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Population decline of the Elfin-woods Warbler *Setophaga angelae* in eastern Puerto Rico

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Summary

We estimated the population density of the globally threatened Elfin-woods Warbler *Setophaga angelae* within two forest types at different elevations in the Luquillo Experimental Forest in north-eastern Puerto Rico. Population densities ranged from 0.01 to 0.02 individuals/ha in elfin woodland and 0.06–0.26 individuals/ha in *palo colorado* forest in 2006, with average rates of decline since 1989 of 0.002–0.01 and 0.003–0.06 individuals/ha respectively. These estimates show a significant general declining trend from c.0.2 individuals/ha in 1989 in elfin woodland to c.0.02/ha in 2006, and from 1 to 0.2 in *palo colorado* forest. Although variation in estimated population density depended on the statistical method used, we document and discuss possible causes of an overall population decline from 1989 to 2006, lending support to previous initiatives to reclassify the species from the IUCN Red List category of "Vulnerable" to "Endangered".

Resumen

Se estimó la densidad poblacional de la reinita de bosque enano ("Elfin-woods Warbler") *Setophaga angelae*, nombrada globalmente como en peligro de desaparición, dentro de los dos tipos de bosques a diferentes alturas del Bosque Experimental de Luquillo en el noreste de Puerto Rico. Las densidades poblacionales variaron de 0.01 a 0.02 individuos por hectárea en bosque enano y 0.06–0.26 individuos por hectárea en bosque de palo colorado en el 2006, con tasas de disminución promedio desde 1989, 0.002–0.01 individuos y 0.003–0.06 individuos por hectárea. Estas estimaciones muestran una baja en la tendencia general significativa de c.0.2 individuos por hectárea en 1989 en bosque enano a c.0.02 por hectárea en 2006, y de 1 a 0.2 en el bosque de palo colorado. Aunque la variación de la densidad poblacional estimada depende del método estadístico utilizado, documentamos y analizamos las posibles causas de un descenso de la población total desde 1989 a 2006, prestando apoyo a las iniciativas para reclasificar la especie de la categoría de la IUCN amenazada "Vulnerable" a "de extinción".

Introduction

One of 34 species in the genus *Setophaga*, the Elfin-woods Warbler *S. angelae* (hereafter EWWA) is the most recently discovered of the New World wood warblers (Family Parulidae). Discovered in 1968 and described in 1972, the endemic and "Vulnerable" (BirdLife International 2010) EWWA is an 8 g (Arendt *et al.* 2004) bird confined to the montane forests of Puerto Rico where it is local and uncommon (Kepler and Parkes 1972, BirdLife International 2010).

Since its discovery and classification, there has been concern regarding the status and future of the species owing to its limited range and dwindling habitat as a result of continuous island-wide development (Kepler and Parkes 1972, Willis 1972, Gochfeld *et al.* 1973, Pérez-Rivera and Maldonado 1977, Dietz 1987) and predicted repercussions of escalating climate change (Wormworth and Mallon 2006). Conservation efforts for the species began by listing it in 1982 as a Federal Candidate Species under the Endangered Species Act. However, preliminary studies shortly thereafter by Cruz and Delannoy (1984) within the 4,150-ha Maricao Forest (18°09′N, 66°58′W) in western Puerto Rico, suggested long-term population viability given no unforeseen substantial reduction or degradation of habitat.

Unfortunately, however, continued habitat loss and alteration, and the indirect consequences of global climate change, such as the increase in Atlantic cyclone events (Goldenberg *et al.* 2001, Webster *et al.* 2005) have produced a different effect. More recent studies (Arroyo-Vázquez 1991, Waide 1995, Miranda-Castro *et al.* 2000, Anadón-Irizarry 2006) have documented the disappearance of the species or at least local population declines from much of its former range throughout Puerto Rico along the Cordillera Central and Sierra de Cayey, including the easternmost population in the Luquillo Mountains. Through extensive island-wide surveys conducted in 2003–2004, Anadón-Irizarry (2006) documented that the EWWA's distribution was limited to two disjunct montane forests separated by about 150 km: the Luquillo Experimental Forest (LEF) in the east and the Maricao Commonwealth Forest in the west. Populations were patchy and occurred at low densities in both forests, thus threatening the long-term survival of the species. The remnant EWWA population has been estimated at 300–1,800 individuals (Anadón-Irizarry 2006, BirdLife International 2010). Anadón-Irizarry (2006) recommended that the species be reclassified as "Endangered" under the Endangered Species Act and IUCN. Most recently (July 2011), in collaboration with BirdLife International, the Puerto Rican Ornithological Society (la "Sociedad Ornitológica Puertorriqueña, or SOPI) began surveying for the warbler in potential habitat in the Carite Commonwealth Forest, hoping to discover a potential third population. Unfortunately, some 25 expeditions failed to detect the species (V. Anadón-Irizarry *in litt*. 2012).

