing reforestation can thus be considered novel ecosystems, with communities that differ from historical plant and animal assemblages (Hobbs et al., 2006, 2009).

A large-scale reforestation effort has been underway at Hakalau Forest National Wildlife Refuge (HFNWR) on the island of Hawaii for over 20 years. This refuge provides one of the highest quality forest habitats for four globally endangered bird species in the state (Scott, Mountainspring, Ramsey, & Kepler, 1986) and also has well-established and widespread non-native plant (Daehler, 2005) and bird species (Camp, Brinck, Gorresen, & Paxton, 2015; Camp, Pratt, Gorresen, Jeffrey, & Woodworth, 2010). The goal of the reforestation effort is explicitly to expand and improve native forest bird habitat by planting trees and understorey plants in corridors and patches. Camp et al. (2010) used bird survey data at HFNWR to discuss how long-term population trends could be influenced by tree planting. Our research complements theirs, focusing instead on the spatial distribution of native and exotic birds as a function of landscape context and to provide insight into the effective design of large-scale reforestation projects.

The objective of our study was to explore to what extent birds occupy this landscape a decade after tree planting and how bird density varies among planted corridors, remnant corridors and mature forest. Specifically, we assessed how landscape context—distance from mature forest, habitat type (e.g., planted or remnant corridor) and tree cover at various scales—impacts the distribution and abundance of native and exotic birds in areas undergoing reforestation. We demonstrated that the factors that predict the relative abundance of native and exotic birds are markedly different and that it is possible to design reforestation to benefit native species in novel ecosystems.

2 | METHODS

2.1 | Study site

HFNWR is a 15,390-ha reserve on Hawaii Island, United States (19°51′N, 155°18′W; Figure 1), established in 1985 to protect high densities of Hawaii's imperilled forest birds (Scott et al., 1986). Our study was located in the upper third of this refuge, which is characterized by mature mesic and wet rain forest at lower elevations (approximately 800–1,900 m), and pastureland (3,500 ha), which was once mesic forest, undergoing active reforestation at upper elevations (approximately 1,650–2,000 m). The average annual rainfall at HFNWR is 2,500 mm, and the mean daily air temperature is 15°C (Juvik & Juvik, 1998).

2.2 | Reforestation and habitat types

There are three distinct forested habitat types in our study area: mature forest, planted corridors and remnant corridors (Figure 2). Mature forest in HFNWR has a canopy dominated by koa (*Acacia koa*) and ohia (*Metrosideros polymorpha*) and a diverse understorey of mostly native shrubs and ferns. The upper portion of the refuge was once similarly forested but was cleared for cattle pasture in the 1800s and planted in non-native pasture grasses. Reforestation efforts began in earnest in the early 1990s, and the USFWS has since planted over 300,000 *A. koa* trees throughout this 3,500 ha area. This tree species was chosen because it occurred historically at these elevations, and it grows rapidly and survives well in conditions of high light and exposure.

The reforested area consists mostly of long, linear "planted corridors" of *A. koa* of variable length, stretching west and upslope from the mature forest to encourage dispersal of birds and plant propagules (Figure 1). Beginning in 2003, understorey species were also planted in these corridors. At the time of this study, there was no natural regeneration of understorey with the exception of ferns and one shrub, *Vaccinium reticulatum*. The planted corridors mimic the shape and location of "remnant corridors" in this landscape, which also vary in length. Remnant corridors were not planted, but rather consist of large *A. koa* and *M. polymorpha* trees growing naturally in and along gulches, and thus protected from cattle over the past several hundred years. These remnant corridors also stretch west and upslope from the native forest at lower elevations and occur less frequently in this landscape relative to planted corridors. Both types of corridors are approximately 40 m wide and between 0.5 and 2.5 km long.

2.3 | Bird surveys

We surveyed birds at HFNWR between May–August in 2007 and 2008, which includes parts of both the breeding and post-breeding period for most Hawaiian forest birds (Ralph & Fancy, 1994). Hawaii is distinct from much of the continental United States in that many bird species have extended breeding periods (December–July), with peak activity for most Hawaii Island species occurring from April to July (Ralph & Fancy, 1994). We observed birds at 125 point count locations distributed among eight planted corridors, four remnant corridors and the mature forest below and adjacent to each of these corridors. We used aerial imagery to select planted and remnant corridors for inclusion in the study, which were relatively evenly distributed across the reforestation area (Gould et al., 2013). Within each corridor, we established fixed point count locations starting 300 m within the mature forest and extending upslope at 150 m intervals along the length of the corridor until the corridor dissipated at the upper edge of the refuge. This 150-m interval between point count locations is standard protocol for forest bird surveys in Hawaii and is designed to minimize the likelihood of double-counting individual birds. We adopted this interval to ensure our findings were comparable to other published studies on Hawaiian forest bird populations (Camp et al., 2010; Paxton et al., 2016; Reynolds, Scott, & Nussbaum, 1980; Scott et al., 1986). This design resulted in 36 points in mature forest, 59 points in planted corridors and 30 points in remnant corridors (Figure 1).

