Urbanization alters the influence of weather and primary productivity on avian populations in the Seattle metropolitan area

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Abstract

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Two novel, abiotic challenges that affect primary productivity, and the biodiversity dependent upon it, are urbanization and climate change. Increased levels of urbanization cause an inversely proportional decrease in primary productivity, while climate change promises concurrent changes in temperature and precipitation. Although the effects of climate change are difficult to predict, the effects of El Niño years in the Pacific Northwest are similar to the changes currently predicted with climate change and may provide an insights into the long-term changes. To this end, I utilized a 250m resolution Normalized Difference Vegetation Index product from the MODIS satellite as an estimate of primary productivity and the Oceanic Niño Index as a way to estimate the strength of the El Niño -Southern Oscillation. Both variables were correlated with ten years of bird richness and relative abundance data to understand how the influence of primary productivity and weather changes with the stage of urbanization. Primary

productivity was found to exert a strong influence on bird populations in landscapes undergoing active development, and much less in areas of established housing development or forested reserves. Relative to primary productivity, weather was much less influential on bird populations at actively changing sites, and more influential than productivity in forest reserves. Birds in established developments are the least influenced by weather, perhaps because anthropogenic subsidies are provided and harsh weather is buffered. This indicates that once the landscaping becomes mature, housing developments are not strongly influenced by primary productivity or weather; thus, developers should be encouraged to minimize the loss of vegetation during development and home owners should attempt to quickly achieve mature landscaping that preferably provides food and shelter for wildlife.

INTRODUCTION

Animals increasingly confront new challenges, many resulting from human activities that are extensive and enduring. While many challenges may be difficult to eliminate in a human-dominated world, by understanding their effects it may be possible to affect minor changes that significantly improve the chances for animals to thrive. Two such novel challenges are urbanization (Miller and Hobbs, 2002) and climate change (IPCC, 2007; Møller, 2013). Both are rapidly changing abiotic factors that affect primary productivity and the biodiversity dependent upon it. Urbanization influences primary productivity in a predictable way, with a decrease in productivity in proportion to the level of urbanization (Bino et al., 2008). Urbanization also interacts with climate, most obviously in forming the urban heat island, a pattern that has been intensifying in recent years (Hoffman and Schlünzen, 2013). Concurrent changes in precipitation are less consistent than increased temperatures associated with the urban heat island, but increased downwind precipitation is a common effect of urbanization (Blake et al., 2011). Climate change has observable effects on plant and animal species as well as the communities and ecosystems they compose; changes include phenological mismatches, shifts in species ranges, and response to disturbance (Walther 2010). Urbanization is exerting an equally pervasive force on ecological communities (Chace and Walsh, 2006; Marzluff et al., 2008), particularly as it removes, fragments, and degrades key habitat elements (Alberti 2005) and changes natural cycles (Coleman et al., 2011; Golman et al 2005). Animals that find themselves in these newly fragmented landscapes must cope with the changes in vegetation cover and the changes in energy provided, either directly or indirectly, by the remaining plants. Yet the interactive effects of urbanization and climate on plant and animal populations, while important, are rarely studied (Liu et al. 2007; Møler, 2013; Sehgal, 2010; Zuckerberg et al., 2011). Investigating the effects of current climatic variability, such as the El Niño -Southern Oscillation (ENSO), in urban ecosystems can help fill this important void.

Suburban temperate forests experience both seasonal and yearly climatic variability and changes in primary productivity associated with urbanization; birds must routinely cope with both. The severity of the extremes and local habitat conditions dictate which species will thrive and which will decline. Numerous recent studies have found primary productivity or available energy, as measured by satellite based remote sensing, to be a good predictor of species richness at various spatial scales (Bino et al., 2008; Goetz et al., 2007; Laurent et al. 2005; Luck, 2006; Marshal et al., 2006;). However, there are relatively few published reports investigating the use of productivity as a predictor of avian species richness in urban landscapes (Gottschalk et al. 2005) and fewer yet that relate this to the effects of climate. In a large-scale study, Luck (2006) found that species richness tracks human population density, despite the effects of urbanization, because humans routinely select the most productive areas for settlement.

Given the inherent variability associated with suburban landscapes, methods that can quickly and accurately measure important variables are imperative. Measuring primary productivity in the patchiness of the suburban landscape lends itself to a satellite-derived index of vegetation greenness known as the Normalized Difference Vegetation Index (NDVI). NDVI, which synthesizes both vegetation quantity and health, has been shown to be an accurate predictor of vegetation cover and productivity (Buyantuyev and Wu, 2008; Piñeiro et al., 2006). Particularly with the release of more complete time series data, recent studies have been commonly making use of Landsat TM or ETM derived NDVI due to the improved temporal resolution and moderate spatial resolution, which is superior to MODIS; however, the temporal resolution is still not as fine as the MODIS data, particularly in the Pacific Northwest (PNW) where frequent cloud cover further reduces the temporal resolution in the winter months (Newton et al., 2009). Along the same lines, aerial photograph interpretation, the traditional and still frequently utilized form of remote sensing, has high spatial resolution, but even poorer temporal resolution than Landsat. The combination of excellent spatial resolution and poor temporal resolution make aerial photography the ideal choice for short-term studies with excellent spatial detail. However, systematic aerial photographs of my study area during the period of bird surveys are only available for one summer time-point in 2002, 2006 and 2009 (WAGDA, 2013). This limitation of poor temporal resolution with Landsat or aerial photography would both limit my ability to accurately assess yearly mean NDVI and chances to find for yearly changes in the relationships between bird populations and primary productivity or weather.

Fortunately, MODIS (MODerate resolution Imaging Spectroradiometer) NDVI products offer an option for greatly improved temporal resolution, without a debilitating sacrifice in spatial resolution over Landsat ETM and aerial photography (Buyantuyev and Wu, 2008). I also considered using the Leaf Area Index data that is available from MODIS, but it suffers from some of the same limitation as NDVI and has a spatial resolution of 500m as opposed to the 250m resolution of the NDVI product. The improved temporal resolution and respectable spatial resolution may provide a more accurate predictor of avian species richness and abundance than simply maximum NDVI of one or two images, particularly in an area undergoing rapid land clearing and subsequent home construction.

Similarly to using a synthetic variable such as NDVI to represent primary productivity, the Oceanic Niño Index (ONI), a measure of ENSO, provides a synthetic climate variable that may represent future patterns if climate change models are accurate. Although it is clear that no single weather variable, such as temperature or precipitation, is adequate to predict changes in productivity or bird populations, a larger climate variable such as the strength of the ENSO may have stronger predictive power.

The Seattle metropolitan area is an excellent location to study the convergence of a variable landscape and climate. The significant climatic effects of ENSO are relatively well understood and predictable (Kogan, 2000). Due to a change in normal storm track El Niño winters in the PNW are drier and warmer than normal which may benefit resident bird survival; however, the decrease in soil moisture content for the subsequent summer (Baker et al., 2010) can reduce primary productivity (Li and Kafatos, 2000), which could negatively effect bird reproduction. In addition, the urbanizing fringes of Seattle are undergoing rapid and extreme changes in land cover, land use and wildlife habitat (Donnely and Marzluff, 2006), which, in the landscape surrounding Seattle, often results in a sharp decline and subsequent, although moderate, rebound in productivity. Distinct changes in the patterns of avian species richness, which are, at least partially, explained by urbanization, have occurred near Seattle (Marzluff, 2005). However, the extent to which interactions between climate, urbanization and primary productivity are shaping this shift is not well understood.

STUDY OBJECTIVES

The abnormal weather that results from ENSO (warm and dry El Niño winters) resembles the predicted effects of sustained climate change and provides an opportunity to examine the interaction of a rapidly changing landscape and climate. By comparing long-established residential developments (Developed sites) and forested reserves (Reserve sites) with sites that were cleared and developed between 2001 and 2010 (Changing sites), I have the opportunity to examine how weather variability associated with ENSO and changes in primary productivity during and following development influence bird populations over time. This is essentially a glimpse into how birds will cope with a rapidly changing world. Correlating productivity and weather with bird population metrics in each of these three site types will allow me to understand how urbanization changes the impact of large scale, abiotic factors on bird populations. I expect that primary productivity will be strongly correlated with bird populations at Changing sites, but will explain much less variation at Developed or Reserve sites: the loss of native vegetation at Changing sites will reach a level at which bird populations are forced to respond. With productivity becoming such an important factor at Changing sites, I predict that weather will have comparatively less influence on birds and on primary productivity. At Reserve and Developed sites, however, I hypothesize that weather will explain more variation in bird population metrics than productivity because productivity is relatively consistent throughout my study and cold Winters and Springs associated with El Niño will decrease bird abundance.

ASSUMPTIONS

This study relies on a few assumptions in order to draw conclusions about the influence of productivity and weather on bird populations. One assumption is that NDVI, as measured and produced by the MODIS satellite and engineers, is an accurate representation of primary productivity. This has been confirmed in numerous papers correlating NDVI and primary productivity (Bino et al., 2008; Buyantuyev and Wu, 2008; Goetz et al., 2007; Piñeiro et al., 2006; Tucker et al., 1985) I also made the assumption that my unadjusted counts of birds accurately represent bird relative abundance and species richness. This is preferable to adjusting for detection probability over a short sampling frame in an heterogeneous landscape (Marzluff et al. in review).

The assumption that ONI, which utilizes ocean buoys to measure sea temperature, accurately predicts the strength of ENSO in the PNW is important for my weather variable to be meaningful, but this is, like NDVI, is commonly used (Chen et al., 2011; Todd et al., 2011; Praskievicz and Chang, 2009)

Two assumption that are more specific to my study are that the 21 sites I selected accurately represent the urban gradient of Reserve, Changing and Developed landscapes and that missing years of data do not significantly alter the results. Given that these sites have been utilized for numerous other studies to draw very meaningful conclusions about birds and urbanization, it is clear that the sites are appropriate. And although there are years of missing data, particularly for the Developed sites, the most annually dynamic Changing sites were very well sampled. Removing years where not every site was sampled would have resulted in an unacceptable reduction in sample size.

METHODS

Within the urbanizing fringe of the Seattle Metropolitan area, I randomly selected 21 one-kilometer study sites spanning a gradient of forest land cover, impervious surface and forest patch connectivity (Figure 1). These sites were all below 1000m in dense urban to sparsely populated exurban and second-growth forest. (Donnelly and Marzluff, 2004, 2006; Blewett and Marzluff, 2005) Land cover and its pattern were classified with a 1998 LANDSAT image (Botsford, 2000). I further classified each site by stage of development, resulting in five Reserve sites, seven Developed sites and nine Changing sites (Farwell and Marzluff 2013). Reserve sites are dominated by mid-successional vegetation with at least 70-year-old Douglas-fir trees interspersed with deciduous trees and an understory of ferns and fruiting shrubs surrounded by suburban matrix. Developed sites are long established housing subdivisions that have been human dominated for at least 20 years. Changing sites were forested either when the study began or cleared in the few years prior but have since become suburban developments. Although minor development may have continued through 2010 at some Changing sites, forest clearing, road building and intense home building typically occurred over three years starting in approximately 2000.

I surveyed bird abundance during the breeding seasons (April to August) of 2001 to 2010 by conducting four 50 m fixed radius point count surveys at four to eight points in each study site (Ralph et al. 1993). I conducted surveys between 0500 and 1200 on days when conditions allowed adequate visibility and audibility of birds. Rarely, I conducted only three surveys per year due to weather or denial of land access; this happened in nine percent of site-years. Additionally, three sites had fewer than eight points; however, as each site was either homogenously forested, small in size or both, fewer points were representative. At all Developed and Changing sites, the majority, typically six of eight, of survey points were located in the far more heterogenous urban matrix and the remaining were located in the remnant forest (Donnelly and Marzluff 2006).

Due to the heterogeneity of the developed areas and high vegetation density in this type and age of forest, between 758 and 1154 trees per hectare (Spies and Franklin, 1991) which make estimations of distance to aural detections unreliable, I utilized small, fixed radius surveys to estimate relative abundance (Farwell and Marzluff 2013). Although this method may create a bias toward underestimation of relative abundance, my detection level was high and not variable by site type (Marzluff, et al. in review). Due to inadequate sampling resulting from fixed radius point counts I did not include nonbreeding birds, raptors, waterfowl, and other species with very specific habitat requirements or large home ranges in my analysis (Ralph et al. 1993).

Bird species were classified into guilds based upon the following life history characteristics: tolerance of human development, migration, diet and use of human food subsidies (Table 1). There are a total of 58 species included in this study and every species was assigned a guild based on each life history trait (Table S1).

To account for differential survey effort between sites and to normalize my data I calculated annual mean relative abundance as the average number of detections per 10 min, fixed-radius survey per year for each of the adequately sampled bird species and guilds known to breed in my study region (Tables S2, S3, S4). Annual species richness was calculated at the total number of separate species observed at each site during the four annual surveys (Table S5).

I used images from NASA's MODIS satellite to obtain productivity values, in the form of NDVI, for each research site over the course of the 10-year study. I downloaded the Version 5 MOD13Q1 250 m resolution 16-day composites of a gridded level-3 product from the NASA Warehouse Inventory Search Tool (WIST) for January 2001 to December 2010. In this product NDVI is calculated using ratios of reflectance in the red (645 nm) and near-infrared (858 nm) bands from the best daily images of each 16-day period. Both bands are atmospherically corrected bi-directional surface reflectances with appropriate feature masking. MODIS13Q1 is a Validated Stage 2 product with extensive accuracy assessments over numerous locations and time points. The MODIS13Q1 product is distributed in Hierachical Data Format–Earth Observation System (HDF-EOS) and visualized in an integerized sinusoidal projection (ISIN) mapping grid (Land Processes Distributed Active Archive Center). I obtained GPS coordinates for each point count location at my study sites and projected them in UTM NAD83 using ARCGIS 9.3.3 (ESRI 2008). The following steps are a generalized method for extracting usable NDVI data from the MODIS13Q1 product, but should provide enough detail to make this approach repeatable in and GIS software. I calculated the geometric mean of these points and created a 1km^2 circular buffer around the geometric mean, which is the area on the landscape I felt was adequately represented by my points; those 1km^2 areas constitute my 21 sites. To obtain the necessary NDVI data, I created a model to extract two raster Subdatasets from the original MODIS13Q1 files, one with the NDVI values and one with Pixel Reliability values, and reproject the Subdatasets into UTM NAD83 using the Project Raster tool, found in the Data Management toolbox. The pixel reliability layer has five classes as assigned by the product engineers: the NDVI data in class zero is considered completely reliable after validation; class one means that NDVI data was produced, but atmospheric or terrestrial interference decreased reliability; no NDVI data was produced for class 2, 3 or -1 because the land surface was covered with snow or ice, the land surface was shadowed by clouds or the reflectance data was otherwise inadequate to yield NDVI values, respectively. With two raster layers in the same projection I used the Set Null tool from the Conditional toolset in the Spatial Analyst toolbox to remove any unreliable data by converting pixels with any reliability class other than zero to No Data in the NDVI layer. The result was an NDVI layer with only the most reliable data for subsequent calculations. Unfortunately NDVI data was lost at some of the time points at some of the sites, but this was necessary to ensure the remaining data was of the highest quality.

The last step of the model was to calculate the mean NDVI for each composite image at each site using Zonal Statistics with the 1 km^2 buffer around each site center as the zone. There was a maximum of 21 NDVI pixels included in the each zone; however, if pixels were previously set to No Data with Set Null they were not included in the Zonal Statistics calculations so the actual average was 18.4 with a standard deviation of 2.82. When sites had less than 10 pixels included in the calculations the data was dropped from the final calculation of annual mean NDVI. Due to unreliable NDVI data each site had an average of 16.5 (S.D.= 1.23) out of a total possible 23 time points, with most of the missing composites coming in the winter months. I calculated the yearly mean NDVI for each site using the values from each composite image. As a result I had mean NDVI for each 1 km^2 site drawn from multiple time-points throughout each year (Figure 2).

I utilized annual mean NDVI because I was interested in the effects productivity throughout the year. Additionally, I used annual mean NDVI rather than mean summer or annual peak NDVI, because it was calculated from approximately 16 time points, rather than approximately six or one, respectively. Mean annual NDVI was strongly correlated with annual peak NDVI at Changing (r=0.93, p<0.01, N=90), Developed (r=0.93, p<0.01, N=70) and Reserve sites (r=0.882, p<0.01, N=50) throughout the study period, indicating that either measure would correlate similarly with my bird population metrics.

The strength of ENSO has a strong effect on weather patterns and has been shown to affect bird populations in the PNW; therefore, it may serve as a good predictor for bird richness and relative abundance in my study. Although microclimate differences may exist between my sites, in general El Niño is known to result in warm and dry winters in the PNW, while La Nina typically results in cooler, wetter winters (NOAA). These deviations from normal winter conditions have been shown to affect avian reproductive success and survival (Bloxton 2002; Nott et al. 2002). Periods of El Niño and La Nina are examples of large-scale climate variations and may serve as a tool for understanding potential long-term effects of global climate change.

I estimated the annual strengths of the El Niño Southern Oscillation using the National Oceanic and Atmospheric Association’s Oceanic Niño Index (ONI). This index is calculated as the difference between a three-month running mean of sea surface temperatures from the historical mean from 1971 to 2000. Numbers greater than 0.5 indicate a strong El Niño and numbers less than -0.5 indicate a strong La Nina. Because the effects of the ENSO are felt more strongly during the winter in my study areas, the yearly metrics are the means from the winter preceding the breeding season. For example the metric for 2010 is the mean of September 2009-February 2010.