Quantifying the observed shifts in EWWA population and habitat range is critical in determining the impact of current threats to its survival and appropriate classification for large-scale conservation schemes. As part of the USFS/International Institute of Tropical Forestry's long-term study to determine forest-bird community response and adaptation to intensifying cyclonic events, a major indicator of global climate change, we present analyses of 17 years of data tracking EWWA population trends within the LEF. Our four main objectives were to: (1) compare population densities among forest types; (2) compare the rapidly evolving statistical methods used in deriving population densities, (3) document and discuss possible causes of an overall population decline from 1989 to 2006; and (4) determine if our results support previous initiatives to reclassify the species from globally Vulnerable to Endangered.

Methods

Study area

We conducted our study from September 1989 to October 2006 within the 11,330-ha Luquillo Experimental Forest (LEF, or El Yunque) in the Luquillo Mountains of eastern Puerto Rico (18° 19′N, 65° 45′W) (Figure 1).

These mountains constitute an isolated range of Cretaceous monadnocks resulting from uparching and faulting (Mitchell 1954) that rise to 1,075 m elevation, 8–15 km from the ocean, depending on location (Weaver and Murphy 1990). Average annual rainfall and temperature range from 3,000 mm and 25.5° C in the foothills to more than 5,000 mm and 18.5° C on peaks higher than 1,000 m, respectively (Brown *et al.* 1983, García-Martinó *et al.* 1996).

The LEF is comprised of four major forest types (*tabonuco*, *palo colorado*, palm, and elfin woodland) that are stratified by elevation and placed into separate life zones (see Wadsworth 1951, Ewel and Whitmore 1973 for a more detailed description). Our study sites traversed subtropical wet forest as well as lower montane wet and rain forest (Holdridge 1967, Brokaw and Grear 1991).

Historically, elfin woodland has been the EWWA's primary habitat; it is confined to higher elevations and peaks above 750–850 m and covers only about 405 ha, or 4% of the LEF. However,

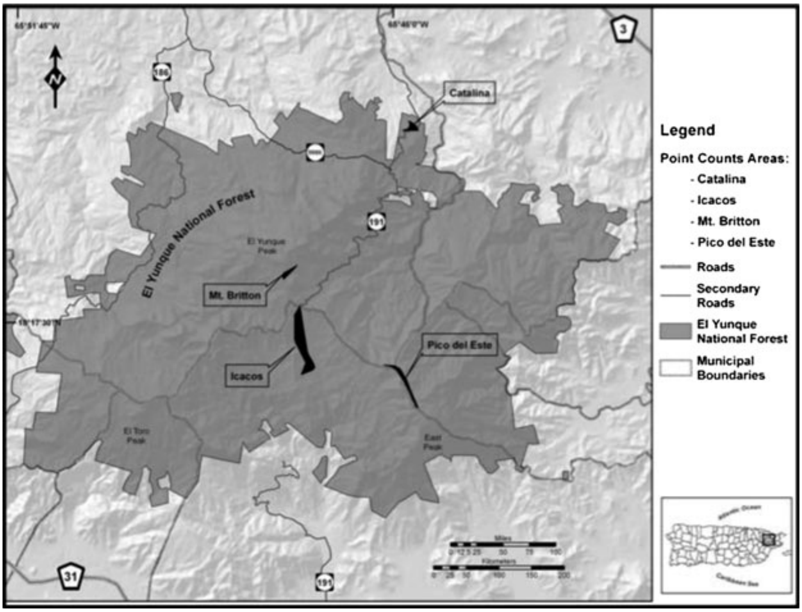

Figure 1. Map of the Luquillo Experimental Forest (El Yunque National Forest), Puerto Rico, portraying avian survey routes within different forest types.

it harbours more endemic trees and shrubs than do the other forest types (Weaver and Murphy 1990, Weaver 1995). Relative humidity beneath forest cover remains almost constant between 99 and 100% (Byer and Weaver 1977). As a result of such high humidity, strong winds, heavy, nearly constant rainfall (> 5,000 mm) and thus saturated, nutrient-drained soils, elfin woodland is comprised of dense stands of short, twisted trees and shrubs with diameters averaging 5–10 cm and heights rarely exceeding 5 m. Five species often account for 95% of the stems of at least 10 cm diameter at breast height (DBH) (Weaver *et al.* 1986). Three dominant species (*Tabebuia rigida* Urban, *Ocotea spathulata* Mez, and *Calyptranthes krugii* Kiaersk) regularly account for 80% of total tree density (Howard 1968).

