Can patterns of habitat use by western Nearctic–Neotropical migratory landbirds in winter inform conservation priorities?

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ABSTRACT—I use point-count survey data collected from 171 locations across 11 vegetation conditions in western Mexico to illustrate common patterns of winter habitat use by 97 Nearctic–Neotropical migratory landbird species. A number of bird species are relatively restricted in their habitat use, with some (e.g., Northern Waterthrush [*Parkesia noveboracensis*], American Redstart [*Setophaga ruticilla*]) occurring only in relatively undisturbed habitats, and others (e.g., Say's Phoebe [*Sayornis saya*], Horned Lark [*Eremophila alpestris*]) occurring only in relatively disturbed lands associated with agriculture. A large number of bird species (e.g., Cassin's Vireo [*Vireo cassinii*], MacGillivray's Warbler [*Geothlypis tolmiei*]) use every one of the vegetation types considered, from low-elevation tropical deciduous forests to high-elevation conifer forests. Bird species showing patterns of restricted habitat use deserve conservation attention, but even the more broadly distributed species might become significantly less abundant in human-altered portions of habitats. Identifying the latter will require the inclusion of a wider spectrum of altered vegetation types/conditions than what I included here, or than what is typically considered in wildlife–habitat relationship programs. *Received 24 December 2018. Accepted 10 December 2019.*

¿Pueden los patrones de uso de hábitat invernal por aves terrestres migratorias Neártico–Neotrópico de occidente informar prioridades de conservación?

RESUMEN (Spanish)—Uso datos de conteos por puntos colectados en 171 localidades en 11 tipos de vegetación en el occidente de México para ilustrar patrones comunes de uso de hábitat invernal de 97 especies de aves terrestres migratorias Neártico–Neotrópico. Ciertas aves tienen uso de hábitat relativamente restringido, con algunas (e.g. los chipes *Parkesia noveboracensis* y *Setophaga ruticilla*) presentes solo en hábitats con poca perturbación, mientras que otros (e.g., el mosquero *Sayornis saya* y la alondra *Eremophila alpestris*) están presentes solamente en tierras con relativa perturbación asociadas con la agricultura. Una gran cantidad de especies de aves (e.g. el vireo *Vireo cassini* y el chipe *Geothlypis tolmiei*) usan cada uno de los tipos de hábitat considerados aquí, desde bosques tropicales deciduos de elevaciones bajas a bosques de coníferas de gran elevación. La conservación de las especies de aves que muestran patrones de uso de hábitat restringido merece atención, si bien las especies más ampliamente distribuidas podrían hacerse significativamente menos abundantes en porciones de hábitat alteradas por humanos. Identificar estas últimas requerirá la inclusión de un espectro más amplio de tipos/condiciones de vegetación alterada que aquéllas que incluyo aquí o de las que son típicamente consideradas en programas de relaciones entre fauna silvestre y su hábitat.

There is continued concern about population declines in Nearctic–Neotropical migrants (Faaborg et al. 2010, Rosenberg et al. 2016) but, unfortunately, we often lack the key information needed to tease apart alternative explanations for reported declines in any given species (Rappole and McDonald 1994, Sherry and Holmes 1996). The source of a population decline for any given species will necessarily be linked to a specific geographic location and habitat, so meaningful conservation action will require that we uncover those key locations and habitats. To do this, we need information on (1) the geographic distribution of species in all seasons, (2) patterns of habitat use within occupied areas, and (3) measures of reproductive or survival success in each season. Concerning geographic distributions, the longitudinal separation of migration pathways and wintering areas of most North American Neotrop-

ical migratory birds have been understood since the turn of the century (Cooke 1904), with western North American migrants wintering largely in western Mexico, as described in greater detail elsewhere (Hutto 1985, 2009; Kelly and Hutto 2005). Recent studies involving year-round tracking with miniature tracking devices has further refined our understanding of the locations and migratory pathways between breeding and winter ranges of select species (McKinnon and Love 2018). With the advent of the citizen-based information on bird locations through eBird (Sullivan et al. 2009, Wood et al. 2011, Sullivan et al. 2014, La Sorte et al. 2017), the relative abundance and geographic distribution of every bird species in every season is becoming better understood with every passing year. This geographical information has resulted in successful conservation action focused on securing the protection of specific locations associated with

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concentrated or restricted use (Sullivan et al. 2017).

Within the geographic areas occupied by migratory landbirds, we still know next to nothing about patterns of habitat use, however, especially in winter and during migration (Faaborg et al. 2010). This is unfortunate because knowledge of the patterns of habitat use can uncover a source of information (restricted habitat use) that can be used to anticipate problems that are likely to emerge from habitat loss and habitat alteration due to human land-use activity—the primary contributor to declining species populations, as is widely acknowledged (www.IUCNredlist.org). Insight into potential habitat condition problems can lead to focused conservation efforts, but only if formal bird surveys are conducted in every possible vegetation type, and only if those vegetation types include subsets that reflect human-altered conditions on top of the vegetation type itself.