I utilized one-way ANOVA with Tukey post-hoc testing to compare means of NDVI, richness and relative abundance data between site types with SPSS 19.0 over the 10 years of my study. For each year of adequate bird data (Table 1), I related annual bird, weather, and productivity metrics at each site using univariate and partial correlations. Although not each study site was monitored each year over the 10-year study period, each site has representative data for the time period. Changing sites, with more variable bird populations were monitored more intensively than Reserve and Developed sites, where bird populations were relatively stable. Correlation coefficients for each site were Fisher-transformed, a variance-stabilizing transformation commonly used to make correlation coefficients suitable for hypothesis testing. The transformed values were averaged by site type to yield single correlations coefficients with standard error for each combination of bird population metric and weather or productivity at each site type.

RESULTS

Primary productivity as assessed by NDVI varied between Reserve, Developed and Changing sites ($F=115.5$, $p<0.01$, $df=2, 207$), but not across years at each site type (Figure 2). Reserve sites had the highest and most consistent annual, mean productivity (0.83,S.E.=0.004; n=50). This exceeded productivity at Developed sites (mean= 0.68; S.E.=0.006; $p<0.01$; n=70) and Changing sites (mean=0.72; S.E.= 0.007; $p<0.01$; n=90). Variance in mean annual productivity was significantly less at Reserve sites relative to

Developed sites (F=5.0, p<0.01, df=4, 6) and Changing sites (F=4.0, p<0.01, df=4, 8), while Changing and Developed sites had similar variance (F=1.25, p=0.15, df= 8, 6).

The large-scale weather pattern of ENSO, which is called ONI, was a uniform variable across all study sites, but was variable from year to year (Figure 2; F=20.4, p<0.01, df=9, 10). The winter of 2001 was a moderate La Nina year with the ONI equal to -0.55; the yearly mean low temperature was 6.72 C° and there was 95.4 cm of precipitation The winter of 2008 was a stronger La Nina with ONI less than -1.0; the yearly mean low temperature was 6.89 C° and there was 78 cm of precipitation (Table 1). Meanwhile, 2003 and 2010 experienced strong El Niño conditions, with ONI greater than1; the yearly mean low temperature was 7.61 C° and 7.67 C° with 106.1 cm and 119.35 cm of precipitation, respectively (Table 1). The pattern of higher temperatures and higher precipitation is a commonly known effect of El Niño . Over the ten years of this study winter ONI, a measure of the strength of the El Niño Southern Oscillation, was strongly positively correlated with mean winter temperature in the Seattle area (r=0.73, p=0.016, N=10), suggesting that winter temperatures were warmer in El Niño years.

Bird species richness differed among site types over time (F=6.34, p<0.01, df=2, 18; Figure 3, Table S5). Using yearly means for each site, the mean richness was 32.7 bird species (S.E.=1.26 , n=9) at Changing sites, 29.3 (S.E.=0.89, n= 7) at Developed sites and 26.0 (S.E.=1.76, n=5) at Reserve sites. Reserve sites had significantly lower mean richness than Changing sites (mean difference= 6.67, q=5.02 ,p=0.007, n= 6.6), but Changing and Developed sites were not different (mean difference=3.38 , q=2.55, p=0.15., n= 6.6)

Bird species richness also varied through time at Changing (F=2.74, p<0.01, df=9, 77) and Developed sites (F=5.01, p<0.01, df=5, 25), but was similar across the 10 years at Reserve sites, which were not undergoing any landscape changes (F= 0.974, p=0.481, df=9, 30 Figure 3). Mean richness at Changing sites ranged from 36.0 in 2005 to 26.2 in 2009, which is the only significant difference in the Tukey HSD post-hoc test (mean difference= 9.83 q=5.62, p=0.02, n=8.6); over ten years the mean was 32.4 and the coefficient of variation was 0.185 (df=9, 77). Mean richness at Developed sites ranged from 23.0 in 2002 to 33.57 in 2003, again the only significant difference in post-hoc testing (mean difference= 10.6, q=6.00, p<0.01, calculated n=4.2); the overall mean was 29.23 and the coefficient of variation was 0.159 (df=5, 25). Mean richness at Developed sites ranged from 23.4 in 2001 to 30.7 in 2002; the 10-year mean was 25.65 and the coefficient of variation was 0.187 (n=40). Richness was not similar between all years at Changing sites (F=2.74, p=0.008, df=9, 77) and Developed sites (F= 5.01, p=0.003, df=5, 25).

Annual variation in richness was correlated with productivity and weather, but this depended on site type (Table 5). At Changing sites, richness increased with productivity (the average of each site's univariate correlation: r=0.26 ±0.10; the average of each site's partial correlation, holding weather constant: r= 0.29 ±0.10), but was very weakly correlated with weather (partial correlation controlling for variable productivity indicates slightly higher diversity in El Niño conditions, r=0.03 ±0.11). At Developed sites richness was greatest in El Niño conditions (mean r=0.44 ±0.15) and the annual change in productivity, which was minimal, had little effect (Table 1). Species richness was not significantly correlated with productivity or weather at Reserve sites (Table 5).

Variation in in richness among replicate Reserve sites obscured a tendency for richness to be greatest in 2002 and 2009, years of relatively low temperature and low rainfall.

There were expected and obvious differences in the total abundance of various guilds in each site type (Table 4). Forest species were approximately twice as abundant in Reserve sites than Developed and Changing sites (mean difference=2.84, 2.50; q=5.98, 5.26; p=0.002, 0.005; n=6.6, 6.6). Synanthropic species were most abundant in Developed and Changing sites (significantly greater in Developed than Reserve sites: mean difference= 2.38, q=13.7, p=0.004, n=6.6), Herbivores were over 60% more abundant at Changing sites than Reserve sites (mean difference=1.46, q=4.17, p=0.024, n=6.6), while Developed sites were not significant different from either. Generalist relative abundance was nearly twice as great at Developed sites than Reserve sites (mean difference= 1.32, q=5.11, p=0.009, n=12), and both were similar in abundance to Changing sites. Subsidy Consumer annual relative abundance was 4.31 at Reserve sites, which was significant less than 6.38 at Changing sites (mean difference= 2.07, q=4.16, p=0.025, n=6.6) and 6.84 at Developed (mean difference, 2.54, q=5.10, p=0.009, n=6.6). Migrant, Resident, Insectivores and Subsidy Avoiders had similar relative abundance at all three site types (Tables S2, S3, S4).

Annual relative abundance of species by guild was most variable at Changing sites and least variable in Reserve sites (Figures 4 and 5). By looking at yearly guild abundance at each site within the site type, a yearly mean abundance was calculated for each site type. For example, all nine Changing sites were sampled for ten years, except in 2009 when only six sites were sampled, so n = 87. At Changing sites all nine guilds, except Synanthropics (F= 1.54, p=0.148, df= 9, 77), exhibit variable abundance from year to year; for example, Forest species (F= 2.62, p=0.011, df= 9, 77), Residents (F=4.51, p<0.01, df= 9, 77) and Generalists (F=2.39, p=0.02, df= 9, 77) were variable over time. There was slightly less yearly variability at Developing sites than Changing sites: only Residents (F=3.17, p=0.02, df=5, 25), Synanthropics (F=2.92, p=0.03, df=5, 25), Herbivores (F=5.76, p<0.01, df=5, 25), Insectivores (F=5.64, p<0.01, df=5, 25), Subsidy Consumers (F=3.53, p=0.02, df=5, 25) and Subsidy Avoiders (F=2.93, p=0.03, df=5, 25) do not have consistent relative abundance from year to year. Unlike Changing and Developed sites, guild abundance was not significantly different from year to year at Reserve sites (Figures 4 and 5).

Annual change in productivity was strongly correlated with the abundance of all guild types in Changing sites (Table 5). The weakest relationship was with Generalists (r=0.27 ±0.102 and the partial correlation, holding weather constant, was r=0.26 ±0.12). In contrast, only 2 of 18 correlations between a guild's abundance and weather were statistically significant. The strongest correlations were negative indicating that Migrant, Synanthropic, Subsidy consumer, and Herbivore guilds were more abundant in La Nina conditions and/or less abundant in El Niño years.

Reserve sites had very few significant correlations between guild abundance and productivity and weather; only 1 of 18 correlations were significant for productivity, 3 of 18 were significant for weather (Table 5). The mean correlation coefficient between Synanthropic species abundance and productivity was moderate (r=0.21 ±0.07; Table 5) when weather was held constant, and the zero-order correlation was not significant. Both weather and, to a lesser extent, productivity were shaping Synanthropic abundance because the mean correlation coefficient between Synanthropic species abundance and weather was strongly negative in the partial correlation (mean r=0.56 ±0.19). There was also a strong negative correlation between Herbivore species abundance and weather (univariate mean r=-0.36 ±0.06) and the correlation improves nearly 15% when productivity was held constant. Although neither weather nor productivity were having a strong influence on guild abundance at Reserve sites, it appears that weather was a dominant influence by increasing bird guild abundance during La Nina year or reducing abundance during El Niño years.

Developed sites resemble Reserve sites more closely than Changing sites, but guild abundance appears to be even less influenced by weather, with 1 of 18 guilds correlated with productivity in partial correlations and 1 of 18 guilds significantly correlated with weather (Table 5). Insectivore abundance was positively correlated with productivity when weather was held constant (r=0.52 ±0.14), suggesting that greater productivity allows for great insectivore abundance. Insectivores were also strongly correlated with weather (r=-0.68 ±0.19), albeit negatively; indicating, in a pattern similar to other site types, that Insectivores were more abundant with La Nina and/or less abundant with El Niño . Given the stronger relationship of Insectivores and weather, it appears that weather was somewhat more influential than productivity in shaping Insectivore abundance at Developed sites. With so few significant correlations it appears that neither productivity nor weather were having a strong influence on guild relative abundance at Developed sites.

At all site types there were very few strong correlations between individual species abundance and weather and there were no significant correlations between individual species and productivity (Table 5). Although there were few significant correlations overall, it was clear that weather was more important than productivity in shaping species abundance.   And with only 7 of 132 correlations significant it was also clear that individual species were much less strongly correlated with productivity and climate than was guild abundance or species richness.

Relatively few species' abundances change through time at a given site type. At Changing sites only American robins (F=2.65, p=0.01, df=9, 77) and Song sparrows (F=2.70, p<0.01, df=9, 77) exhibit changes in relative abundance throughout the 10 years of the study (Figure 6). At Developed sites American crows (F=2.63, p=0.03, df=9, 30), American robins (F=6.41, p<0.01, df=9, 30) and Spotted towhees (F=2.26, p=0.048, df=9, 30) had variable relative abundance from year to year (Figure 6). In contrast, relative abundance did not vary from year to year at Reserve sites for any of the species that I investigated, indicating a very stable community in native forests.

At Changing sites none of the representatives of the guilds were significantly correlated with productivity and only Bewick's wren and American robin abundances were correlated with weather. Bewick's wrens were positively correlated with weather approximately equally in both the univariate (mean r= 0.27 ±0.06) and partial correlation (mean r=0.27 ±0.06), signifying that weather was important in shaping Bewick's Wren abundance. Meanwhile American robins were negatively correlated with weather when productivity was held constant (mean r=-0.13 ±0.06: Table 5), indicating that weather conditions influence American robin abundance, although in an opposite manner of Bewick's wrens. Despite few significant correlations, weather was having more influence than productivity on species abundance.

Similarly to Changing sites, Reserve sites have no significant correlations between individual species and productivity and only three with weather (Table 5). Again Bewick's wrens were positively correlated with weather with (mean r=0.26 ±0.07) and without (mean r=0.24 ±0.07) productivity being held constant, indicating Bewick's wrens were more strongly influenced by weather than productivity. In Reserve sites Pacific wrens, a forest species, were also positively correlated with weather in the zero-order correlation (mean r=0.32 ±0.11), suggesting that both wren species were more abundant following El Niño winters and less abundant following La Nina winters.

Developed sites diverged slightly from Changing and Reserve sites, with significant univariate correlations between productivity and Bewick's wrens (mean r=0.83 ±0.33; Table 5) and Pacific-slope flycatchers (mean r=-0.50 ±0.20; Table 5). Bewick's wrens were positively correlated with weather in the univariate correlation (mean r=0.53 ±0.20; Table 5). These results indicate that Bewick's wrens and Pacific-slope flycatchers species are more abundant at sites with greater productivity and that Bewick's wrens are either less abundant following La Nina and/or more abundant following El Niño years at Developed sites.

DISCUSSION

The process of converting native forests to suburban housing developments significantly changes the influence of primary productivity and climate on bird relative abundance and species richness. Bird relative abundance is influenced strongly by primary productivity and, to a lesser extent, by strength of winter ONSI in the suburban landscapes I studied. Whereas primary productivity is not strongly correlated with guild relative abundance at forested Reserves or Developed sites, the active process of land clearing for human development creates a situation where primary productivity becomes very important in shaping bird guild abundance, likely due to the sharp decline in native forest cover. Alternatively, the conversion from native forest appears to make guild abundance less sensitive to fluctuations in climate of the preceding winter resulting from El Niño or La Nina. While none of my site types showed many significant correlations between bird abundance and ENSO, those at Changing sites were the weakest: the land conversion that was occurring at Changing sites appears to overshadow the influence of winter weather. This does not indicate that winter weather is unimportant to bird populations at Changing sites; in fact, the nearly equivalent number of significant correlations, despite very significant disturbance indicates that ENSO is important. In the face of expected changes in the PNW climate, this finding indicates that the active process of suburban development affects the ability of birds to deal with the predicted warmer and dryer summers. Fortunately, it appears that established landscaping and potentially human subsidies of Developed sites provide adequate habitat to buffer against the effects of El Niño winters. Thus, if housing developments achieve mature landscaping quickly after the construction phase bird populations may be more stable and capable of withstanding climate fluctuations.

Changing sites were by far the most heterogeneous in terms of land cover and productivity over the course of this study, allowing for the greatest number of species to utilize these sites (Hansen et al., 2005). Changing sites offered something for every species I studied: over the course of my study the sites were forest, cleared land and finally early housing developments. As expected, annual richness fluctuated greatly at

Changing sites indicating a high turnover in species though time. Although not as heterogeneous as Changing sites, the combination of houses, landscaped properties and remnant forest at Developed sites supports more species than forest alone. Developed sites are not undergoing any active development; however, species richness is variable from year to year, possibly as a result of changes in landscaping or quantity of subsidies provided. It may also be a reflection of species that do not tolerate human development well undergoing a slow demise to a final local extinction.

Principally homogenous, Reserve sites support the fewest number of species over time, but annual mean richness does not fluctuate from year to year. This is most likely a result of the absence of big disturbances and mild weather conditions of the PNW that allow for consistent yearly habitat conditions. Additionally, the consistency of the productivity in Reserve sites may buffer some of the effects of density-independent factors to allow at least some members of the species to remain at a site from year to year. While subdivisions may support a great number of species, native forest provides a consistent refuge in the face of fluctuating conditions in the matrix and a functional system of reserves should be retained on the landscape as new housing developments are planned.

The mean guild relative abundance was greatest at different site types depending on the natural history of each guild, and which site types present favorable conditions. For instance, those guilds that are adapted to exploit human modifications to the landscape were less abundant at Reserve sites than they were at Developed or Changing sites. This pattern was true of forest species, which are most abundant at Reserve sites; synanthropic species, which are more abundant at Developed sites than Reserve sites;

generalist species, which are more common at Developed sites than Reserve sites; and subsidy consumers, which are the least abundant at Reserve sites. These four guilds have the greatest relative abundance at site types that cater to their natural history traits: primarily guilds that are capable of utilizing intentional or unintentional human provisions are most common at the human dominated site types, a pattern that seems to, at least in part, follow optimal foraging theory. An even more striking pattern was observed in Australia where Catterall et al. (1998) found strong segregation of guilds into either cleared land or bush (native vegetation) based on life history traits. As a possible indication for things to come, all of the “bush species” have experienced significant declines in abundance since European arrived in Australia.

Interestingly, herbivores have a greater relative abundance at Changing sites than Reserve sites, but Developed sites are similar to both. This is likely because Reserve sites are dominated by dense overstory trees, with fewer fruiting shrubs in the understory. Developed sites, in contrast, may have fruit and seed producing shrubs included in the landscaping. The landscaping at Developed sites also includes numerous non-native species, which would increase the plant diversity potentially leading to a wider time span for fruit-bearing and greater overall fruit production. Additionally, Developed sites have more edge that could provide an area for fruiting understory shrubs to thrive. Meanwhile, Changing sites may have a greater number of early successional weeds and shrubs that produce fruit or seeds during land clearing and subsequent landscaping with such plants. Particularly in the PNW, Himalayan blackberries (*Rubus armeniacus*) can become dominant in disturbed landscapes, so if the changing areas remain disturbed for an extended period, herbivores may become more abundant. Again, Catterall et al. (1998)

saw a similar pattern in some frugivore species and hypothesized that the landscaping, with fruiting and flowing plants, in suburban areas benefits these species.

Bird guild abundance appears to be more variable at site types where productivity is more variable over time and between individual sites within the type. Eight of nine guilds do not have consistent abundance through time at Changing sites, the site type where dramatic land cover change took place directly preceding and during this study. Developed sites, while not undergoing land cover change, have variable productivity, perhaps due to maturing vegetation or ongoing homeowner alteration their landscaping. Developed sites have significant yearly variability in six of nine guilds, which is slightly less than Changing sites, but much more than Reserve sites. Reserve sites do not have any significant yearly variability in productivity, and correspondingly no guilds have significantly different abundance over the course of my study. Reserve sites seem to serve as an island of refuge within the suburban matrix and following a particularly bad year can serve as a source for some species to emigrate to Developed and Changing areas. The importance of a stable island within the sea of change can be very important for a stable metapopulation, particularly in mobile species that can more easily move through the matrix (Neuschulz et al., 2013), but may also be influenced by the level of urbanization in the matrix (Meffert et al., 2013).