During our study, the only other habitat in which EWWA was observed in substantial numbers—*palo colorado* forest—is located in the lower montane wet forest zone between roughly 600 and 900 m, encompassing 3,318 ha (c.30% of the LEF). Average annual rainfall is c.3,800 mm (Weaver and Murphy 1990). Although *palo colorado* forest includes more than 50 tree species (Wadsworth 1951), it is named for the *palo colorado* or swamp cyrilla *Cyrilla racemiflora*, which, although rarely exceeding heights of 18 m, may reach almost 3 m in diameter and can survive more than 1,000 years (Weaver 1986). Weaver and Murphy (1990) estimated c.1,850 trees/ha with a total basal area of 40 m^2/ha.

Methodology and survey protocol

Count plots consisted of fixed-radii, concentric circles. Detection distance within a plot was recorded for all detections. Using point transects spaced 100 m apart, data were collected for relative abundance as well as distance sampling density estimation analyses. In total, 130 points were dispersed among the four forest types and a mixed-species plantation (Table 1, Figure 1). Points were distributed along an elevational gradient from a minimum of 90 m along Road 988 near the Mameyes River to a maximum of 1,005 m near East Peak, just outside the perimeter of a former

Table 1. Dispersion of 130 count points among four forest types and a mixed-species plantation in the LEF, Puerto Rico: EW (elfin woodland); PC-PCt (*palo colorado–palo colorado* transition to EW); PF-EW (mixed palm forest-elfin woodland); TA (*tabonunco*); PL (mixed-species plantation).

Survey Route	Forest Type	No. of Points	Elevational range (m)	Latitude-Longitude Range
Road 988	TA	30	90 - 212	18°19′45″N, 65°45′06″W - 18°19′30″N, 65°44′36″W
Catalina Service Center	PL	10	150 - 200	18°20′34″N, 65°45′47″W - 18°20′25″N, 65°45′53″W
El Verde	TA	30	510 - 610	18°18′53″N, 65°49′22″W - 18°18′17″N, 65°49′29″W
Icacos Valley	PC-PCt	30	642 - 748	18°16′46″N, 65°47′19″W - 18°17′51″N, 65°47′25″W
Mt. Britton	PF-EW	15	810 - 900	18°18′31″ N, 65°47′31″W - 18°16′57″N, 65°46′04″W
East Peak	EW	15	900 - 1005	18°16′57″ N, 65°46′04″W - 18°16′20″ N, 65°45′39″W

U.S. Naval radar station. Ten of the 130 points were placed near the USDA Forest Service's Catalina Service Centre in a mixed-species plantation of *Pinus elliottii* var. *Pinus caribaea*; kadam *Neolamarckia cadamba*, and mahogany *Swietenia macrophylla* x *mahagoni* hybrid. However, because no EWWA were observed in the plantation during a 10-year period (1989–1999) and only two birds were observed from 1998 to 2006 in *tabonuco* forest (Road 988 and El Verde), the analyses are limited to elfin woodland and *palo colorado* forest.

Field biologists covered 30 transect points in each forest type in two days (15 points per day) between 05h30 and 09h30 AST (Atlantic Standard Time). Surveys were conducted approximately monthly from 1989 to 2006. To minimise observer bias, three field biologists conducted most of the surveys over the 17-year period. One biologist (Roberto Díaz) conducted virtually all surveys over an 8-year period, almost half of all surveys completed. Occasional substitutions were made when he was absent or ill. A gap in data collection in 2003 led us to remove a portion of that year from our analysis.

Observers recorded the number of birds detected as well as their distance from the count point. From September 1989 to December 1997, a relative abundance fixed-width (≤ 25 and > 25 m) distance-classification method was used (Hutto *et al.* 1986), so individual bird distances from the count point were classified into ≤ 25-m or > 25-m bins. During this time period, exact distance was not estimated. From February 1998 to November 2006, a distance sampling classification method was employed, with exact distances estimated by the observer and binned into five concentric circles of 0–5, 6–10, 11–20, 21–40, and > 40 m (Buckland *et al.* 1993).

Statistical analysis

In order to evaluate EWWA population dynamics in the LEF, we used two methods to estimate the population density for each of the two forest types. These methods were designed to make use of data collected from both sampling periods and to ensure that the estimated long-term population trends are robust. We decided to analyse data from the higher elfin woodland and lower *palo colorado* forest types separately since EWWA vertical migration has been suggested, with birds moving to lower elevation, north-facing forests during seasons of heaviest rainfall (USFWS 2001, CBD 2004).

Population density estimates were calculated for each monthly survey, and then averaged to determine the annual mean population density estimate and associated standard error. In this way, the same bird detected month after month could not falsely inflate the population density estimate. Similarly, keeping the two forest types or elevations separate, contributed to avoiding any multiple counts based on seasonal migration. Population density trends could thus be observed from year to year. As such, the estimated population density then represents the mean number of EWWA per hectare per count survey, consistent with many other reports.