Efforts to determine patterns of habitat use represent a proactive approach to conservation because human-caused changes in land cover types can be used to *anticipate* negative ecological effects on birds, should those land-use trends continue (Hutto and Young 2002, Hutto 2005). Indeed, one of the most important kinds of monitoring information that conservation biologists can provide is a solid description of the land conditions that each species requires for its occurrence and success. It is only through a keen understanding of patterns of habitat use that we can anticipate the likely effects of land-use changes on species. Human alteration of a vegetation type that constitutes the only type used by a species in winter would certainly suggest a problem for that species, should negative land-use practices within, or conversion of, that vegetation type continue unabated (Hutto 1989, 1992, 1995). Thus, an important step toward meaningful conservation efforts involves gaining an understanding of the particular land conditions each species uses in each season in combination with its geographic distribution during the same season. Understanding the land conditions a species uses to the exclusion of other conditions is a necessary precursor to the gathering of more detailed information about survival and/or reproductive success within the conditions occupied.

The earliest attempts (Hutto 1980, 1992) to expose patterns of habitat use by western Nearc-

tic–Neotropical migratory landbirds—species that winter almost exclusively in western Mexico—produced a basic understanding of the patterns of winter habitat use for that geographic group of Nearctic–Neotropical migrants. Nevertheless, patterns of habitat use described in those papers were, in many instances, based on detections on fewer than 5 points, and were based on sampling from a limited number of sites and a limited range of available vegetation categories. Hutto (1992:235) suggested that broad generalizations about patterns of habitat use would have to await the inclusion of data from "a more complete spectrum of disturbance levels and habitat types."

In an effort to provide patterns of habitat use across a more extensive range of vegetation conditions than previously considered, I compiled survey data on western North American migratory landbirds from 171 locations where I conducted formal bird surveys over an 8-year period in western Mexico. Although the complete dataset lacks samples from all geographic regions and all vegetation types used by migrants in western Mexico, my goal in presenting results from all of the surveys is to (1) stimulate research on questions related to patterns that emerge from consideration of a relatively broad range of vegetation conditions, (2) help us understand how habitat relationship patterns can help guide conservation priorities for Nearctic–Neotropical migratory bird species that winter in western Mexico, and (3) encourage the development of a more comprehensive effort to document habitat relationships of Nearctic–Neotropical migrants in winter by way of large sample sizes that are now possible to attain from coordinated citizen-science programs.

Methods

Study sites

I conducted formal point-count bird surveys during 8 winter seasons (mid-November through mid-March between 1975 and 1993) across 171 sites (Supplemental Table S1) that were distributed broadly throughout western Mexico south of Sonora and north of Chiapas (Figure 1). Although I placed each site into one of 27 vegetation type/condition categories when in the field, sample size considerations led to the consideration of a condensed 11 vegetation type/condition combina-
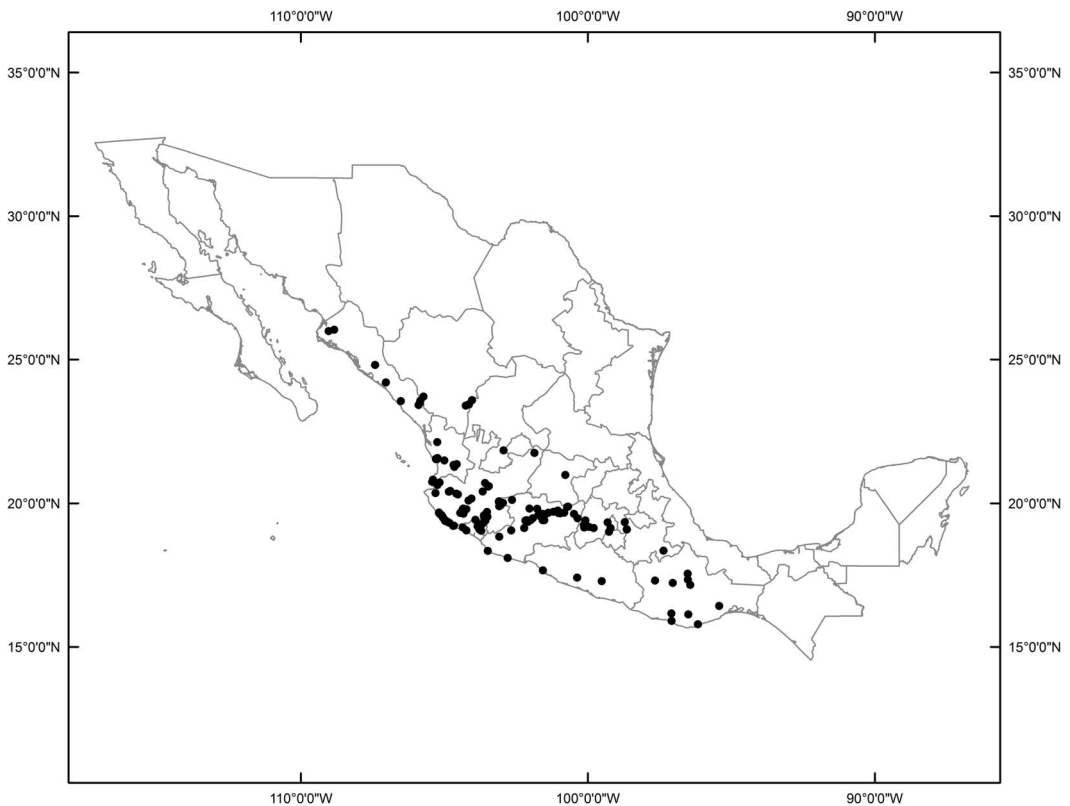
Figure 1. Overview of the distribution of 171 locations within western Mexico at which bird surveys were conducted.