At each point, we used the point transect distance sampling method to survey birds (Buckland et al., 2001; Reynolds et al., 1980). For each bird detected aurally or visually during an eight-minute count (the standard count period for Hawaiian bird surveys; Camp et al., 2010), we recorded species and distance to the individual. Cloud cover, rain, wind, gust and time of day were also recorded at each sampling location. Two expert biologists with years of experience observing birds in Hawaii and extensive training in distance estimation conducted all surveys. We surveyed birds at all points between dawn and 11:00 once in 2007 and twice in 2008 and changed the order of

FIGURE 1 This map illustrates the upper portion of Hakalau Forest National Wildlife Refuge, Hawaii (black line = refuge border), where the effect of reforestation on native and exotic birds was evaluated. Bird survey points are indicated with symbols (triangles = planted corridors; circles = remnant corridors). The mature forest (downslope) and the planted and remnant corridors (upslope) are dark in colour and the former pastureland undergoing reforestation with *Acacia koa* is light grey
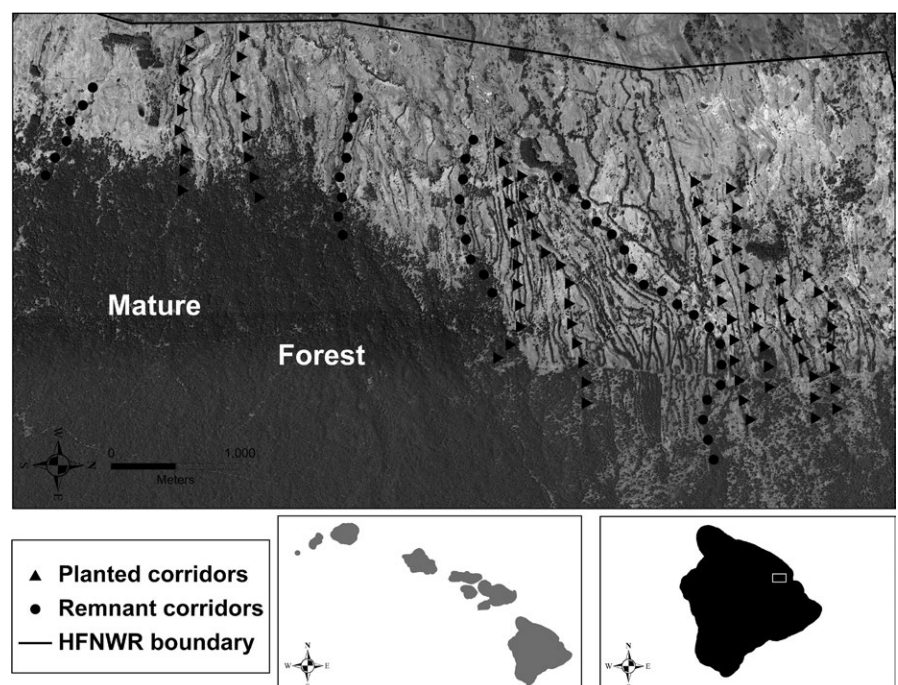
FIGURE 2 Photographs that illustrate the three distinct forested habitat types (a: mature forest; b: remnant corridors; c: planted corridors) in and adjacent to the reforestation area in Hakalau Forest National Wildlife Refuge, Hawaii

our visits such that each site was surveyed at multiple different times. We truncated all data on birds observed in corridor points at 20 m post-survey prior to analysis because 20 m was the average distance from the observer to the edge of the planted or remnant corridor, and we did not want to include observations outside of the habitat type of interest. Bird observations recorded from points within mature forest were truncated at 50 m prior to analysis.