Methods 1 and 2

Both methods are modified based on the standard distance sampling population density estimation equation (Buckland *et al.* 1993). The modification is necessary because our data were not collected to strictly adhere to the requirement of a distance sampling protocol, owing to the rapid evolution of avian survey methodologies. When this study began in late 1989, relative abundance (Hutto *et al.* 1986) was the standard metric. In 1998 we replaced the standard relative abundance protocol with the distance sampling method because of the program's ability to estimate population density and size. Our modification is aimed at capturing the long-term trend of population density and providing a range of population density instead of a definite estimate.

Our first of two estimation methods (eq. 1) is a simplified model based on a distance sampling population density equation:

$$\text{Density} = n\,(1/\tau^2)/(2\pi k) \tag{1}$$

where n = number of birds detected, $\tau^2 = (1/n)\sum d^2$, the mean squared distance of birds detected (assuming a half normal detection probability model), d = distance from transect count point to each bird detected, and k = number of points visited (n = 30) each sampling trip. This equation incorporates an estimated probability curve (the half normal model) that a bird located d distance from the count point will actually be detected during the survey. In this way, we estimated the population density of birds based on the probability of seeing a bird as a function of the distance from the observer. The detection probability model is difficult to decide based on the data because distances are in distance bands, rather than accurate measures. With the reported robustness of the half-normal model and our objective of emphasising the long-term trends, the half-normal assumption is a reasonable compromise.

The difference between methods 1 and 2 reflects the two different sighting-distance recording methods, or classifications, used in data collection. Method 1 classifies sighting distances into two classes (concentric-radii circles of mean radius 12.5 or 35.5 m), and method 2 classifies distances into 5 classes (2.5, 7.5, 15, 30, 45 m mean-radius concentric circles). Data collected before 1998 used a two-category distance classification method and data collected since 1998 used the 5-category distance classification method. As a result, method 2 can only be applied to data collected since 1998. Data collected since 1998 were reclassified into two distance classes when method 1 is used. We note that our data were collected before the standard distance sampling methods were developed. Consequently, we either must discard the historical data (which will lead to the loss of information) or sacrifice accuracy of the estimated population density. A compromise is to analyse the data using two methods, each reflects the limitations of the data collected from different time periods. Such a compromise is necessary in order to understand the long-term trend of population dynamics in the region. To ensure that the estimated population density trend is reasonable, we also analysed the data using a third method.

Method 3

Because any distance sampling method is sensitive to the detection probability model assumed and to inaccuracies in estimating distances, the resulting population density estimate may be unreliable. Such uncertainty may be one explanation for the high year-to-year variability in estimated EWWA population density.

We therefore used just the count data and a bootstrapping technique to estimate the median count per point (including 95% confidence intervals). This method makes no assumption about the detectability of the birds recorded, other than that it was assumed to be similar across the study period. For each of the two habitats considered, 999 bootstrapped samples of the count data were obtained by random sampling with replacement from the original dataset. For each of these 999 samples, a mean count per sample was calculated for each calendar year and median and 2.5 and 97.5 percentiles of these was obtained. Years where the 95% CIs did not overlap can be said to be significantly different from each other.

Results

Distribution and abundance

During this study, although two singing EWWA males (< 1% of all detections) were observed at El Verde on the western slope of the LEF at elevations of 585 m (18°18′21″N, 65°49′26″W) and 600 m (18°18′17″N, 65°49′29″W) in *tabonuco* forest on 8 August 2002 and another male was heard singing near a Puerto Rican Parrot *Amazona vittata* nesting area in April 2011 (W. Arendt pers. obs.), all other EWWA were found in only two of the four forest types: elfin woodland and *palo colorado* forest. In total, over the 17-year period, there were 1,442 EWWA detections: 1,035 (72%) in *palo colorado* forest (Icacos Valley) and 405 (28%) in elfin woodland, 397 at East Peak but only eight at Mt. Britton. EWWA were recorded at all 30 points in Icacos Valley and all 15 points at East Peak, but only six of 15 points at Mt. Britton (elfin woodland), and just two of 30 points in *tabonuco* forest at El Verde. In *palo colorado* forest, EWWA detections decreased from 675 between January 1989 and December 1997 to 360 between February 1998 and October 2006. In elfin woodland during the same two periods, EWWA detections decreased from 333 to 64 at East Peak and from six to two at Mt. Britton.

The El Yunque EWWA population is likely declining. Estimated annual population densities (in number of birds per hectare per count) in dwarf and *palo colorado* forest are shown in Figure 2. These estimates show a general declining trend from c.0.2/ha in 1989 in elfin woodland to c.0.02/ha (Method 1) in 2006 and from 1 to 0.2/ha in *palo colorado* forest (Figure 2). This apparent temporal trend is statistically significant ($\alpha = 0.1$) based on a non-parametric trend test (Mann-Kendall test; Gilbert 1987) done on the results from using methods 2 and 3 for both dwarf and *palo colorado* forests.