tions, which is still more than double the number considered in previous work.

Mangroves/tropical evergreen forest—Mangroves line the coastal and lowland waterways of western Mexico and are dominated by *Rhizophora mangle*, *Avicennia germinans*, and *Conocarpus erectus*. Tropical evergreen forests occur in some coastal lowlands and are viewed (Pesman 1962) as a kind of intermediate forest type between rainforest and tropical deciduous forest. The most common genera are *Ficus*, *Bursera*, *Cecropia*, *Sabal*, *Acacia*, *Ceiba*, and *Lonchocarpus*.

Tropical deciduous forest—This vegetation type is common in the coastal lowlands of western Mexico, but is also one of the most threatened in Mexico (Lerdau et al. 1991). It is relatively tall (to 20 m), and is dense enough that it is difficult to walk through without the presence of a road or well-established trail. The most common genera include *Acacia*, *Bombax*, *Bursura*, *Caesalpinia*, *Ficus*, *Lysiloma*, and *Tabebuia*.

Low-elevation agriculture and second growth— This vegetation category includes lowland (lower than ~2,000 m) vegetation types that had been heavily disturbed by human agricultural and forest clearing practices (plowed field, fallow field, low-statured agricultural field, understory agriculture, tall agricultural plantations, field border strips, second growth following clearcutting). Survey locations included points situated within agricultural fields or plantations themselves, within vegetated border strips surrounding agricultural land, or within second growth following extensive deforestation. There were usually elements of relatively undisturbed vegetation types nearby, so the influence of adjacent native vegetation types on the associated bird communities was apparent.

Riparian—This category includes riverine environments at all elevations.

Village—This category includes the smaller rural villages and larger cities occupied by

humans, and the matrix of vegetation embedded within these settlement areas.

Thornforest—This short-statured vegetation type is generally only 2–3 m in height and is dominated by plants in the genera *Acacia*, *Mimosa*, *Caesalpinia*, and *Prosopis. Lemaireocereus* cacti are generally present as well.

High-elevation agriculture and second growth— This vegetation category includes the same kind of disturbed vegetation types as described above for low-elevation agriculture and second growth types, but the sites occur at higher elevations (above ~2,000 m) and they harbor bird communities that differ noticeably from those associated with the lower-elevation disturbed sites. As was true for the lower-elevation disturbed sites, avifaunal elements associated with nearby higher-elevation undisturbed oak, pine, or fir forests are apparent.

Oak woodlands—These woodlands are dominated by oaks (*Quercus*) and have a relatively open understory.

Pine-oak woodlands—These woodlands are composed of a mixture of oaks (*Quercus*), pines (*Pinus*), and madrones (*Arbutus*); they typically support an herbaceous understory, but are open and easily traversed.

Cloudforest—This is a more mesic version of the pine-oak category where epiphytes are abundant.

Pure pine and pine-fir forests—These are bands of pure pine (*Pinus*) or pine-fir (*Abies*) forests that occur at higher elevations.

Each vegetation type was sampled at a minimum of 5 different geographic locations (see the latitude, longitude, and elevation of each in Supplemental Table S1). During the earlier survey years, sites were often represented by a single point sample. Nonetheless, the total number of point counts conducted in each vegetation type exceeded 30—a number that Ralph et al. (1995) recommend as a minimum needed to generate a reasonable estimate of the occurrence rate of any species within a target vegetation type. Specifically, each vegetation category was sampled at no fewer than 50 survey points, and 7 of the 11 were sampled at more than 200 point locations (Supplemental Table S1).