Weather and productivity were not strongly correlated at my study sites perhaps because Changing sites are undergoing more intense land cover changes of anthropogenic origin and the changes associated with yearly weather fluctuations are relatively insignificant. Developed sites, with their manicured landscaping likely receive enough supplemental water and human care to maintain a stable primary productivity through dryer summers of El Niño . Reserve sites have the greatest and most consistent productivity of the three site types: the established, dense conifer-dominated forests are insensitive to measurable changes resulting from fluctuating weather conditions. Although water may be limiting during the summer of El Niño years at Reserve sites the overstory trees may be able to outcompete the understory for water well enough to maintain a green canopy which is primarily measured with NDVI. Additionally, by using the yearly mean NDVI rather than a yearly peak NDVI some of the summer drought signals may have been masked. I decided to use yearly mean NDVI because the study area is relatively temperate with a long growing season and there are many resident birds included in this study that may be sensitive to changes in productivity outside the summer months.

Additionally, it is known that NDVI can become saturated as the ratio of reflectances approach 1:1 (Wang et al., 2003), so minor changes that might have been correlated with changes in weather at Reserve sites would not be evident due to errors associated with the NDVI measurement. Although beyond the scope of this study, it may be possible to eliminate some of the errors of saturation by utilizing either ground-based or airborne scanning LIDAR to very accurately measure percent canopy cover (PCC) and understory density, utilizing these variable to improve regressions. Despite these limitations, it has been shown that weather is strongly correlated with primary productivity on a large scale (Box et al., 1989), so I believe partial correlations are still appropriate for this study.

The results of the correlations between guild abundance and productivity at my three site types indicate that guild abundance is about equally insensitive to primary productivity at Reserve and Developed sites, while abundance is strongly correlated to productivity at Changing sites. Only Synanthropics are correlated with productivity at Reserve sites, which is a surprising finding because Synanthropic species are typically more abundant in urban landscapes and less abundant in the denser forests. However, when the landscape surrounding the study sites is considered it is apparent that the strongest partial correlations between productivity and Synanthropic abundance are at the two Reserve sites surrounded by the densest suburban development. Although my survey points were located in the forest, the positive correlation may be a result of increased synanthropic abundance in the suburban matrix with individuals that also utilize the forest being detecting during surveys. One of the most prevalent synanthropic species is the American crow, which is also a generalist and commonly makes use of forest patches. There are no significant correlations between individual species and productivity at Reserve sites, supporting the idea productivity is not an important factor in shaping bird abundance. Given the lack of significant correlations, it appears that primary productivity is great enough at Reserve sites as to not be a driving factor in bird guild abundance. Although it may be possible that annual mean NDVI is simply not the correct remote sensing modality for predicting bird abundance in dense forest (Ranganathan et al., 2007), density-dependent factors are likely playing a more important role in shaping bird relative abundance at Reserve sites.

Developed sites, similarly, have only one significant correlation between guild or species abundance and primary productivity, indicating that other factors are controlling bird abundance. In this case, it is only Insectivores that have a strong positive correlation with productivity, potentially because the Developed sites with more vegetation support a greater insect population and thus more of the birds that prey upon them. It should be noted that my Developed sites are not exclusively houses and landscaped yards; there are varying amounts of remnant forest patches at each of the sites. Thus, sites with greater primary productivity are likely reflective of sites with greater native forest cover. Therefore, it is also possible that this guild requires larger patches native vegetation to provide food and nesting locations and may not be very capable of utilizing human-planted vegetation food supplements in Developed sites. This could be particularly true if the human residents of these developments are using insecticides on their property. The results of the correlations between guild abundance and primary productivity at Reserve and Developed sites indicates that productivity is not an important factor in shaping guild abundance.

Changing sites seem to follow a different pattern, with significant partial correlations between productivity and eight of nine guilds. Changing sites are experiencing drastic land cover change leading to the greatest variability in and least amount of primary productivity of the three site types; therefore, richness and guild abundance appears to be driven by productivity. Only Generalists, one of the most adaptable guilds that I studied, were not influenced by productivity, likely because they are capable of finding food independent of foraging in or around plants. This result is supportive of my initial hypotheses and is likely a result of the decrease in primary productivity following forest clearing and subsequent rebound in productivity with landscaping that are drastic and persistent enough to cause productivity to become an in important factor shaping guild abundance; this is a distinctly different pattern than at Reserve and Developed sites. Surprisingly, none of the individual species abundances were correlated with productivity at Changing sites. This may be because there are fewer sightings of individual species than of aggregated guilds during any one year creating greater noise in species data; this is supported by the very high variability in the correlations between individual species and productivity.

These patterns of guild abundance suggest that developers should undertake large-scale developments in stages to allow for landscaping to begin to mature before all the native forest is removed; alternatively, developers could landscape the development with more mature plants and plant species that are known to benefit wildlife (e.g., Washington Department of Fish and Wildlife's Backyard Wildlife Sanctuary Program). Leaving large patches of native forest on the landscape will provide a refuge for native guilds that may serve as source populations when the landscaping in the matrix has reached an adequate level of maturity to again support many of these guilds.

Given that significant correlations between bird abundance and ENSO are relatively few compared to correlations with primary productivity, climate appears to play a secondary role in shaping relative abundance patterns than primary productivity. Only two guilds' abundances were significantly correlated with weather at Reserve sites indicating that winter ENSO strength is not a very influential factor in predicting bird guild abundance. Partial correlations indicate Herbivores are negatively associated with ONI, hence Herbivore abundance is reduced during the breeding season at Reserve sites when the proceeding winter was a strong El Niño , and increased following a La Nina winter. In the typical warm and dry summers of the PNW, water is often a limiting resource to plant growth, leaving plants to compete for moisture stored in the soil from the previous winter. If soil moisture is not replenished during the winter, plants can suffer drought effects, resulting in slower growth (Peterson et al., 2002) and reduced fruit and seed production during the subsequent breeding season (Herrera 1991; Selås 2000); changes in precipitation associated with ENSO have been shown to affect soil moisture content (Nott et al., 2002). It appears that the warmer, dryer winters associated with El Niño in the PNW (Thomas et al. 2003) exacerbate soil-moisture deficiencies for the upcoming breeding season and negatively affect summer Herbivore abundance. Changes in rainfall associated with ENSO are known to be similarly correlated with avian reproductive success in the PNW (Nott et al., 2002). The reduced Herbivore abundance that I witnessed could result from individuals fledging fewer young or moving to areas with more food despite a lower overall primary productivity, such as Developed landscapes, which receive supplemental water. On the other hand, the wetter winters associated with La Nina (Thomas et al., 2003) will ensure the soil is adequately moist to allow for greater fruit and seed production, which would likely result in a greater number of nesting birds and nest productivity. At Reserve sites Herbivores are not influenced by productivity, which indicates that more vegetation cover does not necessarily provide more berries (Oleyar, 2011), but are influenced by yearly weather conditions, which may have a greater influence on yearly food production.

Synanthropic species, in addition to Herbivores, are particularly sensitive to El Niño events at Reserve sites: there is a negative partial correlation between Synanthropic species abundance and weather. Although I did predict that Synanthropic abundance would be influenced by weather at Reserve sites, it is interesting that only Synanthropics and Herbivores respond to changes in climate associated with El Niño . I speculate that Synanthropic species are less capable of coping with adverse vegetative conditions at

Reserve sites than Developed sites because there are fewer human supplements that could buffer the effects of a dry summer. If summer vegetation is less suitable due to low soil-moisture conditions Synanthropic species may easily immigrate to more developed landscapes where conditions are more favorable to their success. Although not significant, the correlation between Synanthropic abundance and weather is much less negative at Developed sites perhaps indicating an influx of individuals from more forested areas.

Bewick's wrens and Pacific wrens are positively correlated with weather, which is the opposite pattern seen for Synanthropic and Herbivore guild abundance. Perhaps because both are year-round residents and not Herbivores the wrens are more negatively influenced by a cold and wet winter than they would be by summer with low soil-moisture. If fewer adults survive the winter, the reduction in species abundance will be further compounded by fewer fledglings being spotted in my late summer surveys. Despite guild abundance displaying a different response to changes in the ONI, the response of individual species to changes in food availability associated with ENSO has been previously documented (Jones et al., 2003). Nott et al. (2002) also found that individual species' reproductive success was positively correlated with warmer, dryer winter and spring conditions.

At Developed sites there is a single significant correlation between weather and guild abundance, which is further confirmation that Reserve and Developed sites are quite similar in the bird population's response to weather and productivity. As stated above, Insectivore guild abundance is significantly correlated with productivity and now weather in the partial correlations, indicating that both vegetation cover and weather are important. Insectivores are strongly dependent on vegetation as a food source for the insects they eat, thus there may be more insectivores at sites with greater productivity. But given that productivity is not simply providing greater food resources (Oleyar, 2011), the stronger influence on food availability may be weather, which has a strong influence on insect numbers. Similarly to Herbivores at Reserve sites, insectivores do poorly in years with dryer winters and better in years with wetter winters because plants have great soil-water reserves during the warm, dry summers, which can support a greater number of insects (Nott et al., 2002). At Reserve and Developed sites the two guilds that would logically suffer the most from plants experiencing summer drought are significantly negatively correlated with El Niño winters. Bewick’s wrens are again positively correlated with weather, another similarity to Reserve sites. I surmise that the same factors causing this relationship in Reserve sites are at work in Developed sites.

When examining the correlations between birds and weather at Changing sites, there appears to follow only a slightly divergent pattern from Developed and Reserve sites; there are two guilds and two species that are significantly correlated with weather at Changing sites; however, the correlations are much weaker than those at Developed and Reserve sites. Contrary to my original hypotheses, Migrants, Herbivores and American robins are significantly negatively correlated with weather. In similarity to Developed and Reserve sites is the positive correlation between weather and Bewick’s wrens. American robins are the only species with a significant negative correlation; perhaps as a non-resident and herbivore the robins are less sensitive to the cold winters associated with La Nina and more negatively affected by the dryer summers that can reduce berry production during the breeding season. Pacific wrens are Bewick’s wrens on the other hand are both residents and neither are herbivores so cold and wet winters are more detrimental than dryer summers.

Although there are an equivalent number of significant correlations between bird abundance and weather at all three sites types, productivity is clearly the more important in shaping abundance at Changing sites. It appears the yearly changes in weather are minor compared to the clearing of a forest; thus, large-scale climate variables are less capable of explaining the variability in bird abundance at Changing sites. This is a strong contrast to Developed and Reserve sites, where productivity has very little correlation with bird abundance and weather has relatively larger influence, albeit not large overall.

CONCLUSIONS

Over the 10-year period of this study the factors that shaped guild abundance are very different at Changing sites than they are at Developed or Reserve sites. Productivity is critical in shaping the species abundance and richness at Changing sites because it is variable and remnant forest patches may not be capable of sustaining all species, and the effects of weather are minor compared to drastic landscape change. The drastic and rapid reduction in forest cover associated with forest clearing has caused primary productivity to become a driver of species presence and guild abundance. At Developed sites, which experienced significant loss of vegetation more than two decades ago, productivity is not nearly as important to bird abundance, though forest cover is still correlated with the most forest-reliant guilds. It seems the maturing landscaping is an adequate replacement for native vegetation for all but a select few guilds, and these guilds would benefit the most from either more mature landscaping or greater areas of forest left on the landscape during development. Developed sites share a mixture of characteristics of Reserve and Changing sites, though more closely resemble Reserve sites which is reflected in the relationships between bird abundance, productivity and weather. Birds are only weakly responding to both weather and productivity, perhaps because of the stable land cover regime and the ability of the suburban areas to buffer the effects of reduced productivity and weather fluctuations with human supplementation. Additionally, the weather is relatively mild in my study area owing to the buffering effect of the Puget Sound. Reserve sites show only two significant relationships between bird abundance and productivity, indicating the vegetation quantity is not as important and not variable over time, while weather is correlated with Herbivore abundance, indicating that weather only plays an important role in shaping abundance of a guild that is most sensitive to adverse plant growing conditions and does not appear to directly cause cold-induced mortality. Overall, bird abundance is being shaped by density independent factors, such as primary productivity and weather, at Changing sites much more strongly than at the more stable Developed and Reserve sites.

Contrary to my hypotheses, none of the individual species were significantly correlated with productivity and very few are correlated with weather, at any of the three site types, despite the 11 selected species being the more abundance members of their guilds. I expected these species to be representative of the guilds; however, it appears that the yearly variability of species abundance does not track that of productivity or weather. Perhaps the numerous other factors influencing species abundance, such as predation and competition are not acting synchronously with productivity or weather, obscuring the large-scale relationships to abundance. Another confounding factor may be the scale of my study: it could be that individual species respond to productivity and weather at either finer (Radford et al., 2005) or coarser (Yamaura et al, 2011) resolution than my 1km scale. Unfortunately, the combination of my remote sensing and bird survey techniques make it impossible to examine the correlations at alternative spatial scales. In this case the individual species may be at low relative density in the 1km study areas that I cannot detect subtle changes in the patterns of interest. By grouping individual species in to guilds some of the discordant factors and issues of scale can be smoothed allowing the relationships between guild abundance, productivity and weather to become apparent.

CONSERVATION IMPLICATIONS

My results suggest that housing developers in the Pacific Northwest would greatly benefit avian populations by limiting the amount of forest cleared at any one time and accelerating the recovery of primary productivity, in the form of bird-friendly vegetation, after the initial development phase. Homeowners in new subdivisions will most greatly benefit current bird residents and provide refuge for birds displaced by the subsequent housing development by planting fruiting shrubs, increasing plant density and structural complexity and even providing direct food and water subsidies. Goddard et al. (2010) found private gardens form a substantial portion of the urban green space and play a vital role in maintaining biodiversity in Britian. In recognition of this fact many conservation NGOs have programs in place to help individuals improve their gardens for wildlife. However, the urban garden is not without its perils for birds, first among them the domestic cat, the excessive use of exotic plants in landscaping and the fragmented nature of the garden patches (Goddard et al., 2010)

While birds may be better at coping with a fragmented landscape than many other species, it is not feasible to rely on individually managed private gardens as the whole solution to loss of native habitat. Although challenging, it would be more beneficial to wildlife if these large planned developments could cooperate with a group such as the Audubon Society to create an organized framework of private gardens, landscaped public areas and reserves of native forest.

The remaining large forest patches should remain intact as it appears that bird populations have adequate productivity and are fluctuating with weather in a predictable way. The negative correlations between bird guild abundance and weather indicate that if climate change predictions of dryer summers and reduced snowpack are correct for the Pacific Northwest bird population could decline. However, it appears that birds are relatively resistant to fluctuations in weather associated with ENSO in landscapes where primary productivity is stable. This makes prioritizing bird conservation in planning and implementing new developments even more important in the face of unpredictable changes in climate.

FUTURE DIRECTIONS

Future studies of the relationships between bird population demographics and large-scale variables such as primary productivity or climate should focus on addressing issues of scale encountered in this study. At a finer scale, site-specific measurements of weather conditions to improve the correlations between productivity and weather and to decrease the variability of the correlations between weather and bird abundance. This could be accomplished by installing relatively simple data loggers to record rainfall, temperature and soil moisture at each site. Understanding changes in land cover and productivity at a smaller scale could be improved by utilizing higher resolution aerial imagery or ground-based LIDAR to quantify the area and distribution gardens and small green spaces over time. Work to assess land cover change at very fine spatial resolution is already ongoing at these study sites and will likely yield an increased understanding of the nuanced factors that determine how birds respond to urbanization. Additionally, to assess not only the primary productivity, but also the "bird-friendliness" of these green spaces, on the ground surveying of the gardens for food, cover and nesting locations could be carried out alongside the bird surveys. The garden surveys would be a good opportunity for a partnership with a backyard wildlife group such as the Audubon Society or Backyard Wildlife Sanctuary Program; the partner group could also assess some of the gardens and make recommended improvements for wildlife. A longer-term study could then investigate if the garden improvements change the relationships between productivity and bird populations at Developed or Changing sites. A finer scale examination of the changes in productivity associated with urbanization may reveal further insights into their impacts on bird abundance and richness.

To understand how larger scale factors may be influencing the correlations between birds, productivity and weather it would be good to examine how the productivity of the land surrounding the study sites differs between sites and site types. Collecting NDVI data from the same MODIS products in 2 km^2 concentric around the bird survey sites would provide some insight about the surrounding land, which likely plays an important role in shaping these relationships.

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TABLES AND FIGURES

Table 1. Weather and climate data utilized in this study. Weather data was collected from Seattle Tacoma International Airport. The station is 370 ft. above sea level with Latitude 47°27'N, Longitude 122°19'W. The Oceanic Niño Index (ONI), a measure of El Niño strength was obtained from NOAA sea temperature monitoring buoys in the Pacific Ocean. ONI below -0.5 indicates La Nina conditions, -0.5 to 0.5 is neutral and above 0.5 indicates El Niño conditions; below -1.0 or above 1.0 is considered a strong La Nina or El Niño , respectively.