The upward jump in estimated density at the beginning of the second survey period (1998–2006) using Method 1 may reflect the effect of the change in counting methods rather than an actual change (increase) in population density, because the estimated density using Method 3 at the beginning of the same time period did not show the same jump. To verify this, we used a more relevant non-parametric test, the Jonckheere-Terpstra trend test (Page 1963), which compares the null (no trend) to the alternative of a consistent trend. The test results ($P < 0.1$) suggest a consistent declining trend and that the large jump in the estimated number in 1999 in *palo colorado* forest is not inconsistent with this trend. In corroboration, the forest's most common species (Bananaquit *Coerba flaveola*) showed no sharp population incline in elfin woodland with the advent of Method 2 (proportions test: z-statistic = 0.9, $P = 0.3$; $n_{(1989\text{-}1998)} = 5{,}908$, proportion = 0.48; $n_{(1998\text{-}2006)} = 4{,}624$, proportion = 0.49). The third method, which uses the count data only, shows a peak in numbers in elfin forest near the start of the study period in 1992 and a consistent decline afterward to very low numbers at the end. In *palo colorado* forest, numbers recorded were generally significantly lower during the latter half of the time series compared with the first half (see Appendix 1 in the online supplementary materials for bootstrapped medians and confidence intervals).

Discussion

Our study supports the perception of an overall declining EWWA population and a decrease not only in occupied habitat types but also in number of occupied areas within a habitat. We reached this conclusion based on imperfect density estimations using two different models because the data we

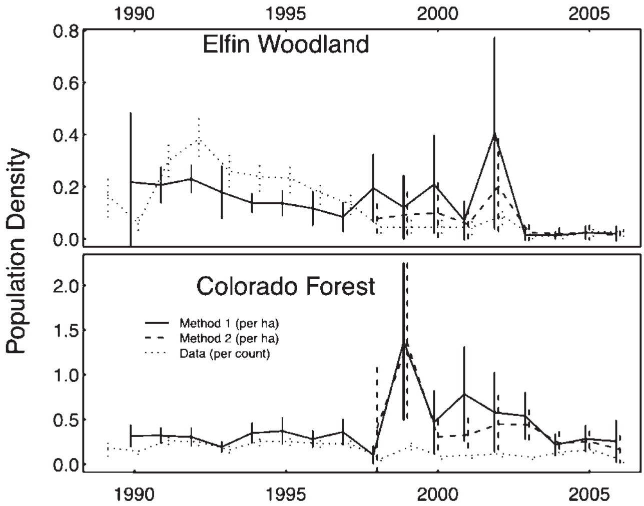

Figure 2. Estimated EWWA population density (number of birds per hectare per count) over time showing a higher density in *palo colorado* forest than in elfin woodland and a declining trend in both forest types.

used were not all collected according to the distance sampling protocol. Accurate density estimation may need a new sampling design, but despite this, the raw count data show a clear decline.

Comparison of population density estimate methodologies

The results of our study show that the difference in estimated population density between method 1 and method 2 is not obvious. Although we hypothesised that method 2 could overestimate population density because of the increased number of distance bins, there was only one set of distance data and the difference between method 1 and method 2 cannot reflect the potential difference between the sampling methods. Consequently, it is unclear whether the change in sampling method has led to any misrepresentations of EWWA populations. The unexpected jump at the beginning of the second survey period starting in 1998 using method 2 suggests that changes in survey methodology may lead to unexpected consequences, albeit not all species, such as the Bananaquit, showed this sharp increase.

When assigning sightings into distance bins, uncertainty associated with the estimate enters when the bins change. We had a relatively stable number of sightings in 1998 and 1999 based on the method 3 estimates (Figure 2). But in 1999, shortly after the survey method was changed, some of these sightings were assigned into the maximum distance bin (> 40 m), resulting in a large jump in estimated population density. Is this increase real or is it simply a statistical artifact of the method? We calculated the summary statistics of all of the species (n = 16) for which there were sufficient sample sizes and there were no significant changes in detections after the change in survey methods. That there is a lack of change in summary statistics in the raw data, whereas the estimates do show a sudden change, is a clear indication of the effect of changing the estimation method and is likely to represent the learning process the observers went through with the advent of a new method. The stable, dwarf-forest Bananaquit population succeeding the change in survey methodologies is exemplary of the fact that methodology does not always cause an apparent artificial incline or decline in all forest-bird species and why it affected EWWA is unknown. Still, the answer to this question is impossible to obtain because we can never truly estimate the detection probability function, a function not only of distance from the count point, but also of general environment that may affect a surveyor's ability to see (or hear) the bird. As a result, our estimate using method 3 can be seen as the lower bound of the population density, whereas the estimates from the two distance sampling methods should be viewed as an indication of potential fluctuations of the upper bound of population density.