Bird survey method

Even though a formal point-count methodology (Hutto et al. 1986) had not been developed until a decade following the earlier bird surveys associated with this work, my methods were consistent throughout the years represented here, and mirrored the consensus methods subsequently described in Ralph et al. (1995). Observers recorded numbers of every bird species detected within a fixed distance (100 m) from a single point in space within a 10-min period. Because major vegetation types hundreds of meters from a survey point can be quite different from the vegetation type near a survey point, I used a fixed distance to maximize the probability that every bird detected occurred in the vegetation type as categorized at the survey point. In general, multiple observers visited a given site, and each went in a different direction to collect survey data independently, stopping roughly every 200 m to conduct a count. Bird surveys during the nonbreeding season present a special challenge associated with a limited time period allotted for data collection from a survey point because birds frequently occur in mixed-species flocks. In western Mexico, these flocks can include more than 30 species and 100 individuals, and are among the largest and most diverse anywhere in the world (Hutto 1987, 1994). Thus, when a flock was detected within the fixed-radius survey area during the 10-min count, it often took additional time to identify and count the flock members that were deemed present during the 10-min count.

During most survey years, we did not record distances to bird detections, so it was not possible to use program DISTANCE (Buckland et al. 2001, Thomas et al. 2010) to calculate a model-based estimate of bird density within a given vegetation type. As described in detail elsewhere (Hutto and Young 2002, 2003; Johnson 2008; Hutto 2016, 2017), there are numerous reasons why the proportion of fixed-radius counts on which a species is detected is likely to be the most biologically meaningful index of abundance that can be gained from point-count data anyway, especially when attempting to uncover habitat associations. Therefore, I considered the presence of a species within 100 m to be the most reliable and meaningful information recorded, and I used the proportion of points during which a species was detected within a given vegetation type as an index of its abundance in that type.

Using the range maps available on the Birds of North America web site (www.birdsna.org), each species was classified as either a (1) Nearctic–

Neotropical migrant if its breeding range occurs primarily in the Nearctic north of the US–Mexico border, and its winter range occurs primarily in the west-Mexican Neotropics; (2) possible Nearctic–Neotropical migrant if it breeds largely in the Nearctic, and is a winter-only resident within the west-Mexican Neotropics where our surveys were located (see Fig. 1); and (3) resident if it is resident year-round within the west-Mexican Neotropics. I included the intermediate "possible migrant" category because I had no way of knowing whether a detected individual of one of these species was a migrant or a resident; I knew only that the more northern breeders migrated southward in winter, and that migrants from the north could have occurred within the areas that I surveyed in winter. Although field technicians and I detected a total of 295 species (Supplemental Table S2), I restricted my focus for this report to the 97 species that were classified as either migrants or possible migrants because of the interest in reported declines in that group of birds. I also restricted my analyses to those species that were detected on more than 5 different points. The raw data on occurrence of all 3 categories of landbird species across a broader range of 27 vegetation type/condition categories are made available, however, through the Dryad Digital Repository (datadryad.org).

Statistical analysis

For the purposes of representing the relative abundance of a given species across vegetation types, I calculated probabilities of occurrence from the pooled sample of all points conducted within each of the 11 vegetation types. In doing so, the overall probability of occurrence for any vegetation type was necessarily biased toward values represented by sites that had the greatest number of sample points, but the alternative (give each site belonging to the same vegetation type equal weight by calculating the percent occurrence within each site before calculating a single mean across sites) would have produced occurrence rates that were biased toward values derived from undersampled sites. Therefore, I chose to calculate probabilities of occurrence based on the pooled samples within each vegetation type. To determine the vegetation types with which a given species was likely to be nonrandomly associated, I used a chi-square contingency analysis to identify those positive associations that contributed significantly ($P < 0.05$) to any nonrandom distribution of occurrence rates across vegetation types.

Results

Field technicians and I conducted a total of 4,596 point counts across the 171 sites (Supplemental Table S1). Even though this represents a relatively large point-count database, a species still had to be detected on a minimum of ~100 points to achieve an acceptably small proportion of cells ($<20\%$) with expected values that were less than 5 for the statistical analyses, so the patterns I describe for the rarer species should be interpreted with care. Most Nearctic–Neotropical migratory landbird species were detected in more than one vegetation type, but some (e.g., Willow Flycatcher [*Empidonax traillii*], Hammond's Flycatcher [*Empidonax hammondii*], Yellow-headed Blackbird [*Xanthocephalus xanthocephalus*], Red-winged Blackbird [*Agelaius phoeniceus*], Northern Waterthrush [*Parkesia noveboracensis*]) were relatively restricted in their habitat use to a single vegetation category (Appendix Table 1). The narrow habitat distributions of these species are illustrated most clearly through histograms that represent the occurrence rate in each vegetation type as a proportion of the maximum rate of occurrence across all vegetation types (Fig. 2). Other Nearctic–Neotropical migrant species (e.g., Cassin's Vireo [*Vireo cassinii*], Black-and-white Warbler [*Mniotilta varia*], Orange-crowned Warbler [*Oreothlypis celata*], Nashville Warbler [*Oreothlypis ruficapilla*], MacGillivray's Warbler [*Geothlypis tolmiei*], Wilson's Warbler [*Cardellina pusilla*]) were common across a broad range of vegetation types (Appendix Table 1), and the evenness of their abundances across multiple types is readily apparent in histograms of their proportionate occurrence rates relative to their highest recorded occurrence rates (Fig. 3).