2.4 | Habitat variables

We determined distance to mature forest from each point by carrying a hand-held GPS and walking the length of the corridors. Thus, our measure of distance to forest reflects the path a bird would move through a corridor (while foraging), rather than the shortest distance to the forest. We measured tree cover using ArcMap 10.0 and a 2010 WorldView II satellite image with 0.5 m resolution to estimate proportion of canopy cover at 10 m radii increments from 0 to 500 m and at 250, 500 and 1,000 m radii around each sampling point (Gould et al., 2013). Finally, we conducted principle components analysis using R (PCA; R Core Team, 2013) to capture dominant patterns of tree cover (e.g., declining or increasing with distance from point) to incorporate into the model described below.

2.5 | Abundance modelling

We used hierarchical open-population binomial mixture models (Kéry & Royle, 2010; Kéry & Schaub, 2012) to infer the abundance of native and exotic birds while taking into account species-specific detection probabilities. We used R (R Core Team, 2013) to conduct all statistical analyses. Our data can be expressed as $y_{i,j,k,t}$ point counts at each sampling location where $i = 1,....,I$, for each species $j = 1,....,J$, on visit $k = 1, 2$, during year $t = 2007, 2008$. Assuming the populations are closed over the course of each year, the observed counts arise as follows:

$$Y_{jkti} \sim \text{binomial}(N_{jti}, p_{jkti}), \qquad (1)$$

where N_{jti} is the total number of individuals for species i, at each site j, in year t, and p_{ijkt} is the species and survey-specific detection probability. Point count surveys were not conducted during rain or winds >2 on a beaufort scale, but cloud cover varied from 0% to 100%. Therefore, we modelled the detection probability for each species as a linear function of cloud cover (c) at the time of each survey using the logit link:

$$\text{logit}(p_{jkti}) = \alpha_{0_j} + \alpha_j c_{jkti}. \qquad (2)$$

We modelled the latent variable N_{jti} as a Poisson random variable,

$$N_{jti} \sim \text{Poisson}(\lambda_{jti}), \qquad (3)$$

where λ_{jti} represents the mean abundance (i.e., intensity) of each species at each site and year. To make inference on potentially influential covariates, we expressed λ_{jti} as a log-linear combination of the effects. The components of the log-linear model include the following: (1) environmental predictor variables (x_j) that help describe the niche for each species in the community and vary by location and (2) community-level interactions (e.g., relative abundance of guild members) to account for potential competition (see Appendix S1). The resulting log-linear model specification can be written as follows:

$$\log(\lambda_{jti}) = x'_j \boldsymbol{\beta}_i + \gamma_{jgjti}, \qquad (4)$$

where the $\boldsymbol{\beta}_i$ coefficients correspond to the affect, on each species, of distance from mature forest, habitat type (remnant or planted corridors), tree canopy cover at various scales and a principal component representation of changes in tree canopy cover. The coefficient γ_i affects the relationship between total guild member frequency g_{jti} and log intensity λ_{jti} for each species.

To implement this model with a Bayesian hierarchical approach, we specified Gaussian priors for coefficients. We fit all models in JAGS using the *runjags* package in R (Denwood, 2016; see Appendix S2). The critical forms of inference to assess the magnitude of effects on the abundance of native and exotic birds while controlling for a potential effect of intraguild competition are marginal posterior means, variances and credible intervals for model parameters ($\boldsymbol{\beta}_j$ and $\boldsymbol{\alpha}_j$) as well as mean square error (MSE) for each model calculated using leave-one-out cross-validation (Hooten & Hobbs, 2015; Link & Sauer, 2016). We also report the direction (positive or negative) of the effect for each bird species in the model, but the strengths of these relationships are not comparable among species due to large differences in abundance.

2.6 | Density estimation by habitat type

To estimate the density of each species by habitat type (mature forest, remnant corridors and planted corridors), we used distance sampling (DISTANCE, version 5.0, release 2; Thomas et al., 2010). Detection functions used for analysis included uniform and hazard rate with cosine and simple polynomial adjustment terms. We based model selection on a comparison of the

relative fit of these models and Akaike's information criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002). Because of limited detections of some species, estimating density in each habitat type was possible for only a subset of the species we recorded. For all other species (detections <75; Buckland et al., 2001), we report the presence–absence of each habitat type (Table 1).