Comparison of results with previous studies

In the LEF, Waide (1995) reported the EWWA rare in the areas of El Yunque Peak and Mt. Britton and more common along the Trade Winds Trail to El Toro, Pico del Este and in the upper part of the Icacos Valley; fewer were detected along the Caimitillo Trail and road to El Yunque summit. EWWA was among the most uncommonly encountered species in elfin woodland. Waide (1995) estimated a population of 138 pairs (or 0.4 pairs/ha) scattered over 329 ha of elfin woodland with considerable activity outside elfin woodland, particularly in *palo colorado* forest. Our estimate of a more current (2006) population density is considerably smaller (Figure 2). The EWWA's aggregated nature and possible seasonal elevational movements within the LEF led Waide (1995) to caution the interpretation and use of his population estimate

Anadón-Irizarry (2006) recorded most EWWA individuals along the Tradewinds Trail (more than half of all detections), and fewer in Icacos Valley, El Toro Trail and East Peak. Individuals were not detected in Mount Britton or El Yunque Trail, which is consistent with Waide's (1995) finding. Individuals were detected from 250 to 949 m elevation but most were recorded between 600 and 800 m, which is very similar to our results. There were notable differences between forest types in Anadón-Irizarry's (2006) study. Mean number of EWWA per count point was highest in *palo colorado* forest, slightly lower in elfin woodland, lowest in *tabonuco* and nil in sierra palm forest. Our results showed a similar trend, but detections in traditional elfin woodland were almost a third less frequent. The density estimate for the LEF resulting from Anadón-Irizarry's 2003–2004 surveys was 0.18 EWWA/ha/count within a surveyed area of 155.2 ha.

Our study corroborates the results of Waide (1995) and Anadón-Irizarry (2006). It suggests that, in elfin woodland, the EWWA population is faring better at East Peak (albeit not appreciably so), but continues to falter in the vicinity of Mt. Britton. Conversely, *palo colorado* forest exhibits mean population densities higher than those in elfin woodland in the areas we surveyed in the Icacos Valley on the mountain's south slope (Figure 2). Beyond previous studies, our study owing to its longevity documents a downward population trend. Intrinsic (physiological, genetic) causes are potential factors contributing to this decline. However, it is more likely that natural habitat conversion and degradation resulting from increasingly regular and more intense cyclonic events in the region (Goldenberg *et al.* 2001, Webster *et al.* 2005) are playing an increasingly more important role in the species' decline in the LEF. Recent hurricanes, two of which occurred only nine years apart (1989, 1998) caused extensive damage in the Mt. Britton area as well as other sections of the forest (Brokaw and Grear 1991).

The recent influx of cyclonic activity has had contrasting impacts on EWWA populations in other areas of the island. Whereas Arroyo-Vázquez (1991) was unable to find the species in the Toro Negro Forest in surveys conducted following Hurricane Hugo in 1989, Tossas (2006), reporting on the effects of Hurricane Georges (1998) on the resident birds of Maricao Forest, stated that the EWWA was the only species able to recover by the end of her study. These contrasting reports may be the result of disproportionate damage caused by the passing storms in their respective forests.

Severity of the population decline, and habitat shift

Traditionally EWWA detections in the vicinity of East Peak have been among the highest of all areas surveyed in the LEF (Waide 1995, Anadón-Irizarry 2006). Conversely, however, our EWWA detections in the LEF over a 17-year period were almost triple in the *palo colorado* forest type than in the species's traditional elfin woodland habitat, in which there was an 80% decrease in the number of EWWA detections from 1998 to 2006 (but it is noteworthy that the number of EWWA detections in *palo colorado* forest also declined almost 50% during the same period). This steep decline in both forest types may likewise reflect the consequences of the hurricanes, such as habitat alteration and degradation of not only the hard-hit elfin woodland (Brokaw and Grear 1991) but also in *palo colorado* forest on the more protected southern slope of the mountain. As an example, following both hurricanes, but especially hurricane Georges, much of the elfin woodland at Mt. Britton surrounding several of our count points was converted to palm brake (Arendt unpubl. data), which invades areas following major disturbance. Whereas destruction of elfin woodland at East Peak was less severe following both hurricanes (unlike the Mt. Britton site, the integrity of the vegetation associations around the East Peak count points was maintained), the sizeable disparity of EWWA detections between *palo colorado* and elfin woodland recorded in our study is nonetheless alarming if it reflects habitat change at East Peak due to cyclonic intensification as an indirect consequence of climate change since this summit forest type can take as along as two centuries to recover following major disturbance (Weaver 2000).