Many species used a range of vegetation types that encompassed a broad elevation zone as well. Indeed, species like the Elegant Trogon (*Trogon elegans*), Dusky-capped Flycatcher (*Myiarchus tuberculifer*), Cassin's Vireo, Black-and-white Warbler, Nashville Warbler, MacGillivray's Warbler, Black-throated Gray Warbler (*Setophaga*
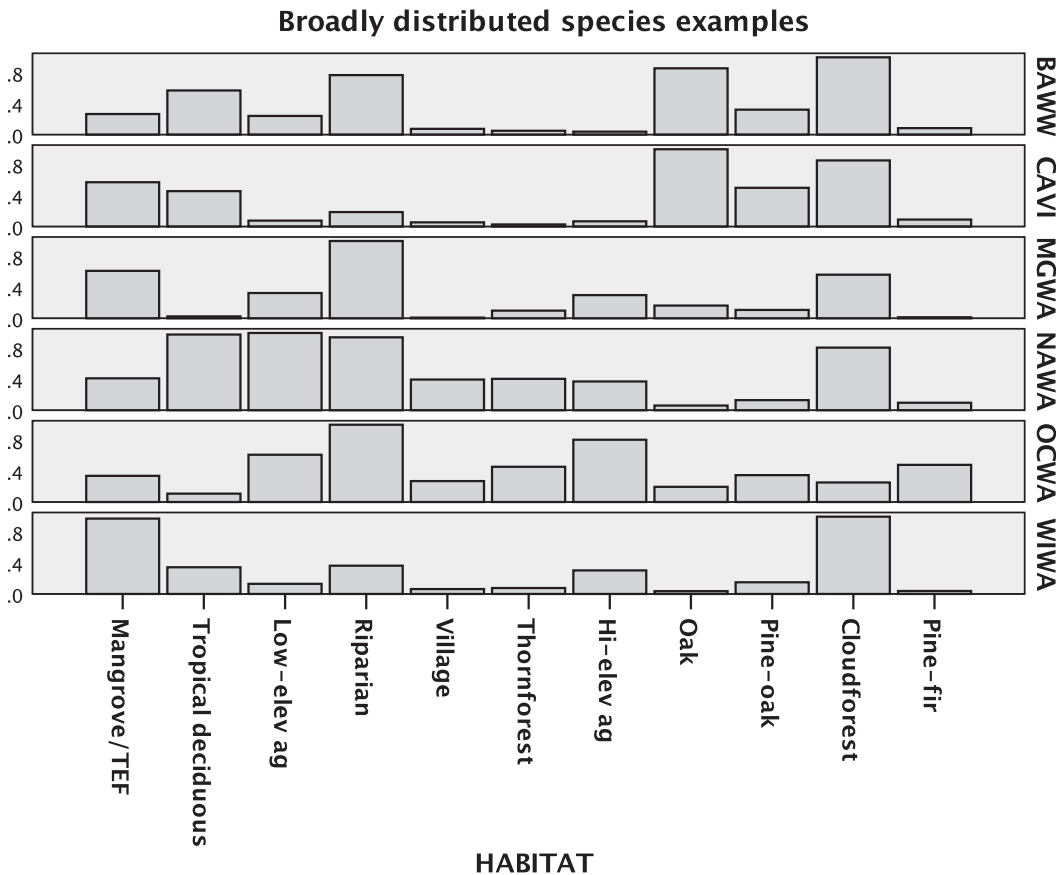
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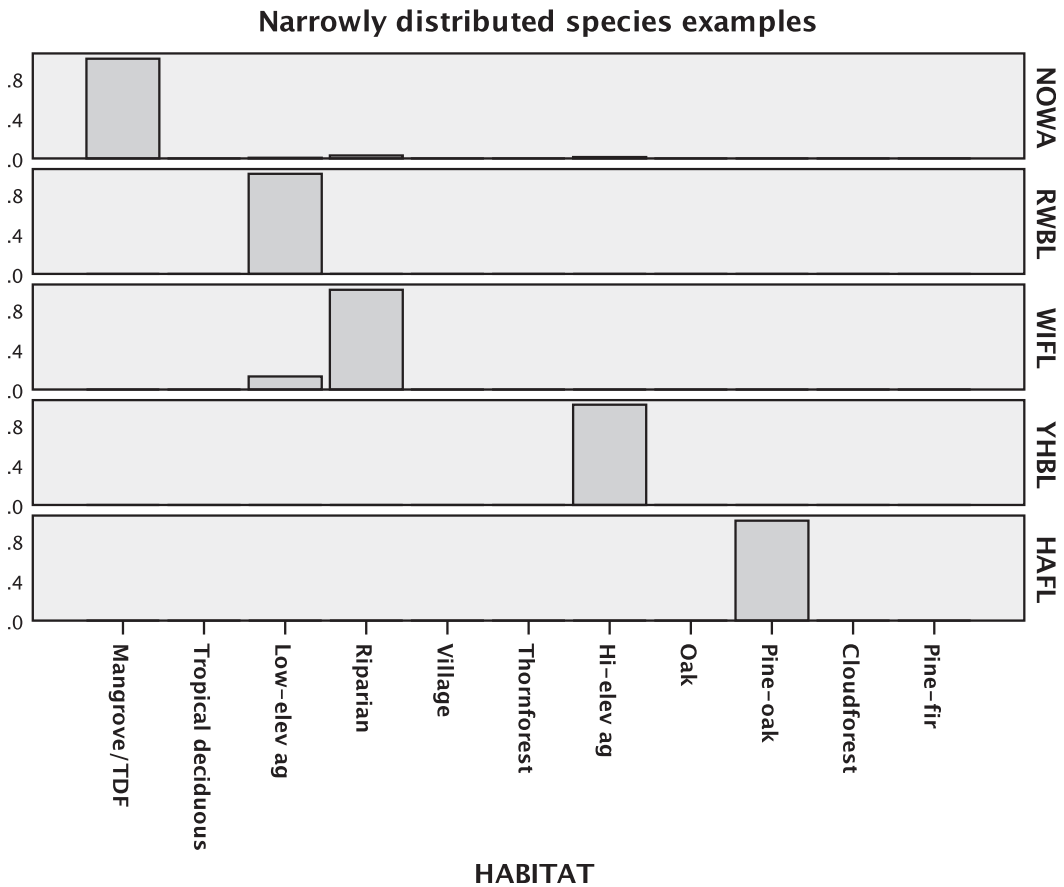
Figure 2. Several examples of Nearctic–Neotropical migratory species that were relatively restricted in their distributions to 1 of 11 vegetation type/condition categories. Species (ordered from occurrence in low- to high-elevation vegetation types) are Northern Waterthrush (*Parkesia noveboracensis*; NOWA), Red-winged Blackbird (*Agelaius phoeniceus*; RWBL), Willow Flycatcher (*Empidonax traillii*; WIFL), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*; YHBL), and Hammond's Flycatcher (*Empidonax hammondii*; HAFL). Bar heights represent occurrence rate as a proportion of the maximum rate of occurrence across all vegetation types.