3 | RESULTS

We observed 5,492 birds (n = 2,781 native, 2,711 exotic) in the reforestation area and adjacent mature forest. These included 20 species (10 native and 10 exotic; Table 1). These observations were comprehensive in that they include all extant bird species known to occur in Hakalau Forest NWR. A subset of native (n = 6) and exotic (n = 8)

TABLE 1 Density estimates for all native and exotic bird species observed in an area undergoing reforestation (planted and remnant corridors) and in adjacent mature forest in Hakalau Forest National Wildlife Refuge, Hawaii[a]

Species	Planted corridors	Remnant corridors	Mature forest
Hawaii Amakihi (N)[b] *Hemignathus virens* (n = 1,791)[c]	39.23 (10.7)	18.74 (14.6)	20.73 (16.3)
Iiwi (N) *Vestiaria coccinea* (n = 471)	0.99 (70.7)	6.87 (22.3)	4.34 (23.3)
Apapane (N) *Himatione sanguinea* (n = 417)	0.78 (43.5)	3.34 (27.2)	7.62 (22.6)
Hawaii Elepaio (N) *Chasiempis s. sandwichensis* (n = 143)	0.27 (78.7)	0.92 (44.5)	1.99 (28.2)
Omao (N) *Myadestes obscurus* (n = 164)	O	X	1.33 (28.7)
Hawaii Creeper* (N) *Oreomystis mana* (n = 41)	O	X	X
Akiapolaau* (N) *Hemignathus munroi* (n = 34)	X	O	X
Hawaii Akepa* (N) *Loxops c. coccineus* (n = 7)	O	O	X
Pueo (N) *Asio flammeus sandwichensis* (n = 6)	X	O	X
Hawaiian Hawk* (N) *Buteo solitaries* (n = 5)	O	X	X
Japanese white-eye (E) *Zosterops japonicus* (n = 1,679)	87.49 (12.8)	57.82 (7.2)	23.76 (14.7)
House Finch (E) *Carpodacus mexicanus* (n = 398)	0.96 (39.3)	1.99 (25.6)	2.21 (67.4)
Red-billed Leiothrix (E) *Leiothrix lutea* (n = 297)	0.27 (29.7)	6.84 (38.2)	8.64 (29.6)
Northern Cardinal (E) *Cardinalis cardinalis* (n = 171)	0.88 (36.5)	1.33 (29.9)	2.50 (46.2)
Erckel's Francolin (E) *Francolinus erckelli* (n = 35)	X	X	X
Kalij Pheasant (E) *Lophura leucomelana* (n = 29)	X	X	X
Barn Owl (E) *Tyto alba* (n = 12)	X	O	X
Wild Turkey (E) *Meleagris gallopavo* (n = 9)	X	X	O
Eurasian Skylark (E) *Alaudia arvensis* (n = 7)	X	O	O
Melodious Laughing-Thrush (E) *Garrulax canorus* (n = 1)	O	O	X

[a]Density estimates (birds/ha [%CV]) are presented for those species with sufficient detections for program DISTANCE (n ≥ ~75; Buckland et al., 2001); the presence or absence in a habitat type is indicated by an "X" and an "O," respectively, for all other species.
[b]N = native, E = exotic and * = federally endangered.
[c]Total number of independent observations for each species.

species with sufficient detections to meet modelling requirements was included in the abundance model to evaluate the influence of landscape context and habitat type on abundance (Appendix S3.1–14). All native and most exotic birds (together 98.4% of total observations) that met the criteria for modelling abundance were forest-affiliated species (Camp et al., 2010).

The abundance and distribution of native and exotic birds in the reforestation area were not influenced by the same variables (Table 2). The top model predicting the abundance of native birds included distance from mature forest and habitat type (planted or remnant corridors). The abundance of Omao (*Myadestes obscurus*), Apapane (*Himatione sanguinea*), Hawaii Amakihi (*Hemignathus virens*), Hawaii Elepaio (*Chasiempis s. sandwichensis*) and Iiwi (*Vestiaria coccinea*) all declined in planted and remnant corridors as distance from mature forest increased (Table 3). Abundance of Apapane and Iiwi increased in remnant corridors, but we did not detect an effect of habitat type on abundance of the other native species. Tree cover was less important for native bird abundance, regardless of scale or pattern.

All models evaluating the influence of landscape context variables such as distance mature forest or surrounding tree cover on exotic species had similar predictive power (Table 2). In contrast to all native birds, abundance of the most common exotic species, Japanese white-eye (*Zosterops japonicus*), increased with distance from mature forest (Table 3). Models that included tree cover at 500 and 1,000-m scales were associated with increased abundance for Red-billed Leiothrix (*Leiothrix lutea*) and Northern Cardinal (*Cardinalis cardinalis*). Habitat type was a less important predictor of abundance for exotic compared with native species.