Does the fact that *palo colorado* forest exhibits a larger population of EWWA than elfin woodland cast doubt as to the species's optimum habitat, or is the EWWA simply adapting to environmental changes? While EWWA populations have declined overall in both forest types, the decline appears to be more prominent in the elfin woodland population. Based on higher population density estimates in *palo colorado* forest, populations are beginning to show a preference for habitats at lower elevations. Further studies should compare EWWA population dynamics in the LEF with those in the Maricao Commonwealth Forest surveyed by Cruz and Delannoy (1984), Anadón-Irizarry (2006) and others, in order to determine not only whether both populations are faring similarly, but also whether any long-distance movements and thus gene pool diversification may be occurring. The extent and type of habitat degradation, along with a study of various life-history parameters and habitat characteristics, could also be compared across the two areas in order to better understand causes of population density trends. Insight could also be gained concerning the question of EWWA affinity to a specific forest type or habitat condition.

Conclusions

By determining EWWA population density, we documented its continuous decline in eastern Puerto Rico over a period of 17 years (1989–2006). The species showed a significant general declining trend from c.0.2 individuals/ha in 1989 in elfin woodland to c.0.02/ha in 2006, and from 1 to 0.2 in *palo colorado* forest. It is imperative that further research and management programmes be undertaken island-wide, and that the EWWA be reclassified as globally "Endangered", especially in light of increasing climate change. Over the last century, temperatures in the Caribbean have increased by 1°F (0.56°C) and during this century are expected to increase to 4°F (2.22°C) (DOI 2010). Decreased rainfall will reduce habitat for high-elevation species and result in breeding failures. Consequently almost 50% of Caribbean birds show medium or high vulnerability to climate change (DOI 2010). The continued existence of the EWWA has implications beyond the protection of a single species, as the health of songbird populations is generally accepted to be a good indicator of overall environmental quality (Carson 1962, Wormworth and Mallon 2006, Stutchbury 2007, Wilson *et al.* 2007).

Supplementary Material

The supplementary materials for this article can be found at journals.cambridge.org/bci

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References

Anadón-Irizarry, V. (2006) *Distribution, habitat occupancy and population density of the Elfin-woods Warbler (Dendroica angelae) in Puerto Rico*. Thesis. Mayagüez, USA: University of Puerto Rico.

Arendt, W. J., Faaborg, J., Wallace, G. E. and Garrido, O. H. (2004) Biometrics of birds throughout the Greater Caribbean Basin. *Proc. West. Found. Vert. Zool.* 8: 1–33.

Arroyo-Vázquez, B. (1991) *Comparative study of foraging behavior and habitat selection of resident wood warblers (Dendroica) in southwestern Puerto Rico*. Thesis. Fayetteville, USA: University of Arkansas.

BirdLife International (2010) *Dendroica angelae*. In: IUCN 2010. *2010 IUCN Red List of threatened species*. <http://www.iucnredlist.org/details/full/106009123/0>. Downloaded on 30 January 2013.

Brokaw, N. V. L. and Grear, J. S. (1991) Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica* 23: 386–392.

Brown, S., Lugo, A. E., Silander, S. and Liegel, L. (1983) *Research history and opportunities in the Luquillo Experimental Forest*. New Orleans, Louisiana, USA: USDA Forest Service. (General Technical Report SO-44 volume 1)

Buckland, S. T., Anderson, D. R., Burnham, K. P. and Laake, J. L. (1993) *Distance sampling: estimating abundance of biological populations*. London, UK: Chapman and Hall.

Byer, M. D. and Weaver, P. L. (1977) Early secondary succession in an elfin woodland in the Luquillo Mountains of Puerto Rico. *Biotropica* 9: 35–47.

Carson, R. (1962) *Silent spring*. Boston, MA, USA: Houghton Mifflin.

CBD (Center for Biological Diversity) (2004) <www. biologicaldiversity.org/swcbd/species/elfin/index.html>. Downloaded on 26 January 2009.

Cruz, A. and Delannoy, C. A. (1984) Ecology of the Elfin Woods Warbler (*Dendroica angelae*): I. distribution, habitat usage, and population densities. *Caribb. J. Sci.* 20: 89–96.

Dietz, J. L. (1987) *Economic history of Puerto Rico: institutional change and capitalist development*. Princeton, USA: Princeton University Press.

DOI (Department of the Interior, USA) (2010) *State of the birds* 2010. <http://www.doi.gov/upload/State-of-the-Birds-2010.pdf>. Downloaded on 22 October 2010.

Ewel, J. J. and Whitmore, J. L. (1973) The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Río Piedras, Puerto Rico, USA: USDA Forest Service. (Research Paper ITF-18).