nigrescens), and Wilson's Warbler were each detected significantly more frequently than expected due to chance in both a low-elevation and a high-elevation vegetation type (Appendix Table 1). Six of the 97 migrant species used every one of the 11 vegetation types, spanning a range of elevations from sea level to more than 3,000 m, and 60 of the 97 species used more than half the vegetation types considered.

A final pattern contrast worth noting is that many species (e.g., Say's Phoebe [*Sayornis saya*], Horned Lark [*Eremophila alpestris*], Yellow-headed Blackbird, Red-winged Blackbird, American Pipit [*Anthus rubescens*], Savannah Sparrow

[*Passerculus sandwichensis*], Grasshopper Sparrow [*Ammodramus savannarum*], Brown-headed Cowbird [*Molothrus ater*]) occurred exclusively in heavily disturbed vegetation types, while many others (e.g., Elegant Trogon, Gray Flycatcher [*Empidonax wrightii*], Northern Waterthrush, Virginia's Warbler [*Oreothlypis virginiae*], Grace's Warbler [*Setophaga graciae*], Hermit Warbler [*Setophaga occidentalis*], Summer Tanager [*Piranga rubra*]) were relatively restricted to undisturbed vegetation types (Appendix Table 1). More than half of all species sampled achieved their greatest abundance in one of the three categories of heavily disturbed vegetation types (Appendix

Broadly distributed species examples

Figure 3. Several examples of Nearctic–Neotropical migrant species that were broadly distributed across all 11 vegetation type/condition categories. Species (listed alphabetically) are Black-and-white Warbler (*Mniotilta varia*; BAWW), Cassin's Vireo (*Vireo cassinii*; CAVI), MacGillivray's Warbler (*Geothlypis tolmiei*; MGWA), Nashville Warbler (*Oreothlypis ruficapilla*; NAWA), Orange-crowned Warbler (*Oreothlypis celata*; OCWA), Wilson's Warbler (*Cardellina pusilla*; WIWA). Bar heights represent occurrence rate as a proportion of the maximum rate of occurrence across all vegetation types.