Year	ONI Winter	ONI Breeding	Mean High (C°)	Mean Low (C°)	Yearly Mean (C°)	Precipitation (cm)
2001	-0.55	0	14.67	6.72	10.72	95.40
2002	-0.05	0.65	14.89	6.89	10.94	79.65
2003	1.25	0.25	15.78	7.61	11.67	106.12
2004	0.45	0.45	15.89	7.89	11.89	78.99
2005	0.75	0.4	15.61	7.56	11.61	90.02
2006	-0.4	0.1	16.11	7.39	11.78	122.99
2007	0.85	-0.1	15.11	7.17	11.11	98.93
2008	-1.2	-0.45	14.72	6.89	10.78	78.05
2009	-0.4	0.3	15.50	6.89	11.22	97.64
2010	1.45	0.1	15.33	7.67	11.50	119.35

Table 2. Bird species were separated in to guilds based on the following life history traits. Yearly abundances of each guild were calculated for each site taking in to account survey effort. The number of species in each guild is in parentheses. Fifty-eight species total were included in this study. A table that details which species fall into each guild is provided in the supplemental material.

Development	**Migration**	**Diet**	**Food Subsidies**
Forest (21)	Neoptropical (24)	Herbivore (18)	Consumer (28)
Early Succession (39)	Short Distance (7)	Insectivore (35)	Avoider (30)
Synanthropic (8)	Resident (27)	Generalist (5)	

Table 3. Total number of years of data for each site type and site. Every site was not monitored over the 10-year study period, but each has data from representative years.

Site type and name	Years of data
Changing sites	87
Beaver Cleaver	10
Cougar Neighborhood	9
Issaquah Highlands	10
Montare	10
Redmond Ridge	10
Snoqualmie Ridge	10
Treemont Estates	10
Union Hill	9
Uplands	9
Developed sites	35
Beardslee	5
Forster Woods	4
Hawthorne	5
Highlands	3
Old Black Nugget	6
Somerset	4
Totem Falls	4
Westwood	4
Reserve sites	40
Cedar Watershed Preserve	7
Cougar Mountain Park	9
Lee Forest	10
Redmond Watershed Preserve	9
Squak Mountain	5

Table 4. Guild abundance varies by site type. Birds were assigned into guilds based on life history traits. Guild abundance was averaged for each site of the study period and then averaged again by site type and is reported as mean abundance ±S.E. For Changing sites df=9, 77, Developed sites N=35 and Reserve sites N=40.

Site Type	Forest	Synthropic	Migrant	Resident	Insectivores	Herbivores	Generalists	Subsidy Consumer	Subsidy Avoider
Changing	2.41±0.33	1.84±0.31	2.57±0.31	5.96±0.60	4.72±0.56	3.86±0.44	2.00±0.25	6.38±0.48	4.19±0.48
Developed	2.07± 0.38	2.74±0.82	1.55±0.31	7.01±0.92	3.64±0.61	3.61±0.68	2.85±0.46	6.85±0.96	3.24±0.57
Reserve	4.91±0.51	0.36±0.11	1.70±0.20	5.57±0.56	4.29±0.48	2.40±0.32	1.53±0.21	4.31±0.48	3.90±0.42

Table 5. Bird richness and abundance was primarily correlated with primary productivity at Changing Sites, weather at Reserve Sites and weakly by both factors at Developed Sites. I monitored bird richness and abundance for 10 years in the urbanizing fringe of Seattle using point counts and estimated productivity (NDVI) and weather (ONI) using remote sensing. In addition to zero-order correlations, partial correlations were computed for each independent variable, while holding the other constant; for example, the Weather Held Constant column is the correlation between bird guild and productivity with weather held constant. Correlations were computed for each site over the study period, Fisher transformed and averaged by site type. Values reported are r ±S.E. (p-value). Mean correlation coefficients significantly different than 0 are designated with a *. For Changing Sites n=9, Developed Sites n=7 and Reserve Sites n=5.

Changing Sites

	Productivity	Weather Held Constant	Weather	Productivity Held Constant
Richness	0.256 ±0.096(p=0.028)*	0.293 ±0.100(p=0.019)*	0.056 ±0.096(p=0.579)	0.032 ±0.111(p=0.777)
Forest	0.303 ±0.096(p=0.013)*	0.337 ±0.097(p=0.008)*	-0.024 ±0.111(p=0.837)	-0.082 ±0.120(p=0.514)
Synthropic	0.294 ±0.081(p=0.007)*	0.327 ±0.094(p=0.008)*	-0.148 ±0.087(p=0.129)	-0.205 ±0.099(p=0.073)
Migrant	0.297 ±0.089(p=0.010)*	0.357 ±0.092(p=0.005)*	-0.200 ±0.088(p=0.053)	-0.243 ±0.105(p=0.049)*
Resident	0.409 ±0.079(p=0.001)*	0.442 ±0.087(p=0.001)*	-0.066 ±0.081(p=0.443)	-0.135 ±0.098(p=0.207)
Generalist	0.269 ±0.102(p=0.029)*	0.257 ±0.115(p=0.057)	0.023 ±0.103(p=0.833)	-0.047 ±0.112(p=0.683)

Herbivore	0.317 ±0.093(p=0.009)*	0.341 ±0.117(p=0.019)*	-0.203 ±0.097(p=0.069)	-0.279 ±0.113(p=0.039)*
Insectivore	0.355 ±0.111(p=0.013)*	0.323 ±0.086(p=0.006)*	-0.124 ±0.094(p=0.222)	-0.171 ±0.123(p=0.204)
Subsidy Consumer	0.371 ±0.083(p=0.002)*	0.505 ±0.121(p=0.003)*	-0.105 ±0.081(p=0.228)	-0.186 ±0.099(p=0.097)
Subsidy Avoider	0.310 ±0.090(p=0.009)*	0.288 ±0.062(p=0.002)*	-0.171 ±0.116(p=0.178)	-0.215 ±0.132(p=0.141)
AMCR	0.073 ±0.140(p=0.619)	0.048 ±0.148(p=0.756)	-0.001 ±0.096(p=0.989)	-0.021 ±0.102(p=0.841)
AMRO	0.110 ±0.180(p=0.558)	0.113 ±0.182(p=0.552)	-0.100 ±0.059(p=0.126)	-0.133 ±0.056(p=0.044)*
BEWR	0.164 ±0.163(p=0.343)	0.154 ±0.168(p=0.385)	0.273 ±0.056(p=0.001)*	0.271 ±0.063(p=0.003)*
BHGR	-0.032 ±0.231(p=0.894)	-0.031 ±0.237(p=0.900)	0.063 ±0.116(p=0.602)	0.012 ±0.126(p=0.929)
EUST	0.067 ±0.168(p=0.698)	0.063 ±0.179(p=0.734)	-0.073 ±0.067(p=0.305)	-0.039 ±0.089(p=0.675)
PAWR	-0.116 ±0.206(p=0.588)	-0.107 ±0.207(p=0.620)	-0.058 ±0.048(p=0.258)	-0.027 ±0.053(p=0.625)
PSFL	-0.137 ±0.187(p=0.483)	-0.106 ±0.200(p=0.610)	0.002 ±0.108(p=0.987)	0.002 ±0.122(p=0.989)
SOSP	0.032 ±0.216(p=0.887)	0.055 ±0.215(p=0.806)	-0.038 ±0.061(p=0.546)	0.012 ±0.061(p=0.854)
SPTO	0.186 ±0.177(p=0.324)	0.195 ±0.176(p=0.301)	-0.026 ±0.057(p=0.660)	-0.058 ±0.056(p=0.330)
SWTH	-0.013 ±0.217(p=0.952)	-0.007 ±0.211(p=0.976)	-0.096 ±0.121(p=0.449)	-0.106 ±0.113(p=0.377)
WIWA	0.010 ±0.166(p=0.952)	0.008 ±0.172(p=0.964)	0.039 ±0.129(p=0.768)	0.089 ±0.134(p=0.525)

Developed Sites

	Productivity	Weather Constant	Weather	Productivity Constant
Richness	0.381 ±0.226(p=0.143)	0.188 ±0.466(p=0.701)	0.439 ±0.148(p=0.025)*	0.353 ±0.244(p=0.199)

Forest	0.395 ±0.226(p=0.130)	0.501 ±0.240(p=0.082)	0.600 ±0.446(p=0.227)	0.019 ±0.480(p=0.970)
Synthropic	0.298 ±0.223(p=0.230)	0.318 ±0.219(p=0.197)	-0.025 ±0.175(p=0.893)	0.003 ±0.175(p=0.985)
Migrant	0.263 ±0.169(p=0.171)	1.006 ±0.542(p=0.113)	-0.359 ±0.213(p=0.143)	-0.999 ±0.566(p=0.128)
Resident	0.259 ±0.260(p=0.358)	0.441 ±0.373(p=0.282)	-0.093 ±0.182(p=0.627)	-0.380 ±0.275(p=0.216)
Generalist	0.109 ±0.271(p=0.701)	-0.100 ±0.417(p=0.818)	-0.093 ±0.282(p=0.752)	-0.099 ±0.433(p=0.826)
Herbivore	0.301 ±0.280(p=0.323)	0.237 ±0.341(p=0.513)	0.038 ±0.171(p=0.830)	-0.095 ±0.243(p=0.709)
Insectivore	0.047 ±0.103(p=0.661)	0.520 ±0.143(p=0.011)*	-0.382 ±0.163(p=0.058)	-0.681 ±0.187(p=0.011)*
Subsidy Consumer	0.242 ±0.300(p=0.450)	0.344 ±0.453(p=0.476)	-0.110 ±0.201(p=0.604)	-0.314 ±0.327(p=0.374)
Subsidy Avoider	0.128 ±0.074(p=0.135)	0.444 ±0.202(p=0.070)	-0.276 ±0.208(p=0.232)	-0.559 ±0.295(p=0.107)
AMCR	0.061 ±0.346(p=0.867)	-0.318 ±0.584(p=0.606)	0.124 ±0.148(p=0.435)	0.332 ±0.202(p=0.152)
AMRO	0.080 ±0.245(p=0.754)	0.324 ±0.510(p=0.548)	0.112 ±0.202(p=0.599)	0.307 ±0.248(p=0.262)
BEWR	0.830 ±0.327(p=0.044)	0.424 ±0.612(p=0.514)	0.533 ±0.203(p=0.039)*	0.406 ±0.308(p=0.235)
BHGR	-0.009 ±0.269(p=0.974)	-0.115 ±0.460(p=0.810)	0.042 ±0.166(p=0.807)	-0.208 ±0.231(p=0.403)
EUST	0.351 ±0.401(p=0.414)	0.442 ±0.410(p=0.323)	-0.233 ±0.232(p=0.354)	-0.147 ±0.248(p=0.574)
PAWR	-0.131 ±0.244(p=0.610)	0.060 ±0.302(p=0.848)	-0.247 ±0.140(p=0.129)	-0.220 ±0.197(p=0.307)
PSFL	-0.501 ±0.201(p=0.047)	-0.229 ±0.588(p=0.711)	-0.245 ±0.189(p=0.244)	0.032 ±0.267(p=0.910)
SOSP	-0.108 ±0.206(p=0.619)	-0.249 ±0.295(p=0.431)	-0.029 ±0.207(p=0.892)	0.092 ±0.247(p=0.721)
SPTO	0.475 ±0.463(p=0.344)	0.955 ±0.783(p=0.268)	0.087 ±0.142(p=0.562)	0.406 ±0.245(p=0.148)
SWTH	0.208 ±0.316(p=0.534)	0.419 ±0.344(p=0.269)	0.101 ±0.223(p=0.668)	-0.053 ±0.263(p=0.848)

WIWA	0.116 ±0.183(p=0.548)	0.156 ±0.235(p=0.533)	0.079 ±0.232(p=0.745)	-0.058 ±0.240(p=0.816)

Reserve Sites

	Productivity	Weather Constant	Weather	Productivity Constant
Richness	0.245 ±0.196(p=0.279)	0.287 ±0.206(p=0.236)	0.015 ±0.195(p=0.942)	-0.030 ±0.207(p=0.890)
Forest	0.278 ±0.234(p=0.300)	0.278 ±0.248(p=0.326)	-0.098 ±0.131(p=0.498)	-0.217 ±0.124(p=0.157)
Synthropic	0.176 ±0.143(p=0.286)	0.209 ±0.073(p=0.046)*	-0.559 ±0.224(p=0.067)	-0.560 ±0.188(p=0.040)*
Migrant	0.319 ±0.332(p=0.391)	0.258 ±0.325(p=0.472)	-0.025 ±0.163(p=0.887)	-0.049 ±0.126(p=0.718)
Resident	0.363 ±0.169(p=0.097)	0.296 ±0.181(p=0.177)	0.087 ±0.138(p=0.564)	0.020 ±0.124(p=0.878)
Generalist	0.168 ±0.122(p=0.240)	0.141 ±0.166(p=0.442)	-0.136 ±0.125(p=0.338)	-0.139 ±0.160(p=0.435)
Herbivore	0.301 ±0.256(p=0.305)	0.364 ±0.258(p=0.231)	-0.355 ±0.064(p=0.005)*	-0.396 ±0.093(p=0.013)*
Insectivore	0.516 ±0.311(p=0.173)	0.471 ±0.333(p=0.230)	0.200 ±0.171(p=0.308)	0.185 ±0.168(p=0.334)
Subsidy Consumer	0.223 ±0.191(p=0.308)	0.200 ±0.219(p=0.412)	-0.049 ±0.116(p=0.692)	-0.066 ±0.145(p=0.675)
Subsidy Avoider	0.434 ±0.262(p=0.173)	0.765 ±0.611(p=0.279)	-0.093 ±0.167(p=0.605)	-0.592 ±0.510(p=0.310)
AMCR	0.001 ±0.258(p=0.996)	-0.044 ±0.234(p=0.859)	-0.149 ±0.175(p=0.443)	-0.094 ±0.160(p=0.590)
AMRO	0.285 ±0.293(p=0.385)	0.211 ±0.322(p=0.548)	0.147 ±0.143(p=0.361)	0.032 ±0.177(p=0.865)
BEWR	0.056 ±0.256(p=0.837)	0.050 ±0.262(p=0.859)	0.242 ±0.073(p=0.030)*	0.256 ±0.074(p=0.026)*
BHGR	0.151 ±0.225(p=0.540)	0.047 ±0.255(p=0.861)	0.034 ±0.211(p=0.880)	-0.037 ±0.221(p=0.876)
EUST	0.079 ±0.079(p=0.374)	0.093 ±0.093(p=0.374)	-0.074 ±0.074(p=0.374)	-0.086 ±0.086(p=0.374)

PAWR	-0.018 ±0.259(p=0.947)	-0.102 ±0.229(p=0.680)	0.321 ±0.112(p=0.046)*	0.245 ±0.122(p=0.115)
PSFL	0.181 ±0.269(p=0.538)	0.256 ±0.324(p=0.475)	0.156 ±0.180(p=0.434)	0.085 ±0.238(p=0.739)
SOSP	0.522 ±0.356(p=0.216)	0.502 ±0.359(p=0.234)	0.166 ±0.088(p=0.133)	-0.031 ±0.103(p=0.776)
SPTO	0.113 ±0.292(p=0.719)	0.100 ±0.259(p=0.718)	0.183 ±0.208(p=0.428)	0.187 ±0.183(p=0.363)
SWTH	0.241 ±0.433(p=0.608)	0.249 ±0.416(p=0.582)	0.098 ±0.126(p=0.479)	-0.038 ±0.096(p=0.712)
WIWA	0.029 ±0.093(p=0.768)	0.029 ±0.090(p=0.767)	-0.036 ±0.116(p=0.774)	-0.030 ±0.114(p=0.804)

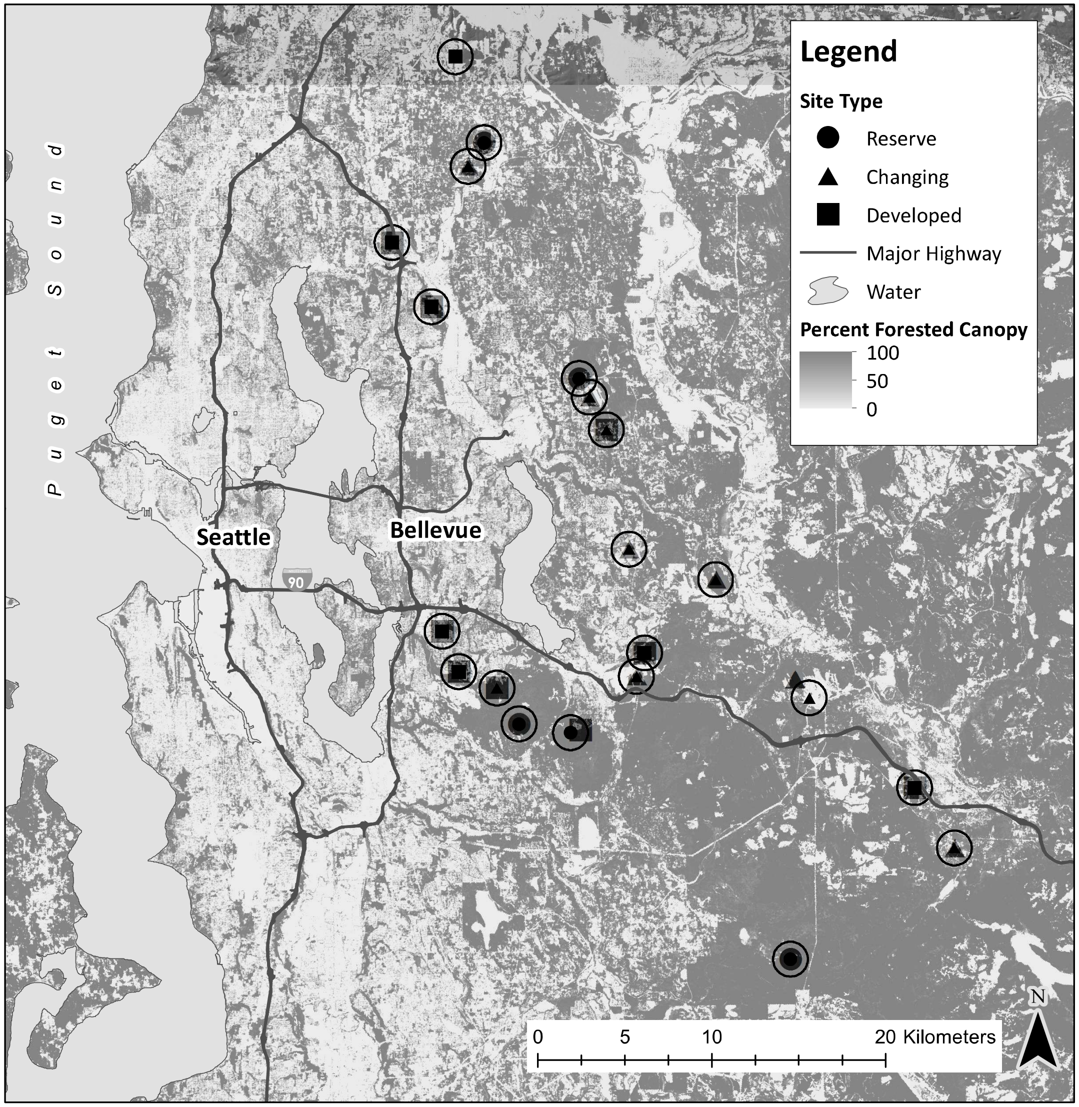

Figure 1. Study sites are spread throughout the Seattle Metropolitan area and across a range of canopy coverage. Canopy cover was obtained from the National Land Cover Database 2001 (Homer et al., 2007).