TABLE 2 Hierarchical binomial mixture models and mean squared error (*MSE*) predicting the abundance of native and exotic birds as a function of landscape context, tree cover and habitat type in the large-scale reforestation of the upper portion of Hakalau Forest National Wildlife Refuge, Hawaii

Model	MSE
Native bird abundance	
Distance from mature forest+habitat type	1.377
Habitat type	1.392
Distance from mature forest	1.576
Tree cover (500m)	1.578
Tree cover (250m)	1.579
Tree cover (1,000m)	1.581
PCA (tree cover pattern)	1.598
Exotic bird abundance	
Distance from mature forest	0.176
Tree cover (1,000m)	0.177
Tree cover (500m)	0.179
Habitat type	0.179
Tree cover (250m)	0.180
PCA (tree cover pattern)	0.180
Distance from mature forest+habitat type	0.180

TABLE 3 The influence of habitat type (remnant or planted corridor), tree cover at various scales, patterns of tree cover and distance from mature forest on the abundance of forest birds in the reforestation of pastureland at Hakalau Forest National Wildlife Refuge, Hawaii[a]

Species (common name; feeding guild)	Distance from mature forest	Habitat Type (planted corridors)	Tree Cover (250 m radius)	Tree cover (500 m radius)	Tree cover (1,000 m radius)	PCA1 (pattern of tree cover)	PCA2 (increase in tree cover)
Hawaii Amakihi (N) (omnivore)	−	.	.	.	.	.	.
Apapane (N) (nectarivore)	−	−	.	.	.	.	.
Iiwi (N) (nectarivore)	−	−	.	+	+	.	.
Hawaii Elepaio (N) (insectivore)	−	.	+	+	+	.	.
Omao (N) (frugivore)	−	.	.	.	.	.	.
Japanese white-eye (E) (omnivore)	+	.	.	.	.	−	−
Red-billed Leiothrix (E) (omnivore)	.	−	+	+	+	−	.
Northern Cardinal (E) (granivore)	.	.	+	+	+	−	+

[a]Positive (+) effects, negative (−) effects and no effect (.) are indicated with symbols. Only forest-dependent species with sufficient detections to model effects are shown. N, native and E, exotic.

The highest estimated densities of both the native Hawaii Amakihi and the exotic Japanese white-eye were in the planted corridors, but most other forest bird species were at highest estimated densities in the remnant corridors and mature forest (Table 1). Several species were rarely detected in planted corridors, but were present in remnant corridors within the reforestation area, as well as the mature forest. These include Red-billed Leiothrix, Omao and two federally endangered species, Hawaiian Hawk (*Buteo solitarius*) and Hawaii Creeper (*Oreomystis mana*). A third endangered species, Hawaii Akepa (*Loxops c. coccineus*), was observed only in the mature forest. Two additional native species, Pueo (*Asio flammeus sandwichensis*) and Akiapolaau (*Hemignathus munroi*), a federally endangered species, were detected both in planted corridors and mature forest (Table 1).

4 | DISCUSSION

The widespread establishment of exotic species poses challenges in achieving traditional restoration outcomes such as replicating historical community composition (Norton, 2009). In many cases, we will need to sustain native species within novel ecosystems that include exotic species (Seastedt, Hobbs, & Sudling, 2008). This study demonstrates that both native and exotic species have occupied an area undergoing large-scale reforestation in Hawaii. We show, however, that these species have responded in distinct ways. We produce strong evidence that there are features of the reforestation area that are positively associated with the abundance and distribution of native birds, but that the several common exotic birds at this site were not consistently associated with these same habitat and landscape characteristics.

Our findings suggest that reforestation projects can be designed to favour native species. For example, trees planted adjacent to native forest are likely to support a greater abundance of native species, compared with more isolated plantings used primarily by exotic birds. In addition, where remnant corridors persist, they can be used to guide restoration strategies for mobile species such as birds. For example, in our system, remnant corridors more closely resembled mature forest in canopy structure and species composition, but also mimicked planted corridors in their long, linear shape and spatial context (Figure 1). Adding understorey diversity to planted corridors, an effort that is already underway at HFNWR, is likely to favour native species as planted corridors mature.