Table 1), which include various kinds of agricultural land and surrounding hedgerows, second-growth, and the matrix of vegetation embedded within human settlements (villages).

Discussion

It is clear that some Nearctic–Neotropical landbird species use a very narrow range of vegetation types in winter, while others use an extremely wide breadth of vegetation types. It is also clear that some species are relatively restricted to disturbed vegetation type/conditions, and that other species are relatively restricted to undisturbed vegetation type/conditions. I could have used fewer vegetation categories to increase statistical rigor, but doing so would not have exposed some finer resolution patterns that informal birdwatching experience suggests are not sampling artifacts. Thus, I used number of vegetation types deemed sufficient to cover both disturbed and undisturbed types, as well as types that covered a broad elevation range. The emergent patterns described here should serve to encourage future citizen participation in winter habitat–focused bird survey programs designed to compile observational data from across an even more comprehensive range of vegetation types and land conditions, which could, in turn, yield the sample sizes needed to test the veracity of these patterns.

Species restricted to relatively undisturbed vegetation types

The bird species that were restricted to relatively undisturbed vegetation types include those that are most likely to suffer from the effects of human activity in the respective vegetation types with which they are associated, so those species would serve well as indicator species for the same vegetation types, as Villaseñor-Gómez (2008) illustrated for wintering birds in Sonora, Mexico. It is imperative that we understand the extent to which different vegetation types are threatened by human activity, and that we use key indicator species to monitor the health of those vegetation types as well. Examples of species that were narrowly restricted in their winter habitat distribution include the Northern Waterthrush and American Redstart (*Setophaga ruticilla*), which were relatively restricted to the mangrove/tropical evergreen forest vegetation category. Although the point-count sample size was limited to 20 in mangroves, waterthrushes were present on 75% of those counts and on only 9.1% of the 33 counts conducted in tropical evergreen forest (resulting in the combined 34% occurrence rate reported for the combined category in Appendix Table 1). Indeed, a high relative abundance of the Northern Waterthrush in mangrove environments elsewhere in winter has been well documented (Lefebvre et al. 1994, Lefebvre and Poulin 1996, Warkentin and Hernandez 1996, Whitaker and Eaton 2014). Except for a roosting preference for mangroves (Smith et al. 2008), there is no published information on the relative occurrence or abundance of the Northern Waterthrush in mangroves (vs. other vegetation types) in winter, however. The fact that the waterthrush occurs rarely (on <10% of the survey points) outside mangroves in this study begs the question of whether the non-mangrove vegetation types serve as suitable winter habitat as well, or whether such areas act as ecological traps (sensu Robertson and Hutto 2006).

Although the American Redstart was most commonly detected in mangroves in this study (on 80% of 20 counts), it also occurred on more than half the counts in tropical evergreen forest openings (55% of 33 counts). If the sexual segregation in habitat use by eastern populations of this species in Jamaica (Marra et al. 1993,

Parrish and Sherry 1994) is any indication, it may be that one sex winters predominantly in mangroves and the other in the scrub edges associated with tropical evergreen forest; the lack of information on sex of each bird detected prevents me from answering definitively, but my informal recollection is that I detected mostly males in the mangroves in western Mexico as well. Habitat segregation by sex in the American Redstart (Ornat and Greenberg 1990) could be a product of dominance by males in mangroves (Marra et al. 1998, Marra 2000, Marra and Holmes 2001) or could reflect different habitat preferences by the 2 sexes independent of male dominance. Either way, we need to focus conservation attention on the undisturbed vegetation type because second growth is in no danger of disappearing (although overwinter survival may be less therein). Whatever our approach, it is important to recognize that habitat distribution information takes us a step beyond simple geographic distribution information and can be used to focus conservation attention more narrowly toward mangroves and one or two additional vegetation conditions that may actually be preferred by one sex or age group.

Undisturbed tropical deciduous forest is perhaps the most endangered vegetation type in western Mexico (Lerdau et al. 1991) and, although no migratory landbird species was restricted in its occurrence to that single vegetation type (Appendix Table 1), 15 species were significantly more abundant in that vegetation type than one would expect on the basis of their average occurrence rate across all vegetation types (chi-square contingency tests, $P < 0.05$). Once again, depending on estimates of overwinter survivorship across all of the habitats occupied, it is impossible to know whether their use of other vegetation types reflects the presence of satisfactory alternatives to tropical deciduous forest or not.