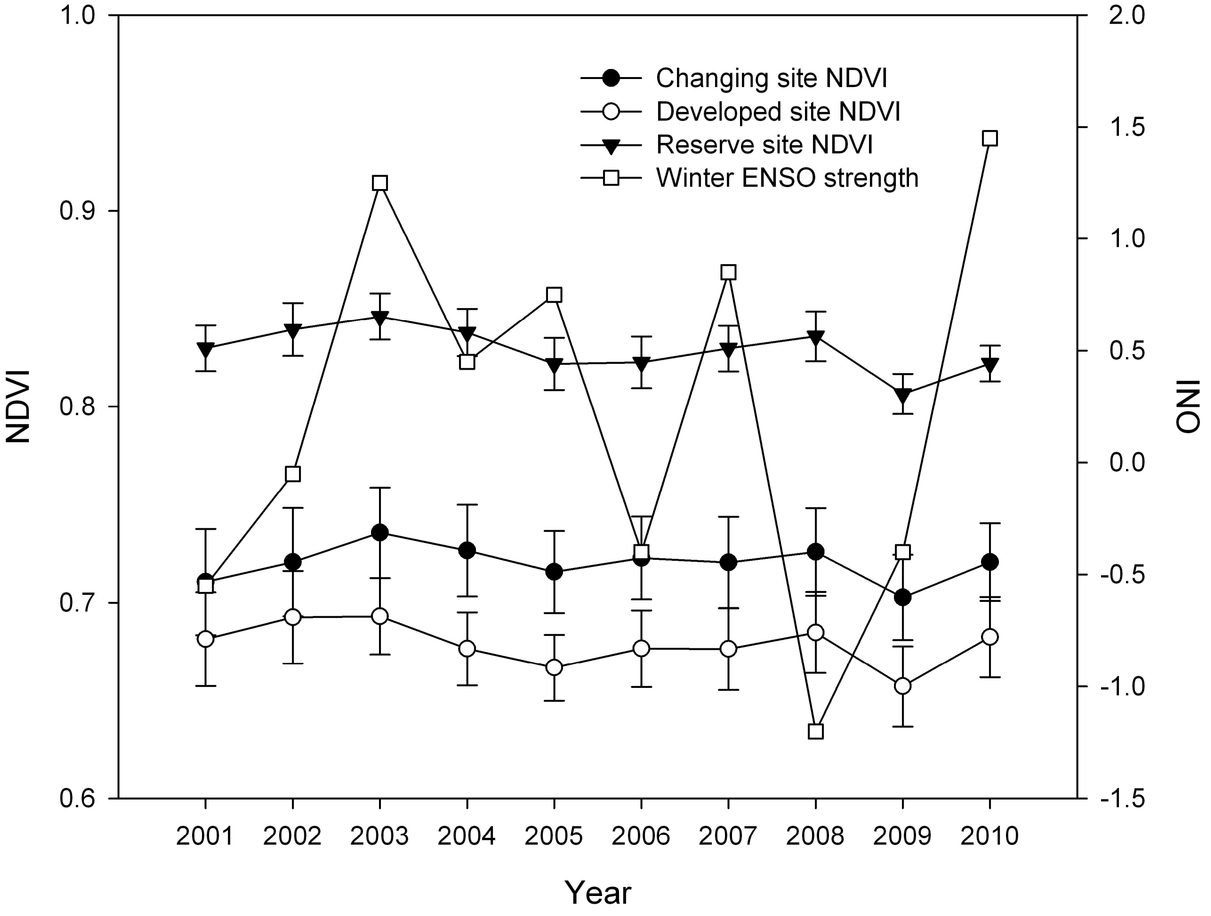

Figure 2. Mean NDVI is significantly greater at forest sites (n=5) than Developed (n=7; p=0.01) and Changing sites (n=9; p=0.02). Reserve variance is less than Changing (F= 4.0, p<0.01 df=9, 19) and Developed (F= 5.0, p<0.01, df=9, 19) variances. NDVI was assessed 23 times yearly at each site from MODIS satellite images, and error free data was averaged to produce yearly data for each site. Error bars represent 95% confidence intervals around the mean. ONI is a measure of ENSO strength; data given here represents ENSO strength of the winter preceding the breeding season.

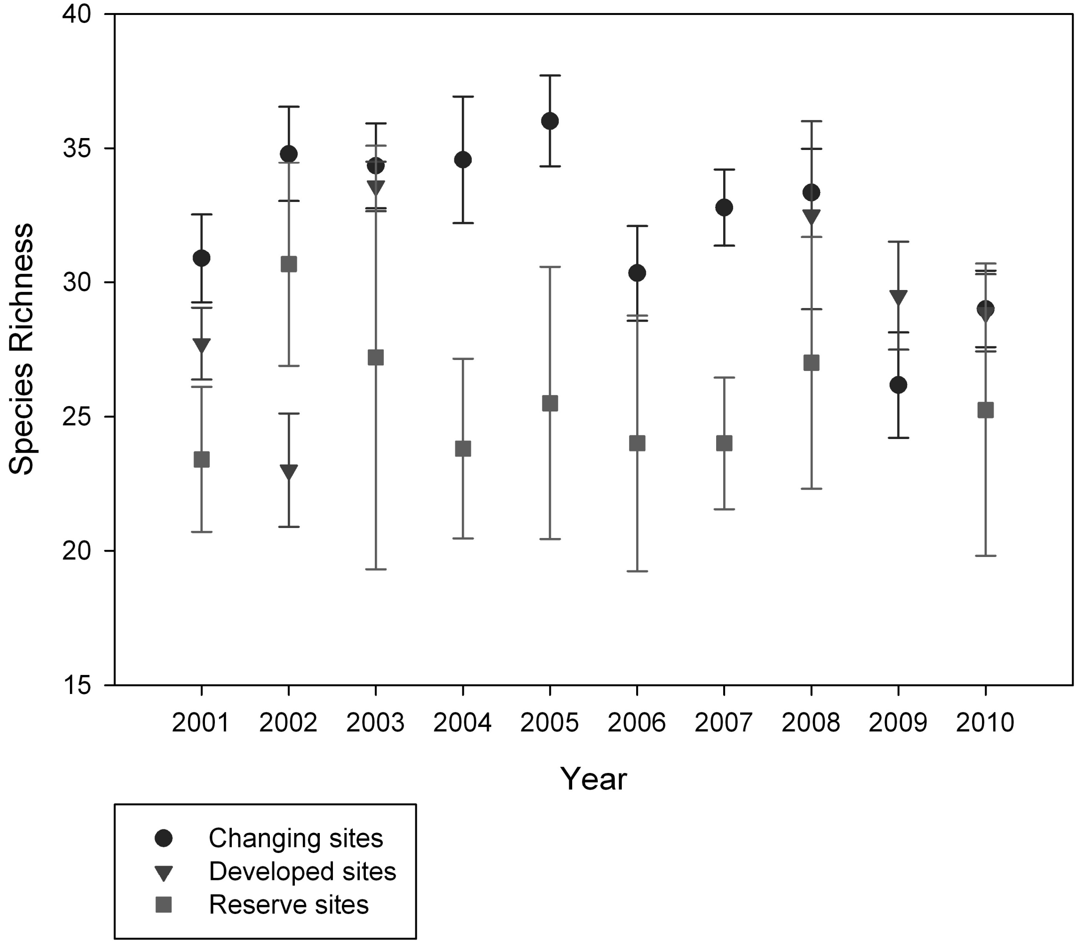

Figure 3. Species richness is greater at Changing sites than it is at Reserve sites. Point counts were conducted during the breeding season and species richness was calculated at the presence of any species in at least one of the point counts. Annual richness for each site was averaged by site type and the error bars are the standard error of those means.

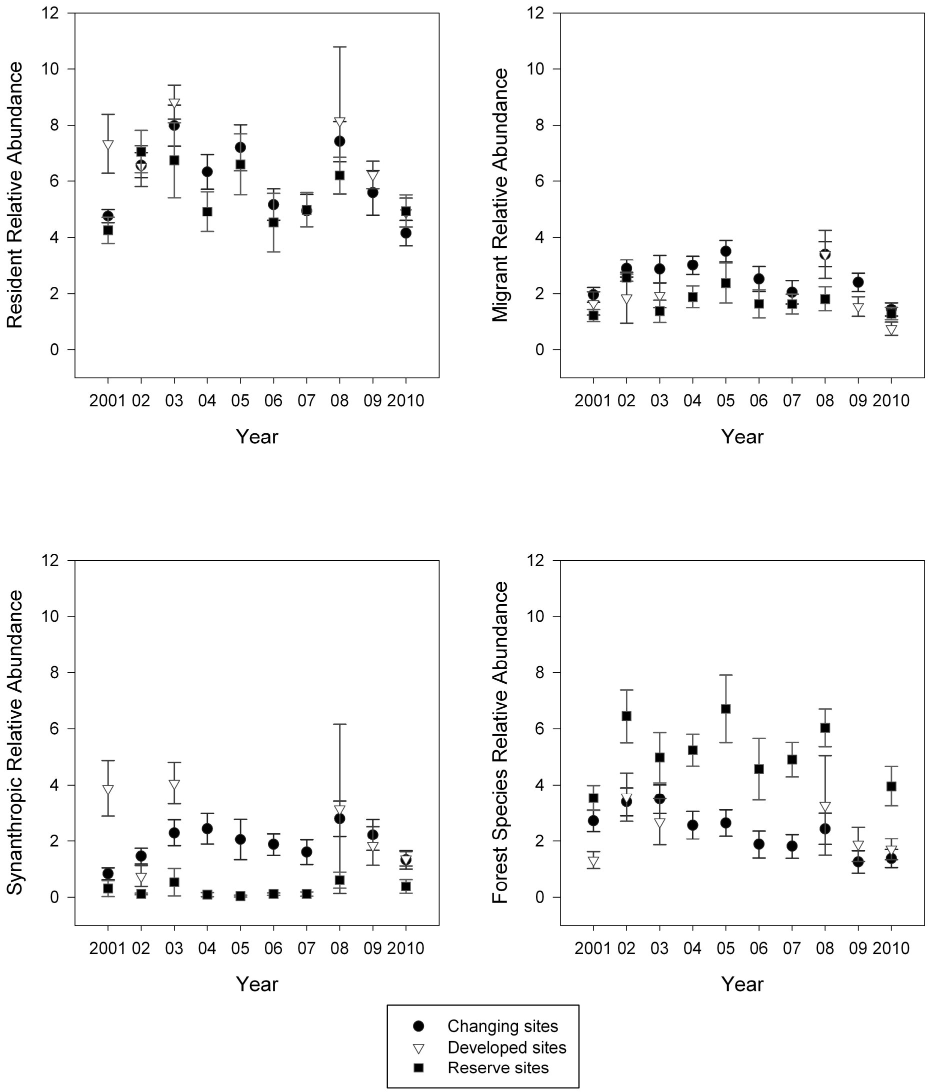

Figure 4. Mean guild abundance was most variable at Changing sites and least variable at Reserve sites. Point counts were conducted during the breeding season and relative abundance was calculated for each site. Sites were averaged by site type for each year. Those means are presented here with standard error as error bars.

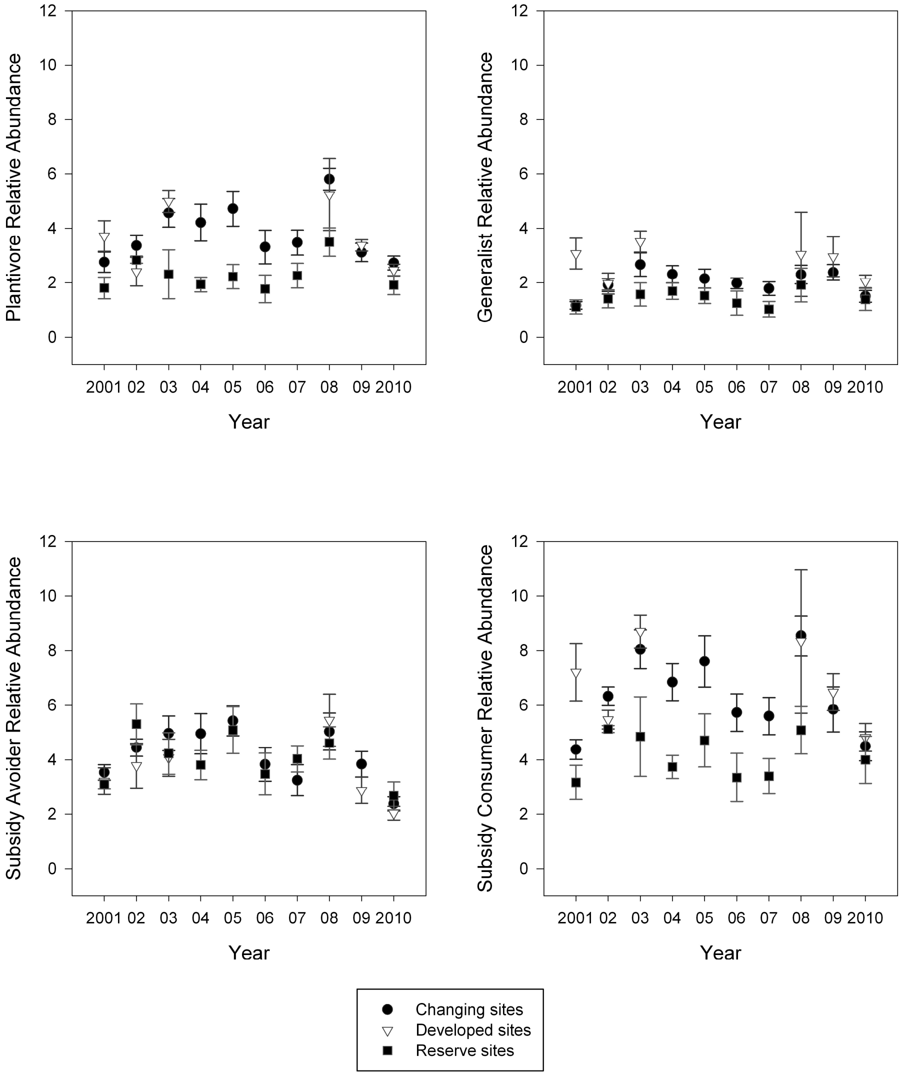

Figure 5. Mean guild abundance was most variable at Changing sites and least variable at Reserve sites. Point counts were conducted during the breeding season and relative abundance was calculated for each site. Sites were averaged by site type for each year. Those means are presented here with standard error as error bars.