García-Martinó, A. R., Warner, G. S., Scatena, F. N. and Civco, D. L. (1996) Rainfall, runoff, and elevation relationships in the Luquillo Mountains of Puerto Rico. *Caribb. J. Sci.* 32: 413–424.

Gilbert, R. O. (1987) *Statistical methods for environmental pollution monitoring*. New York, USA: van Nostrand Reinhold.

Gochfeld, M., Hill, D. O. and Tudor, G. (1973) A second population of the recently described Elfin Woods Warbler and other bird records from the West Indies. *Caribb. J. Sci.* 13: 231–235.

Goldenberg, S. B., Landsea, C. W., Mestas-Nuñez, A. M. and Gray, W. M. (2001) The recent increase in Atlantic hurricane activity: causes and implications. *Science* 293: 474–479.

Holdridge, L. R. (1967) *Life zone ecology*. Revised edition. San José, Costa Rica: Tropical Science Center.

Howard, R. A. (1968) The ecology of an elfin forest in Puerto Rico: 1. introduction and composition studies. *J. Arnold Arboretum* 50: 225–267.

Hutto, R. L., Pletschet, S. M. and Hendricks, P. (1986) A fixed-radius point count method for nonbreeding and breeding season use. *Auk* 103: 593–602.

Kepler, C. B. and Parkes, K. C. (1972) A new species of warbler (Parulidae) from Puerto Rico. *Auk* 89: 1–18.

Miranda-Castro, L., Puente-Rolón, A. R. and Vega-Castillo, S. (2000) First list of the vertebrates of Los Tres Picachos State Forest, Puerto Rico, with data on relative abundance and altitudinal distribution. *Caribb. J. Sci.* 36: 117–126.

Mitchell, R. C. (1954) *A survey of the geology of Puerto Rico*. Río Piedras, USA: University of Puerto Rico Agricultural Experiment Station. (Technical Paper 13).

Page, E. B. (1963) Ordered hypotheses for multiple treatments: a significance test for linear ranks. *J. Am. Stat. Assoc.* 58: 216–230.

Pérez-Rivera, R. and Maldonado, L. A. (1977) Lista de cotejo de las aves de Cayey y algunos comentarios sobre estas. *Rev. Cayey* 9: 129–136.

Stutchbury, B. (2007) *Silence of the songbirds*. New York, USA: Walker and Company.

Tossas, A. G. (2006) Effects of Hurricane Georges on the resident avifauna of Maricao State Forest, Puerto Rico. *Caribb. J. Sci.* 42: 81–87.

USFWS (U.S. Fish and Wildlife Service) (2001) Candidate and listing priority assignment form, *Dendroica angelae*. <www.fws.gov/southeast/es/pdf/EWW.pdf>. Downloaded on 26 January 2009.

Wadsworth, F. H. (1951) Forest management in the Luquillo Mountains: I. The setting. *Caribb. Forest.* 12: 93–114.

Waide, R. B. (1995) *Status and conservation of the Elfin-woods Warbler (Dendroica angelae) in the Luquillo Experimental Forest*. Final report submitted to the U.S. Fish and Wildlife Service, Caribbean Field Office, Cabo Rojo, Puerto Rico.

Weaver, P. L. (1986) Growth and age of *Cyrilla racemiflora* L. in montane forest of Puerto Rico. *Interciencia* 11: 221–228.

Weaver, P. L. (1995) The colorado and dwarf forests of Puerto Rico's Luquillo Mountains. Pp. 109–141 in Lugo, A. E. and Low, C., eds. *Tropical forests: management and ecology*. New York, USA: Springer Verlag. (Ecological studies 112).

Weaver, P. L. (2000) Elfin woodland recovery 30 years after a plane wreck in Puerto Rico's Luquillo Mountains. *Caribb. J. Sci.* 36: 1–9.

Weaver, P. L. and Murphy, P. G. (1990) Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* 22: 69–82.

Weaver, P. L., Medina, E., Pool, D., Dugger, K., Gonzáles-Liboy, J. and Cuevas, E. (1986) Ecological observations in the dwarf cloud forest of the Luquillo Mountains in Puerto Rico. *Biotropica* 18: 79–85.

Webster, P. J., Holland, G. J., Curry, J. A. and Chang, H.-R. (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 293: 474–479.

Willis, E. O. (1972) Local distribution of mixed species flocks in Puerto Rico. *Wilson Bull.* 85: 175–177.

Wilson, S., Norris, D. R., Wilson, A. G. and Arcese, P. (2007) Breeding experience and population density affect the ability of a song-bird to respond to future climate variation. *Proc. R. Soc. B* 274: 2669–2675.

Wormworth, J. and Mallon, K. (2006) *Bird species and climate change: a climate risk report*. The global status report. <www.climaterisk.net>. Downloaded on 2 October 2009.

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