Many of the bird species we observed in the reforestation area are capable of flying across the mosaic of planted and remnant corridors and pastureland, as well as linearly through the corridors. Our distance to forest measure was designed to capture the relative importance of moving through corridors for species that may be more reluctant to move across forest gaps and to test whether some species can only persist within the reforestation area if they are in woodlands that are connected and in close proximity to a large tract of contiguous mature forest. Indeed, we found that our measure of distance to forest was important for all native birds. Our study captured some of the influence of adjacent corridors by measuring all tree cover around each survey point (including all planted and remnant trees). Our results indicate that proximity to tree cover (e.g., other corridors) is likely to be more important for exotic birds than native birds.

Restoration at HFNWR appears to favour Japanese white-eye, the most abundant exotic species. However, the abundance of Japanese white-eye is negatively associated with proximity to mature forest. This finding is encouraging, suggesting that Japanese white-eye may decline in abundance and native bird species may increase over the long-term, as the plant communities in the reforestation area mature and diversify. Future research priorities include understanding the mechanisms behind these patterns, including potential interspecific interactions (Duncan, 1997).

Six of ten native birds at HFNWR were observed in planted corridors, and seven of the ten species were recorded in the remnant corridors. These results strongly indicate that reforestation has achieved success in providing breeding and/or foraging habitat for most forest bird species on Hawaii Island (Strommer, 2011). There may be a relationship between feeding guild and the potential for native and exotic birds to colonize planted corridors. Omnivorous birds and generalist insectivores (e.g., Hawaii Amakihi, Japanese white-eye) were generally abundant in planted corridors, while frugivores, nectarivores and specialist insectivores (e.g., Omao, Iiwi and Apapane) tended to be more abundant in remnant corridors and mature forest (Table 3). Of the four federally endangered species, Akiapolaau, which forages preferentially on *A. koa* (Pejchar, Holl, & Lockwood, 2005), was the only species using planted corridors. In contrast, Hawaii Creeper and Hawaiian Hawk occurred only in remnant corridors and mature forest, which offer foraging substrates (e.g., ohia) and cover for food and nesting for these species (Klavitter, Marzluff, & Vekasy, 2003; Vanderwerf, 1998) that are not yet available in the planted corridors. However, our study was not designed for the optimal detection of raptors and our sample size for Hawaiian Hawk was small (*n* = 5). Previous research indicates that this species uses a wide variety of habitat types, including young planted stands and open habitat (Gorresen et al., 2008). Finally, Hawaii Akepa was the only endangered species observed exclusively in mature forest, probably because it is an obligate cavity nester (Sincock & Scott, 1980).

Long-term survey data are needed to understand the full consequences of large-scale reforestation efforts (Camp et al., 2010). Although variation associated with density estimates in each habitat type varied substantially by bird species in this study, our findings provide a useful baseline for long-term monitoring. Monitoring may also reveal thresholds at which species colonize or increase rapidly in abundance as stands age (Gardali et al., 2006). Information on population dynamics would also provide a better measure of reforestation success (Block et al., 2001; Strommer, 2011). Expanding the number of survey stations located in the planted area would more fully address these questions through HFNWR's annual bird surveys. More generally, incorporating monitoring for desirable and undesirable outcomes in the initial design stages of future restoration projects will be helpful.

We have shown that birds can respond rapidly to large-scale reforestation, with native and exotic species occupying stands as far as a kilometre away from mature forest within a decade. This rapid return of bird activity after planting of a single species supports

the idea that such efforts can potentially "jump start" ecosystem recovery (Passell, 2000), particularly if the return of these birds catalyses the recovery of ecological processes such as pest control, pollination and seed dispersal. This approach could work particularly well at large scales and where resources are limited (Brown & Lugo, 1994). As in HFNWR, a small number of skilled and highly motivated restoration professionals could mobilize a large number of volunteers and/or employ local people. A well-designed reforestation programme can thereby meet multiple objectives: providing new insights into community assembly in novel ecosystems, improving habitat for native species in the presence of established exotic species, contributing to the local economy, and engaging society in the science and practice of ecological recovery.

ORCID

Liba Pejchar 🄳 http://orcid.org/0000-0002-9253-9884

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BIOSKETCH

Liba Pejchar (sites.warnercnr.colostate.edu/liba/) pairs ecology with other disciplines to pursue innovative solutions to sustaining and restoring biodiversity and ecosystem services. Her research often focuses on the factors that shape species distribution, community composition and ecological processes on human-dominated lands. The team of authors is broadly interested in using field ecology along with advanced quantitative methods to address global conservation challenges and achieve benefits for nature and people.

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SUPPORTING INFORMATION

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