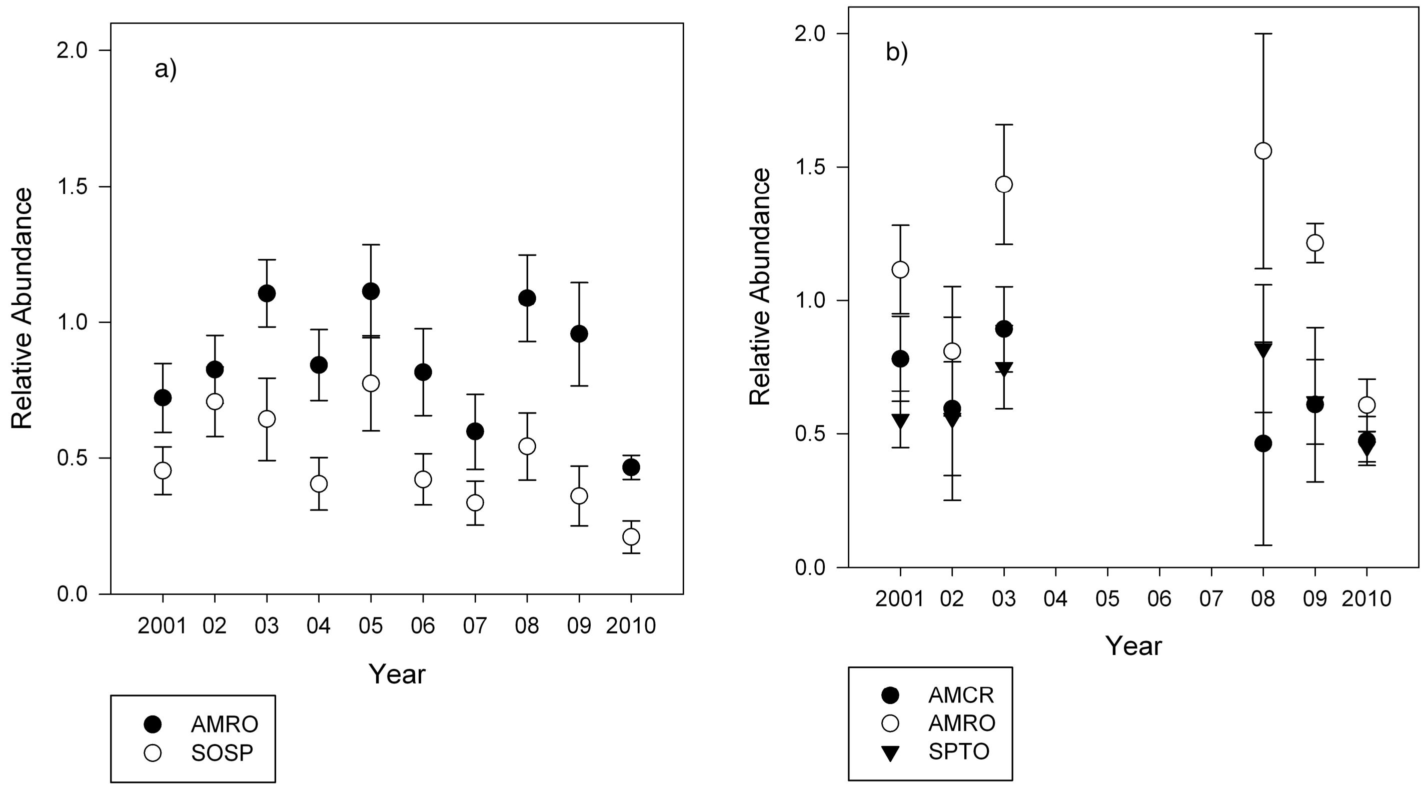

Figure 6. Few species exhibited variable relative abundance over the course of my study at Changing (a) and Developed sites (b). There was no significant variability at Reserve sites. Point counts were conducted during the breeding season and relative abundance was calculated for each site. Sites were averaged by site type for each year. Those means are presented here with error bars as standard error.

SUPPLEMENTAL DATA

Table S1: Each bird species was assigned into guilds for the following five categories based on life history traits. Developmental guilds are based on the stage of urbanization the species prefers. Food subsidies refers to intentional feeding with bird food.

Species	Species	Developmental Guilds	Migratory	Foraging	Nesting	Food Subsidies
AMCR	*Corvus brachyrhynchos*	Synthropic	Resident	Generalist	Canopy	Consumer
AMGO	*Carduelis tristis*	Early Succession	Short Distance	Plantivore	Canopy	Consumer
AMRO	*Turdus migratorius*	Early Succession	Short Distance	Plantivore	Shrub	Avoider
ANHU	*Calypte anna*	Synthropic	Short Distance	Plantivore	Shrub	Consumer
BARS	*Hirundo rustica*	Synthropic	Neotropical	Insectivore	Human Structure	Avoider
BCCH	*Poecile atricapillus*	Early Succession	Resident	Generalist	Secondary Cavity	Consumer
BEWR	*Thryomanes bewickii*	Early Succession	Resident	Insectivore	Shrub	Avoider
BHCO	*Molothrus ater*	Synthropic	Neotropical	Plantivore	Canopy	Consumer
BHGR	*Pheucticus melanocephalus*	Early Succession	Neotropical	Plantivore	Shrub	Consumer
BRBL	*Euphagus cyanocephalus*	Early Succession	Resident	Insectivore	Shrub	Avoider
BRCR	*Certhia americana*	Forest	Resident	Insectivore	Secondary Cavity	Avoider
BTPI	*Columba fasciata*	Early Succession	Resident	Plantivore	Canopy	Consumer
BTYW	*Dendroica nigrescens*	Forest	Neotropical	Insectivore	Canopy	Avoider
BUSH	*Psaltriparus minimus*	Early Succession	Resident	Insectivore	Shrub	Consumer
CAVI	*Vireo cassinii*	Early Succession	Neotropical	Insectivore	Shrub	Avoider
CBCH	*Poecile rufescens*	Forest	Resident	Generalist	Secondary Cavity	Consumer
CEDW	*Bombycilla cedrorum*	Early Succession	Short Distance	Insectivore	Shrub	Avoider
DEJU	*Junco hyemalis*	Early Succession	Resident	Plantivore	Ground	Consumer
DOWO	*Picoides pubescens*	Forest	Resident	Insectivore	Primary Cavity	Consumer
EUST	*Sturnus vulgaris*	Synthropic	Resident	Generalist	Secondary Cavity	Consumer
EVGR	*Coccothraustes vespertinus*	Early Succession	Short Distance	Plantivore	Canopy	Consumer
GCKI	*Regulus satrapa*	Forest	Resident	Insectivore	Canopy	Avoider
HAFL	*Empidonax hammondii*	Forest	Neotropical	Insectivore	Shrub	Avoider
HAWO	*Picoides villosus*	Forest	Resident	Insectivore	Primary Cavity	Consumer

HOFI	*Carpodacus mexicanus*	Synthropic	Resident	Plantivore	Canopy	Consumer
HOSP	*Passer domesticus*	Synthropic	Resident	Plantivore	Human Structure	Consumer
HUVI	*Vireo huttoni*	Forest	Resident	Insectivore	Shrub	Avoider
KILL	*Charadrius vociferus*	Early Succession	Neotropical	Insectivore	Ground	Avoider
MODO	*Zenaida macroura*	Early Succession	Neotropical	Plantivore	Canopy	Consumer
NOFL	*Colaptes auratus*	Early Succession	Resident	Insectivore	Primary Cavity	Consumer
OCWA	*Vermivora celata*	Early Succession	Neotropical	Insectivore	Shrub	Avoider
OSFL	*Contopus cooperi*	Early Succession	Neotropical	Insectivore	Secondary Cavity	Avoider
PAWR	*Troglodytes pacificus*	Forest	Resident	Insectivore	Shrub	Avoider
PISI	*Carduelis pinus*	Early Succession	Resident	Plantivore	Canopy	Consumer
PSFL	*Empidonax difficilis*	Forest	Resident	Insectivore	Primary Cavity	Consumer
PUFI	*Carpodacus purpureus*	Forest	Neotropical	Plantivore	Canopy	Consumer
RBNU	*Sitta canadensis*	Forest	Resident	Insectivore	Secondary Cavity	Consumer
RBSA	*Sphyrapicus ruber*	Forest	Resident	Insectivore	Primary Cavity	Avoider
RCKI	*Regulus calendula*	Forest	Resident	Insectivore	Canopy	Avoider
RECR	*Loxia curvirostra*	Forest	Short Distance	Plantivore	Canopy	Avoider
ROPI	*Columba livia*	Synthropic	Resident	Plantivore	Human Structure	Consumer
RUHU	*Selasphorus rufus*	Early Succession	Neotropical	Plantivore	Shrub	Consumer
SAVS	*Passerculus sandwichensis*	Early Succession	Neotropical	Insectivore	Ground	Avoider
SOSP	*Melospiza melodia*	Early Succession	Resident	Insectivore	Shrub	Consumer
SPTO	*Pipilo maculatus*	Early Succession	Resident	Insectivore	Ground	Consumer
STJA	*Cyanocitta stelleri*	Forest	Resident	Generalist	Canopy	Consumer
SWTH	*Catharus ustulatus*	Forest	Neotropical	Plantivore	Shrub	Avoider
TOSO	*Myadestes townsendi*	Forest	Neotropical	Plantivore	Shrub	Avoider
TOWA	*Dendroica townsendi*	Forest	Neotropical	Insectivore	Canopy	Avoider
VASW	*Chaetura vauxi*	Early Succession	Neotropical	Insectivore	Secondary Cavity	Avoider
VGSW	*Tachycineta thalassina*	Early Succession	Neotropical	Insectivore	Secondary Cavity	Avoider
WAVI	*Vireo gilvus*	Early Succession	Neotropical	Insectivore	Shrub	Avoider
WCSP	*Zonotrichia leucophrys*	Early Succession	Short Distance	Insectivore	Shrub	Avoider
WETA	*Piranga ludoviciana*	Forest	Neotropical	Insectivore	Canopy	Avoider
WEWP	*Contopus sordidus*	Early Succession	Neotropical	Insectivore	Shrub	Avoider

WIFL	*Empidonax traillii*	Early Succession	Neotropical	Insectivore	Shrub	Avoider
WIWA	*Wilsonia pusilla*	Forest	Neotropical	Insectivore	Ground	Avoider
YRWA	*Dendroica coronata*	Early Succession	Neotropical	Insectivore	Canopy	Consumer

Table S2. The mean relative abundance for each species at Changing sites over the course of this study. Relative abundance was assessed by conducting four 50 m fixed radius point counts at four to eight points in each study site. Each year of data represents the mean of all sites (N) that were measured that year.

	YEAR																			
	2001 N=9		2002 N=9		2003 N=9		2004 N=9		2005 N=9		2006 N=9		2007 N=9		2008 N=9		2009 N=6		2010 N=9	
Species	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
AMCR	0.22	0.06	0.36	0.08	0.90	0.31	0.69	0.13	0.54	0.12	0.70	0.16	0.57	0.12	0.88	0.19	0.80	0.14	0.55	0.11
AMGO	0.05	0.04	0.11	0.06	0.34	0.11	0.51	0.21	0.44	0.21	0.47	0.28	0.60	0.23	0.73	0.24	0.31	0.12	0.32	0.09
AMRO	0.72	0.13	0.83	0.13	1.11	0.12	0.84	0.13	1.11	0.17	0.82	0.16	0.60	0.14	1.09	0.16	0.96	0.19	0.47	0.04
ANHU	0.03	0.02	0.00	0.00	0.03	0.02	0.02	0.01	0.02	0.02	0.00	0.00	0.03	0.02	0.03	0.01	0.01	0.01	0.00	0.00
BARS	0.04	0.03	0.01	0.01	0.10	0.07	0.12	0.07	0.04	0.02	0.03	0.02	0.04	0.01	0.06	0.04	0.07	0.03	0.02	0.01
BCCH	0.19	0.07	0.34	0.09	0.25	0.10	0.24	0.09	0.18	0.04	0.31	0.11	0.20	0.05	0.23	0.07	0.51	0.22	0.28	0.07
BEWR	0.09	0.03	0.16	0.05	0.23	0.05	0.15	0.06	0.11	0.05	0.11	0.05	0.08	0.03	0.09	0.03	0.09	0.05	0.13	0.04
BHCO	0.17	0.03	0.21	0.06	0.17	0.08	0.28	0.05	0.22	0.05	0.17	0.05	0.19	0.06	0.25	0.09	0.01	0.01	0.09	0.03
BHGR	0.06	0.03	0.20	0.06	0.14	0.05	0.09	0.04	0.11	0.03	0.10	0.05	0.10	0.04	0.13	0.04	0.13	0.03	0.09	0.02
BRBL	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.06	0.06	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BRCR	0.13	0.04	0.29	0.09	0.28	0.06	0.11	0.04	0.08	0.03	0.13	0.05	0.07	0.03	0.08	0.03	0.02	0.02	0.09	0.03
BTPI	0.05	0.04	0.00	0.00	0.04	0.04	0.04	0.02	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
BTYW	0.10	0.03	0.20	0.10	0.07	0.03	0.04	0.01	0.09	0.03	0.04	0.02	0.07	0.03	0.08	0.03	0.06	0.05	0.01	0.01
BUSH	0.06	0.02	0.04	0.02	0.07	0.05	0.03	0.03	0.08	0.05	0.03	0.02	0.01	0.01	0.16	0.06	0.05	0.02	0.04	0.02
CAVI	0.03	0.02	0.04	0.02	0.03	0.02	0.00	0.00	0.02	0.02	0.01	0.01	0.03	0.03	0.02	0.02	0.00	0.00	0.00	0.00
CBCH	0.44	0.04	0.36	0.08	0.81	0.12	0.73	0.16	0.65	0.16	0.51	0.12	0.51	0.10	0.61	0.20	0.14	0.12	0.43	0.12
CEDW	0.21	0.05	0.10	0.03	0.49	0.13	0.79	0.46	0.39	0.18	0.34	0.12	0.36	0.10	0.35	0.09	0.19	0.09	0.16	0.06
DEJU	0.41	0.09	0.43	0.09	0.71	0.10	0.70	0.17	0.77	0.18	0.43	0.07	0.55	0.10	0.98	0.18	0.80	0.14	0.68	0.10
DOWO	0.02	0.02	0.08	0.02	0.03	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
EUST	0.21	0.09	0.69	0.20	0.43	0.11	0.48	0.19	0.67	0.36	0.38	0.15	0.43	0.22	0.51	0.22	0.90	0.36	0.20	0.09
EVGR	0.02	0.01	0.05	0.03	0.00	0.00	0.02	0.02	0.08	0.04	0.05	0.05	0.06	0.02	0.10	0.05	0.04	0.04	0.09	0.07
GCKI	0.15	0.03	0.13	0.04	0.12	0.03	0.05	0.02	0.13	0.05	0.09	0.04	0.05	0.02	0.09	0.04	0.03	0.02	0.06	0.02
HAFL	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
HAWO	0.05	0.02	0.06	0.03	0.04	0.02	0.04	0.02	0.03	0.02	0.03	0.01	0.05	0.02	0.01	0.01	0.05	0.03	0.02	0.01
HOFI	0.13	0.07	0.02	0.02	0.26	0.11	0.23	0.07	0.12	0.06	0.10	0.04	0.08	0.02	0.36	0.10	0.13	0.05	0.13	0.04
HOSP	0.00	0.00	0.00	0.00	0.01	0.01	0.07	0.05	0.10	0.08	0.09	0.06	0.09	0.09	0.10	0.09	0.09	0.07	0.05	0.04

HUVI	0.02	0.01	0.13	0.04	0.07	0.03	0.02	0.01	0.04	0.02	0.01	0.01	0.02	0.01	0.03	0.01	0.00	0.00	0.01	0.01
KILL	0.01	0.01	0.03	0.01	0.04	0.02	0.02	0.01	0.01	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.08	0.05	0.00	0.00
MODO	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NOFL	0.03	0.02	0.04	0.01	0.10	0.04	0.04	0.02	0.02	0.01	0.07	0.03	0.05	0.02	0.06	0.03	0.08	0.03	0.03	0.01
OCWA	0.00	0.00	0.03	0.02	0.02	0.02	0.03	0.02	0.03	0.02	0.03	0.02	0.01	0.01	0.05	0.02	0.00	0.00	0.00	0.00
OSFL	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00
PAWR	0.48	0.16	0.46	0.15	0.19	0.06	0.15	0.07	0.19	0.07	0.10	0.05	0.20	0.07	0.11	0.05	0.16	0.10	0.04	0.02
PISI	0.41	0.12	0.57	0.12	0.58	0.14	0.28	0.17	0.78	0.24	0.08	0.04	0.53	0.20	0.61	0.14	0.12	0.11	0.16	0.07
PSFL	0.40	0.12	0.42	0.11	0.29	0.08	0.23	0.06	0.30	0.09	0.11	0.03	0.11	0.02	0.21	0.07	0.17	0.06	0.13	0.05
PUFI	0.05	0.01	0.11	0.04	0.16	0.06	0.03	0.02	0.09	0.02	0.13	0.05	0.08	0.05	0.14	0.04	0.05	0.03	0.02	0.01
RBNU	0.03	0.02	0.13	0.02	0.31	0.10	0.25	0.10	0.17	0.04	0.07	0.02	0.05	0.01	0.10	0.04	0.10	0.05	0.11	0.03
RBSA	0.00	0.00	0.00	0.00	0.01	0.01	0.03	0.02	0.04	0.01	0.03	0.01	0.04	0.02	0.08	0.03	0.01	0.01	0.02	0.02
RCKI	0.01	0.01	0.02	0.02	0.00	0.00	0.00	0.00	0.03	0.02	0.00	0.00	0.03	0.02	0.02	0.02	0.01	0.01	0.00	0.00
RECR	0.01	0.01	0.01	0.01	0.01	0.01	0.08	0.04	0.01	0.01	0.01	0.01	0.00	0.00	0.15	0.09	0.00	0.00	0.02	0.02
ROPI	0.05	0.03	0.09	0.06	0.38	0.22	0.53	0.22	0.33	0.20	0.39	0.09	0.17	0.06	0.59	0.31	0.20	0.10	0.28	0.08
RUHU	0.11	0.06	0.15	0.05	0.11	0.04	0.08	0.03	0.10	0.03	0.10	0.05	0.06	0.03	0.09	0.03	0.00	0.00	0.06	0.03
SAVS	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.02	0.00	0.00	0.01	0.01	0.02	0.02	0.05	0.05	0.05	0.05
SOSP	0.45	0.09	0.71	0.13	0.64	0.15	0.40	0.10	0.77	0.18	0.42	0.09	0.33	0.08	0.54	0.12	0.36	0.11	0.21	0.06
SPTO	0.56	0.10	0.75	0.13	0.90	0.21	0.60	0.09	0.83	0.14	0.74	0.23	0.62	0.16	0.85	0.20	0.71	0.25	0.41	0.13
STJA	0.10	0.04	0.09	0.03	0.26	0.09	0.15	0.06	0.10	0.03	0.07	0.03	0.07	0.03	0.07	0.03	0.02	0.01	0.04	0.02
SWTH	0.45	0.10	0.48	0.12	0.48	0.13	0.37	0.11	0.37	0.10	0.35	0.11	0.31	0.10	0.41	0.12	0.25	0.11	0.25	0.09
TOSO	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
TOWA	0.00	0.00	0.05	0.03	0.04	0.03	0.03	0.02	0.02	0.01	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00
VASW	0.02	0.02	0.00	0.00	0.04	0.03	0.09	0.04	0.03	0.02	0.00	0.00	0.01	0.01	0.04	0.03	0.00	0.00	0.00	0.00
VGSW	0.59	0.13	0.73	0.17	1.02	0.23	1.46	0.27	1.91	0.42	1.15	0.13	0.87	0.17	1.61	0.29	1.47	0.40	0.61	0.12
WAVI	0.01	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.03	0.01	0.03	0.02	0.03	0.03	0.02	0.01	0.00	0.00	0.02	0.01
WCSP	0.14	0.06	0.18	0.07	0.17	0.06	0.18	0.08	0.25	0.10	0.18	0.07	0.19	0.07	0.29	0.13	0.18	0.10	0.22	0.10
WETS	0.07	0.02	0.15	0.02	0.19	0.06	0.13	0.03	0.14	0.04	0.10	0.04	0.06	0.02	0.10	0.03	0.08	0.06	0.03	0.01
WEWP	0.00	0.00	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
WIFL	0.06	0.04	0.10	0.04	0.10	0.06	0.07	0.03	0.08	0.03	0.09	0.06	0.06	0.04	0.06	0.05	0.03	0.02	0.04	0.02
WIWA	0.13	0.04	0.14	0.03	0.12	0.04	0.09	0.03	0.09	0.04	0.05	0.02	0.07	0.02	0.10	0.03	0.09	0.04	0.06	0.02
YRWA	0.02	0.02	0.11	0.04	0.01	0.01	0.01	0.01	0.01	0.01	0.12	0.12	0.01	0.01	0.14	0.06	0.02	0.02	0.04	0.01

Table S3. The mean relative abundance for each species at Developed sites over the course of this study. Relative abundance was assessed by conducting four 50 m fixed radius point counts at four to eight points in each study site. Each year of data represents the mean of all sites (N) that were measured that year. Some years are missing data because no sites were sampled that year.

	YEAR																			
	2001 N=7		2002 N=4		2003 N=7		2004		2005		2006		2007		2008 N=2		2009 N=4		2010 N=7	
Species	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
AMCR	.78	.16	.59	.34	.89	.16									.46	.38	.61	.29	.47	.09
AMGO	.04	.02	.00	.00	.15	.02									.37	.34	.15	.03	.12	.04
AMRO	1.12	.17	.81	.24	1.43	.22									1.56	.44	1.22	.07	.61	.10
ANHU	.03	.02	.00	.00	.07	.04									.03	.03	.03	.02	.11	.04
BARS	.08	.08	.00	.00	.07	.05									.00	.00	.00	.00	.00	.00
BCCH	.49	.10	.56	.21	.55	.14									.66	.46	.94	.17	.56	.15
BEWR	.18	.06	.47	.26	.28	.06									.29	.17	.11	.04	.28	.06
BHCO	.12	.04	.06	.03	.19	.06									.43	.39	.01	.01	.09	.03
BHGR	.07	.02	.19	.15	.10	.04									.25	.16	.10	.04	.08	.02
BRBL	.00	.00	.00	.00	.00	.00									.00	.00	.05	.05	.00	.00
BRCR	.04	.02	.25	.07	.18	.07									.14	.11	.01	.01	.15	.04
BTPI	.06	.04	.06	.06	.05	.03									.00	.00	.00	.00	.00	.00
BTYW	.02	.02	.09	.06	.03	.03									.10	.07	.03	.03	.01	.01
BUSH	.35	.14	.09	.06	.21	.10									.00	.00	.13	.07	.00	.00
CAVI	.00	.00	.00	.00	.01	.01									.00	.00	.01	.01	.00	.00
CBCH	.27	.04	.56	.28	.69	.18									.86	.27	.09	.06	.47	.11
CEDW	.18	.08	.06	.06	.31	.12									.27	.02	.10	.03	.25	.11
DEJU	.24	.09	.12	.05	.32	.12									.64	.24	.78	.07	.58	.13
DOWO	.00	.00	.19	.11	.01	.01									.00	.00	.01	.01	.00	.00
EUST	1.34	.47	.06	.06	.94	.33									.94	.94	.80	.43	.28	.10
EVGR	.03	.03	.00	.00	.02	.02									.00	.00	.09	.09	.01	.01
GCKI	.12	.06	.38	.07	.09	.03									.16	.12	.02	.01	.06	.02
HAFL	.00	.00	.00	.00	.00	.00									.00	.00	.00	.00	.01	.01
HAWO	.03	.01	.00	.00	.00	.00									.04	.04	.02	.02	.00	.00
HOFI	1.01	.34	.03	.03	1.34	.28									1.11	1.11	.08	.04	.23	.06

HOSP	.47	.20	.00	.00	.48	.22	.16	.16	.09	.07	.12	.08
HUVI	.00	.00	.06	.06	.03	.03	.02	.02	.03	.03	.01	.01
KILL	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
MODO	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
NOFL	.10	.06	.09	.03	.22	.06	.15	.11	.14	.04	.09	.03
OCWA	.02	.01	.00	.00	.00	.00	.02	.02	.00	.00	.00	.00
OSFL	.00	.00	.13	.13	.03	.01	.02	.02	.00	.00	.00	.00
PAWR	.10	.05	.34	.12	.15	.06	.41	.38	.12	.10	.05	.05
PISI	.25	.05	.41	.06	.25	.07	.25	.25	.18	.04	.09	.04
PSFL	.14	.08	.19	.12	.10	.09	.31	.31	.25	.20	.07	.04
PUFI	.01	.01	.03	.03	.07	.07	.10	.10	.24	.06	.04	.03
RBNU	.03	.01	.16	.09	.22	.06	.14	.11	.07	.01	.18	.04
RBSA	.00	.00	.00	.00	.01	.01	.02	.02	.01	.01	.03	.01
RCKI	.00	.00	.06	.06	.01	.01	.00	.00	.02	.02	.00	.00
RECR	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.10	.10
ROPI	.04	.04	.00	.00	.08	.06	.02	.02	.01	.01	.05	.02
RUHU	.02	.01	.16	.09	.04	.03	.04	.01	.01	.01	.06	.02
SAVS	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
SOSP	.50	.13	1.09	.34	.47	.08	.43	.10	.50	.19	.36	.06
SPTO	.55	.11	.56	.21	.75	.16	.82	.24	.62	.16	.45	.06
STJA	.18	.03	.18	.06	.43	.14	.12	.04	.32	.12	.25	.05
SWTH	.19	.09	.53	.28	.37	.22	.28	.22	.39	.21	.15	.08
TOSO	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00
TOWA	.03	.03	.00	.00	.01	.01	.00	.00	.00	.00	.00	.00
VASW	.00	.00	.00	.00	.01	.01	.06	.06	.00	.00	.02	.01
VGSW	.90	.29	.03	.03	.63	.19	1.52	1.23	.42	.19	.14	.05
WAVI	.00	.00	.00	.00	.00	.00	.02	.02	.00	.00	.02	.02
WCSP	.03	.03	.00	.00	.02	.02	.00	.00	.00	.00	.01	.01
WETS	.06	.03	.19	.08	.14	.07	.45	.30	.08	.03	.04	.01
WEWP	.00	.00	.03	.03	.03	.02	.00	.00	.00	.00	.01	.01
WIFL	.03	.03	.00	.00	.06	.04	.00	.00	.06	.04	.00	.00
WIWA	.08	.03	.34	.19	.09	.03	.11	.02	.18	.07	.07	.03
YRWA	.00	.00	.06	.06	.01	.01	.00	.00	.01	.01	.00	.00

Table S4. The mean relative abundance for each species at Reserve sites over the course of this study. Relative abundance was assessed by conducting four 50 m fixed radius point counts at four to eight points in each study site. Each year of data represents the mean of all sites (N) that were measured that year. There is no standard error for 2008 because only one site was sampled that year.

YEAR

	2001 N=5		2002 N=3		2003 N=5		2004 N=5		2005 N=4		2006 N=4		2007 N=4		2008 N=5		2009 N=1		2010 N=4	
Species	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
AMCR	.04	.04	.07	.03	.10	.06	.09	.07	.03	.03	.05	.03	.08	.06	.18	.09	.06		.15	.11
AMGO	.00	.00	.00	.00	.08	.05	.00	.00	.00	.00	.03	.03	.04	.04	.02	.01	.00		.00	.00
AMRO	.66	.14	.74	.03	.77	.22	.58	.07	.74	.19	.61	.20	.74	.23	.66	.18	.62		.29	.04
ANHU	.01	.01	.00	.00	.01	.01	.00	.00	.01	.01	.00	.00	.00	.00	.03	.02	.00		.02	.02
BARS	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00		.00	.00
BCCH	.03	.02	.48	.20	.14	.08	.08	.04	.00	.00	.15	.08	.12	.07	.13	.06	.25		.17	.10
BEWR	.02	.01	.13	.04	.21	.17	.05	.03	.10	.06	.05	.04	.09	.08	.05	.05	.12		.01	.01
BHCO	.01	.01	.04	.03	.01	.01	.00	.00	.00	.00	.02	.02	.00	.00	.02	.01	.00		.04	.03
BHGR	.14	.03	.32	.06	.15	.07	.18	.10	.23	.07	.24	.12	.15	.09	.25	.11	.12		.13	.07
BRBL	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00		.00	.00
BRCR	.25	.08	.48	.24	.53	.22	.40	.24	.38	.06	.40	.13	.50	.11	.38	.12	.62		.31	.08
BTPI	.01	.01	.00	.00	.05	.03	.03	.01	.04	.01	.00	.00	.00	.00	.00	.00	.06		.00	.00
BTYW	.04	.03	.21	.10	.05	.03	.11	.04	.23	.09	.11	.04	.06	.03	.02	.02	.12		.04	.01
BUSH	.01	.01	.00	.00	.07	.07	.00	.00	.05	.05	.00	.00	.00	.00	.00	.00	.00		.00	.00
CAVI	.00	.00	.01	.01	.01	.01	.00	.00	.05	.04	.00	.00	.00	.00	.00	.00	.00		.00	.00
CBCH	.68	.06	.60	.04	.82	.12	1.33	.25	1.31	.19	.96	.41	.65	.14	1.27	.28	1.25		.82	.12
CEDW	.09	.05	.01	.01	.08	.07	.02	.02	.06	.04	.03	.02	.03	.03	.07	.04	.06		.01	.01
DEJU	.15	.07	.21	.08	.36	.21	.25	.04	.21	.11	.11	.04	.23	.12	.42	.14	.31		.49	.23
DOWO	.00	.00	.05	.03	.03	.02	.00	.00	.00	.00	.00	.00	.00	.00	.01	.01	.00		.01	.01
EUST	.17	.17	.00	.00	.17	.17	.00	.00	.00	.00	.00	.00	.00	.00	.12	.12	.00		.02	.02
EVGR	.01	.01	.02	.02	.00	.00	.00	.00	.01	.01	.00	.00	.00	.00	.06	.06	.00		.09	.06
GCKI	.17	.04	.34	.17	.23	.06	.10	.06	.33	.27	.04	.03	.04	.01	.29	.14	.31		.21	.14
HAFL	.06	.06	.00	.00	.01	.01	.01	.01	.01	.01	.00	.00	.00	.00	.00	.00	.00		.00	.00
HAWO	.07	.03	.07	.01	.11	.03	.10	.03	.07	.03	.08	.01	.09	.04	.14	.06	.12		.05	.02
HOFI	.08	.08	.00	.00	.22	.22	.00	.00	.00	.00	.00	.00	.00	.00	.06	.06	.00		.09	.09

HOSP	.00	.00	.00	.00	.01	.01	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00		.00	.00
HUVI	.02	.02	.06	.03	.11	.08	.02	.01	.09	.06	.06	.03	.04	.01	.02	.02	.06		.02	.01
KILL	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00		.00	.00
MODO	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00		.00	.00
NOFL	.01	.01	.01	.01	.08	.05	.00	.00	.02	.02	.00	.00	.01	.01	.03	.03	.00		.05	.05
OCWA	.00	.00	.02	.02	.01	.01	.00	.00	.00	.00	.01	.01	.01	.01	.00	.00	.00		.00	.00
OSFL	.00	.00	.03	.03	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00		.00	.00
PAWR	.83	.17	1.53	.25	1.10	.31	.83	.14	1.41	.17	1.14	.17	1.37	.17	.88	.25	1.37		.77	.28
PISI	.22	.18	.24	.08	.12	.10	.03	.03	.06	.05	.00	.00	.28	.08	.23	.08	.12		.04	.04
PSFL	.42	.08	.80	.03	.46	.09	.55	.10	.86	.28	.57	.15	.60	.10	.56	.18	.62		.48	.11
PUFI	.02	.02	.16	.13	.07	.03	.03	.02	.18	.06	.14	.10	.18	.11	.10	.04	.18		.06	.03
RBNU	.07	.02	.20	.04	.28	.08	.23	.06	.21	.01	.08	.04	.09	.04	.22	.07	.43		.10	.01
RBSA	.01	.01	.03	.02	.02	.01	.01	.01	.03	.01	.02	.01	.02	.02	.02	.01	.06		.02	.02
RCKI	.01	.01	.00	.00	.04	.02	.00	.00	.04	.02	.00	.00	.01	.01	.04	.02	.00		.00	.00
RECR	.03	.03	.04	.04	.00	.00	.14	.09	.00	.00	.00	.00	.00	.00	.83	.40	.31		.05	.03
ROPI	.00	.00	.00	.00	.01	.01	.00	.00	.00	.00	.04	.02	.03	.02	.19	.05	.06		.09	.06
RUHU	.05	.03	.06	.03	.02	.01	.04	.02	.06	.03	.08	.03	.02	.02	.06	.04	.06		.05	.05
SAVS	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00		.00	.00
SOSP	.39	.15	.82	.20	.38	.11	.30	.10	.60	.30	.24	.15	.12	.08	.24	.09	.12		.30	.10
SPTO	.36	.11	.61	.09	.71	.25	.29	.09	.57	.13	.41	.15	.42	.13	.46	.12	1.18		.51	.07
STJA	.18	.09	.24	.14	.32	.13	.17	.07	.18	.08	.07	.02	.17	.12	.20	.14	.18		.23	.07
SWTH	.40	.16	.95	.20	.40	.15	.65	.20	.67	.24	.50	.22	.59	.21	.53	.22	1.00		.48	.17
TOSO	.00	.00	.00	.00	.01	.01	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00		.00	.00
TOWA	.01	.01	.05	.04	.01	.01	.06	.03	.05	.03	.02	.02	.03	.02	.04	.02	.12		.03	.03
VASW	.02	.02	.00	.00	.02	.01	.04	.04	.00	.00	.00	.00	.00	.00	.01	.01	.00		.02	.02
VGSW	.22	.22	.01	.01	.26	.26	.27	.14	.18	.12	.08	.06	.00	.00	.28	.23	.00		.13	.13
WAVI	.00	.00	.04	.02	.00	.00	.02	.02	.05	.05	.05	.05	.05	.04	.03	.03	.00		.02	.02
WCSP	.00	.00	.00	.00	.01	.01	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00		.00	.00
WETS	.08	.02	.20	.06	.20	.05	.18	.04	.30	.08	.16	.07	.24	.05	.20	.06	.25		.08	.03
WEWP	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00		.00	.00
WIFL	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.01	.01	.01	.01	.00	.00	.00		.00	.00
WIWA	.14	.04	.36	.08	.14	.07	.26	.13	.34	.12	.18	.06	.19	.07	.22	.11	.18		.19	.13
YRWA	.00	.00	.05	.04	.00	.00	.00	.00	.00	.00	.04	.04	.09	.09	.02	.01	.06		.00	.00

Table S5. Mean species richness for each year that data was collected at each site type. A "-" represents years when data was not collected.

Changing

	2001 N=9		2002 N=9		2003 N=9		2004 N=9		2005 N=9		2006 N=9		2007 N=9		2008 N=9		2009 N=6		2010 N=9	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Species Richness	30.89	1.64	34.78	1.75	34.33	1.58	34.56	2.35	36.00	1.69	30.33	1.76	32.78	1.41	33.33	1.64	26.17	1.97	29.00	1.42

Developed

	2001 N=7		2002 N=4		2003 N=7		2004 N=0		2005 N=0		2006 N=0		2007 N=0		2008 N=2		2009 N=4		2010 N=7	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Species Richness	27.71	1.34	23.00	2.12	33.57	0.92	-	-	-	-	-	-	-	-	32.50	3.50	29.50	2.02	28.86	1.44

Reserve

	2001 N=5		2002 N=3		2003 N=5		2004 N=5		2005 N=4		2006 N=4		2007 N=4		2008 N=5		2009 N=1		2010 N=4	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Species Richness	23.40	1.21	30.67	2.19	27.20	3.53	23.80	1.50	25.50	2.53	24.00	2.38	24.00	1.22	27.00	2.10	32.00	-	25.25	2.72

Table S6. Presence and Absence information for each species at each site type through the course of this study. A "-" represents a year that data was not collected for that site type.
Abbreviations: C= Changing sites , D= Developed sites , R= Reserve sites P= Present and A= Absent

	2001			2002			2003			2005			2005		
	C	D	R	C	D	R	C	D	R	C	D	R	C	D	R
AMCR	P	P	P	P	P	P	P	P	P	P	-	P	P		P
AMGO	P	P	A	P	A	A	P	P	P	P	-	A	P	-	A
AMRO	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
ANHU	P	P	P	P	A	A	P	P	P	P	-	A	P	-	P
BARS	P	P	A	P	A	A	P	P	A	P	-	A	P	-	A
BCCH	P	P	P	P	P	P	P	P	P	P	-	P	P	-	A
BEWR	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
BHCO	P	P	P	P	P	P	P	P	P	P	-	A	P	-	A
BHGR	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
BRBL	A	A	A	A	A	A	A	A	A	P	-	A	P	-	A
BRCR	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
BTPI	P	P	P	P	P	A	P	P	P	P	-	P	P	-	P
BTYW	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
BUSH	P	P	P	P	P	A	P	P	P	P	-	A	P	-	P
CAVI	P	A	A	P	A	P	P	P	P	P	-	A	P	-	P
CBCH	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
CEDW	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
DEJU	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
DOWO	P	A	A	P	P	P	P	P	P	P	-	A	A	-	A
EUST	P	P	P	P	P	A	P	P	P	P	-	A	P	-	A
EVGR	P	P	P	P	A	P	P	P	P	P	-	A	P	-	P
GCKI	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
HAFL	A	P	P	P	A	A	A	A	P	P	-	P	P	-	P
HAWO	P	P	P	P	A	P	P	P	P	P	-	P	P	-	P
HOFI	P	P	P	P	P	A	P	P	P	P	-	A	P	-	A
HOSP	A	P	A	A	A	A	P	P	P	P	-	A	P	-	A
HUVI	P	A	P	P	P	P	P	P	P	P	-	P	P	-	P
KILL	P	A	A	P	A	A	P	P	A	P	-	A	P	-	A

MODO	A	A	A	A	A	A	P	P	A	A	-	A	A	-	A
NOFL	P	P	P	P	P	P	P	P	P	P	-	A	P	-	P
OCWA	P	P	A	P	A	P	P	A	P	P	-	A	P	-	A
OSFL	A	P	A	P	P	P	P	P	A	P	-	A	A	-	A
PAWR	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
PISI	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
PSFL	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
PUFI	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
RBNU	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
RBSA	P	A	P	A	A	P	P	P	P	P	-	P	P	-	P
RCKI	P	A	P	P	P	A	A	P	P	A	-	A	P	-	P
RECR	P	A	P	P	A	P	P	P	P	P	-	P	P	-	A
ROPI	P	P	A	P	A	A	P	P	P	P	-	A	P	-	A
RUHU	P	P	P	P	P	P	P	P	P	P	-	P	P	-	A
SAVS	A	A	A	A	A	A	A	P	A	P	-	A	P	-	A
SOSP	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
SPTO	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
STJA	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
SWTH	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
TOSO	A	A	A	A	A	A	A	A	A	A	-	A	P	-	A
TOWA	A	P	P	P	A	P	P	P	P	P	-	P	P	-	P
VASW	P	A	P	A	A	A	P	P	P	P	-	P	P	-	A
VGSW	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
WAVI	P	A	A	P	A	P	A	P	A	P	-	P	P	-	P
WCSP	P	P	A	P	A	A	P	P	P	P	-	A	P	-	A
WETS	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
WEWP	A	A	A	P	P	A	P	P	A	P	-	A	P	-	A
WIFL	P	P	A	P	A	A	P	P	A	P	-	A	P	-	A
WIWA	P	P	P	P	P	P	P	P	P	P	-	P	P	-	P
YRWA	P	A	A	P	P	P	P	P	A	P	-	A	P	-	A

	2006			2007			2008			2009			2010		
	C	D	R	C	D	R	C	D	R	C	D	R	C	D	R
AMCR	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
AMGO	P	-	P	P	-	P	P	P	P	P	P	A	P	P	A
AMRO	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
ANHU	P	-	A	P	-	A	P	P	P	P	P	A	A	P	P
BARS	P	-	A	P	-	A	P	A	A	P	A	A	P	A	A
BCCH	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
BEWR	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
BHCO	P	-	P	P	-	A	P	P	P	P	P	A	P	P	P
BHGR	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
BRBL	P	-	A	A	-	A	A	A	A	A	P	A	A	A	A
BRCR	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
BTPI	A	-	A	A	-	A	A	A	A	A	A	P	A	A	A
BTYW	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
BUSH	P	-	A	P	-	A	P	A	A	P	P	A	P	P	A
CAVI	P	-	A	P	-	A	P	A	A	A	P	A	A	A	A
CBCH	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
CEDW	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
DEJU	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
DOWO	P	-	A	A	-	A	A	A	P	P	P	A	P	A	P
EUST	P	-	A	P	-	A	P	P	P	P	P	A	P	P	P
EVGR	P	-	A	P	-	A	P	A	P	P	P	A	P	P	P
GCKI	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
HAFL	A	-	A	A	-	A	P	A	A	A	A	A	P	P	A
HAWO	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
HOFI	P	-	A	P	-	A	P	P	P	P	P	A	P	P	P
HOSP	P	-	A	P	-	A	P	P	A	P	P	A	P	P	A
HUVI	P	-	P	P	-	P	P	P	P	A	P	A	P	P	P
KILL	P	-	A	P	-	A	P	A	A	P	A	A	A	A	A
MODO	A	-	A	A	-	A	A	A	A	A	A	A	A	A	A
NOFL	P	-	A	P	-	P	P	P	P	P	P	A	P	P	P
OCWA	P	-	P	P	-	P	P	P	A	A	A	A	A	A	A

OSFL	A	-	A	P	-	A	P	P	A	A	A	A	A	A	A
PAWR	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
PISI	P	-	A	P	-	P	P	P	P	P	P	P	P	P	P
PSFL	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
PUFI	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
RBNU	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
RBSA	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
RCKI	P	-	A	P	-	P	P	A	P	P	P	A	A	A	A
RECR	P	-	A	A	-	A	P	A	P	A	A	P	P	P	P
ROPI	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
RUHU	P	-	P	P	-	P	P	P	P	A	P	A	P	P	P
SAVS	P	-	A	P	-	A	P	A	A	P	A	A	P	A	A
SOSP	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
SPTO	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
STJA	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
SWTH	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
TOSO	A	-	A	A	-	A	P	A	A	A	A	A	A	A	A
TOWA	P	-	P	P	-	P	A	A	P	A	A	P	A	A	P
VASW	A	-	A	P	-	A	P	P	P	A	A	A	P	P	P
VGSW	P	-	P	P	-	A	P	P	P	P	P	A	P	P	P
WAVI	P	-	P	P	-	P	P	P	P	A	A	A	P	P	P
WCSP	P	-	A	P	-	A	P	A	A	P	A	A	P	P	A
WETS	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
WEWP	A	-	A	A	-	A	A	A	A	A	A	A	P	P	A
WIFL	P	-	P	P	-	P	P	A	A	P	A	A	P	P	A
WIWA	P	-	P	P	-	P	P	P	P	P	P	P	P	P	P
YRWA	P	-	P	P	-	P	P	A	P	P	P	P	P	A	A

Table S7. Summary of F statistics from ANOVAs and q-values from post hoc Tukey HSD tests. Analysis was run between site types over all ten years and between years at each site type; post hoc tests are reported for analysis between site types for species richness, guild relative abundance and species relative abundance.

SPECIES RICHNESS

Richness between types

ANOVA	Between groups df	within groups df	F value	p value
Richness	2	18	6.34	0.008
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	3.38	2.55	0.149
Changing-Reserve	6.61	6.67	5.02	0.007
Developed-Reserve	6.61	3.29	2.47	0.253

Richness between years

ANOVA	Between groups df	within groups df	F value	p value
Changing	9	77	2.74	0.008
Developed	5	25	5.01	0.003
Reserve	9	30	0.974	0.481

GUILD ABUNDANCE

Guilds between types

ANOVA	Between groups df	within groups df	F value	p value
Forest Abundance	2	18	9.11	0.002
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	0.337	0.71	0.849
Changing-Reserve	6.61	-2.5	5.27	0.005
Developed-Reserve	6.61	-2.84	5.98	0.002

ANOVA	Between groups df	within groups df	F value	p value
Synanthropic Abundance	2	18	7.25	0.005
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	-0.901	2.16	0.243
Changing-Reserve	6.61	1.48	3.56	0.057
Developed-Reserve	6.61	2.38	5.72	0.004

ANOVA	Between groups df	within groups df	F value	p value
Migrant Abundance	2	18	3.42	0.055
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	1.02	3.13	0.065
Changing-Reserve	6.61	0.876	2.69	0.174
Developed-Reserve	6.61	-0.143	0.44	0.954

ANOVA	Between groups df	within groups df	F value	p value
Resident Abundance	2	18	2.53	0.108
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	-1.06	2.29	0.210
Changing-Reserve	6.61	0.387	0.84	0.831
Developed-Reserve	6.61	1.44	3.12	0.124

ANOVA	Between groups df	within groups df	F value	p value
Insectivore Abundance	2	18	3.73	0.044
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	1.08	3.54	0.035
Changing-Reserve	6.61	0.427	1.40	0.599
Developed-Reserve	6.61	-0.65	2.13	0.345

ANOVA	Between groups df	within groups df	F value	p value
Herbivore Abundance	2	18	4.46	0.027

TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	0.257	0.74	0.839
Changing-Reserve	6.61	1.46	4.18	0.024
Developed-Reserve	6.61	1.21	3.46	0.083

ANOVA	Between groups df	within groups df	F value	p value
Generalist Abundance	2	18	6.28	0.009
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	-0.849	3.29	0.051
Changing-Reserve	6.61	0.470	1.82	0.429
Developed-Reserve	6.61	1.32	5.11	0.009

ANOVA	Between groups df	within groups df	F value	p value
Subsidy Consumer Abundance	2	18	6.29	0.009
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	-0.478	0.96	0.752
Changing-Reserve	6.61	2.07	4.16	0.025
Developed-Reserve	6.61	2.54	5.11	0.009

ANOVA	Between groups df	within groups df	F value	p value
Subsidy Consumer Abundance	2	18	1.74	0.204
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	0.950	2.40	0.182
Changing-Reserve	6.61	0.291	0.73	0.867
Developed-Reserve	6.61	-0.660	1.66	0.523

<u>Guilds between years</u>

Forest Abundance

ANOVA	Between groups df	within groups df	F value	p value

Changing	9	77	2.62	0.011
Developed	5	25	1.64	0.187
Reserve	9	30	1.76	0.119

Synanthropic Abundance

ANOVA	Between groups df	within groups df	F value	p value
Changing	9	77	1.54	0.148
Developed	5	25	2.92	0.033
Reserve	9	30	0.61	0.779

Migrant Abundance

ANOVA	Between groups df	within groups df	F value	p value
Changing	9	77	4.507	0.003
Developed	5	25	2.03	0.109
Reserve	9	30		

Resident Abundance

ANOVA	Between groups df	within groups df	F value	p value
Changing	9	77	4.51	<0.001
Developed	5	25	3.17	0.024
Reserve	9	30	1.41	0.227

Insectivore Abundance

ANOVA	Between groups df	within groups df	F value	p value
Changing	9	77	4.31	<0.001
Developed	5	25	5.64	0.001
Reserve	9	30	1.98	0.079

Herbivore Abundance

ANOVA	Between groups df	within groups df	F value	p value

Changing	9	77	4.05	<0.001
Developed	5	25	5.76	0.001
Reserve	9	30	1.118	0.381

Generalist Abundance

ANOVA	Between groups df	within groups df	F value	p value
Changing	9	77	2.39	0.019
Developed	5	25	1.58	0.202
Reserve	9	30	0.469	0.884

Subsidy Consumer Abundance

ANOVA	Between groups df	within groups df	F value	p value
Changing	9	77	4.65	<0.001
Developed	5	25	3.53	0.015
Reserve	9	30	0.726	0.681

Subsidy Avoider Abundance

ANOVA	Between groups df	within groups df	F value	p value
Changing	9	77	3.22	0.002
Developed	5	25	2.93	0.032
Reserve	9	30	1.728	0.126

SPECIES ABUNDANCE

Species between types

ANOVA	Between groups df	within groups df	F value	p value
AMCR	2	18	7.3	0.005
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	-0.131	1.26	0.607
Changing-Reserve	6.61	0.451	4.32	0.02

Developed-Reserve	6.61	0.581	5.57	0.004

ANOVA	Between groups df	within groups df	F value	p value
AMRO	2	18	2.72	0.093
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	-0.168	1.68	0.414
Changing-Reserve	6.61	0.181	1.81	0.433
Developed-Reserve	6.61	0.35	3.50	0.078

ANOVA	Between groups df	within groups df	F value	p value
BEWR	2	18	4.37	0.028
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	-0.086	2.33	0.185
Changing-Reserve	6.61	0.072	1.95	0.363
Developed-Reserve	6.61	0.158	4.28	0.024

ANOVA	Between groups df	within groups df	F value	p value
BHGR	2	18	1.94	0.173
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	0.044	1.19	0.638
Changing-Reserve	6.61	-0.065	1.76	0.447
Developed-Reserve	6.61	-0.109	4.04	0.149

ANOVA	Between groups df	within groups df	F value	p value
EUST	2	18	3.58	0.049
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	-0.416	2.36	0.191
Changing-Reserve	6.61	0.273	1.55	0.539
Developed-Reserve	6.61	0.69	3.91	0.046

ANOVA	Between groups df	within groups df	F value	p value

PAWR	2	18	11.8	0.001
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61		0.00	
Changing-Reserve	6.61		0.00	
Developed-Reserve	6.61		0.00	

ANOVA	Between groups df	within groups df	F value	p value
PSFL	2	18	5.58	0.013
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	0.137	1.88	0.338
Changing-Reserve	6.61	-0.23	3.16	0.100
Developed-Reserve	6.61	-0.367	5.04	0.010

ANOVA	Between groups df	within groups df	F value	p value
SOSP	2	18	0.705	0.507
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	0.076	0.91	0.767
Changing-Reserve	6.61	0.138	1.65	0.492
Developed-Reserve	6.61	0.063	0.76	0.872

ANOVA	Between groups df	within groups df	F value	p value
SPTO	2	18	1.24	0.312
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	0.124	1.15	0.655
Changing-Reserve	6.61	0.239	2.21	0.293
Developed-Reserve	6.61	0.115	1.07	0.76

ANOVA	Between groups df	within groups df	F value	p value
SWTH	2	18	1.52	0.245
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	0.181	1.72	0.397

Changing-Reserve	6.61	-0.077	0.73	0.868
Developed-Reserve	6.61	-0.258	2.46	0.259

ANOVA	Between groups df	within groups df	F value	p value
WIWA	2	18	2.21	0.138
TUKEY HSD	harmonic mean n	mean difference	q value	p value
Changing-Developed	6.61	0.02	0.57	0.897
Changing-Reserve	6.61	-0.084	2.41	0.228
Developed-Reserve	6.61	-0.104	2.99	0.137

Species between years

AMCR	Between groups df	within groups df	F value	p value
Changing	9	77	1.69	0.107
Developed	5	25	2.74	0.042
Reserve	9	30	0.543	0.831

AMRO	Between groups df	within groups df	F value	p value
Changing	9	77	2.32	0.023
Developed	5	25	6.26	0.001
Reserve	9	30	0.27	0.978

BEWR	Between groups df	within groups df	F value	p value
Changing	9	77	0.857	0.567
Developed	5	25	1.28	0.303
Reserve	9	30	0.896	0.541

BHGR	Between groups df	within groups df	F value	p value
Changing	9	77	0.494	0.874
Developed	5	25	1.047	0.412
Reserve	9	30	0.301	0.969

EUST	Between groups df	within groups df	F value	p value
Changing	9	77	0.779	0.637
Developed	5	25	1.79	0.151
Reserve	9	30	0.488	0.87

PAWR	Between groups df	within groups df	F value	p value
Changing	9	77	2.53	0.014
Developed	5	25	0.855	0.525
Reserve	9	30	1.17	0.349

PSFL	Between groups df	within groups df	F value	p value
Changing	9	77	2.43	0.017
Developed	5	25	0.551	0.736
Reserve	9	30	0.756	0.656

SOSP	Between groups df	within groups df	F value	p value
Changing	9	77	2.31	0.023
Developed	5	25	0.597	0.702
Reserve	9	30	1.16	0.355

SPTO	Between groups df	within groups df	F value	p value
Changing	9	77	0.682	0.723
Developed	9	25	2.63	0.048
Reserve	9	30	0.841	0.585

SWTH	Between groups df	within groups df	F value	p value
Changing	9	77	0.604	0.79
Developed	5	25	0.507	0.768
Reserve	9	30	0.449	0.897

WIWA	Between groups df	within groups df	F value	p value

Changing	9	77	0.963	0.477
Developed	5	25	0.757	0.589
Reserve	9	30	0.495	0.866

Figure S1. Diagram of the tools utilized in ARCGIS 9.3.3 (ESRI 2008) to extract the NDVI data at each of my 21 sites from the MODIS product. NDVI data is the first layer of the .HDF file so there is no need to extract it as a subdataset; however, the pixel reliability needed to be extracted because it is the fourth layer. I utilized the Set Null tool to remove any unreliable NDVI data, utilizing the new Pixel Reliability subdataset as the basis for removal; unreliable pixels were classified as “No Data” excluding them from Zonal Statistics calculations. With the reliable NDVI layer prepared, I created a one kilometer circle around the center of each site using Mean Center and Buffer tools. The final output, produced with the Zonal Statistics as Table tool, is a table for each date that NDVI was collected by the MODIS satellite in my study area.