Although there is some overlap in use of tropical deciduous forest and the short-statured thornforest vegetation types, there were 18 species that used thornforest more than expected due to chance (Appendix Table 1), and 11 of those (e.g., Mourning Dove [*Zenaida macroura*], Ruby-throated Hummingbird [*Archilochus colubris*], Black-chinned Hummingbird [*Archilochus alexandri*], Ash-throated Flycatcher [*Myiarchus cinerascens*], Western Kingbird, Least Flycatcher [*Empidonax minimus*], Gray Flycatcher, Northern

Mockingbird [*Mimus polyglottos*], Green-tailed Towhee [*Pipilo chlorurus*], Clay-colored Sparrow [*Spizella pallida*], Virginia's Warbler) were nowhere more abundant than in thornforest environments.

Species occupying a broad range of vegetation types

The extreme breadth of vegetation types occupied by many species is as striking as the restricted distributions illustrated by others. No fewer than a dozen small insectivorous species occupy a range of vegetation types that span the complete elevation gradient from sea level to more than 3,000 m (Appendix Table 1). It is noteworthy that many of these species are relatively specialized in habitat use during the breeding season. Indeed, the pattern of a broad range in habitat use in winter compared with summer for western Neotropical migrants has been discussed previously (Hutto 1995, 2009), and may be a result of (or may cause) the relatively small geographic winter (vs. breeding) ranges occupied by western Nearctic–Neotropical migrants. Extremely broad habitat distributions beg the question of whether different subspecies (e.g., Catry et al. 2016, Valdez-Juárez et al. 2018), ages (e.g., Latta and Faaborg 2002), or sexes (e.g., Marra 2000) might occupy different ends of such a broad vegetation spectrum. Does an identifiable subset of any one of these species occur in, say, the low-elevation, tropical deciduous forest, and another subset occur in the high-elevation pine-oak-fir forest? Or, is it true that any individual of one those species is able to occupy any of the combined physiological and vegetation structural conditions that occurs across the entire vegetation spectrum? There are theoretical reasons why we might expect different ages and sexes to use different habitat types (Hutto 1998), and empirical evidence for sex- and age-based differences in use of adjacent vegetation type alternatives by both western (Valdez-Juárez et al. 2018) and eastern (Holmes et al. 1986, Petit et al. 1995, Marra 2000, Latta and Faaborg 2002) North American migrants. Nevertheless, we have no evidence that an expanded geographic form of sex- or age-biased habitat use might serve to explain the extreme breadth of habitat use across a wide elevation range in western migrants. These

fundamental questions related to patterns of habitat use are as yet unanswered.

For now, it would seem that those species with relatively broad distributions across vegetation types in winter are more likely to benefit from conservation attention directed toward places, times of year, and vegetation types that lie outside rather than inside those associated with the winter period. Indeed, the discovery of high densities of many Nearctic–Neotropical migrants in disturbed habitats on their wintering grounds in western Mexico (Hutto 1980) helped stimulate a broadening of conservation attention from what was, at that point in time, a narrow focus on the effects of tropical deforestation, to one that began to include deforestation and fragmentation effects on the northern breeding grounds (Hutto 1988) and on en-route stopover sites (Hutto 2000). The caveat here, and it is an important one, is that even when a species uses a broad range of habitat types, subsets of those vegetation types might still be of conservation concern for that species because patterns of habitat use might vary significantly between sexes and among age groups or subspecies. Thus, a given subgroup of that species might be using a much more limited range of habitats. Alternatively, all individuals of such species could be remarkably flexible in their habitat use in winter, and an individual in any age/sex category may be able to winter successfully in anything from a patch of coastal second-growth to a high-elevation fir forest.

Species restricted to heavily disturbed vegetation types

The apparent restriction of some species to heavily disturbed vegetation types is remarkable, and leaves one wondering which vegetation types these species used prior to the widespread distribution of agricultural croplands. Although not apparent from presence/absence data alone, there were times and places where harvested agricultural fields were filled with thousands of flocking Yellow-headed Blackbirds (Supplemental Material Video 1) and Brown-headed Cowbirds. The huge numbers of Lark Sparrows (*Chondestes grammacus*), Vesper Sparrows (*Pooecetes gramineus*), and Savannah Sparrows along dirt roads bordering agricultural fields were also impressive (Supplemental Material Video 2), and reflect an

immense concentration of individuals in both low- and high-elevation agricultural fields that is not apparent from simple probabilities of occurrence. The conservation potential of agricultural lands for migratory landbirds is high (Villaseñor and Hutto 1995), and for species that are relatively abundant in, or even restricted to, disturbed sites in winter, tropical deforestation would not seem to be the driving force behind any reported declines that emerge from breeding season monitoring programs (Hutto 1988). This is because disturbed conditions are only getting more and more extensive due to the ever-increasing human population. However, disturbed lands may also function as ecological traps (Robertson and Hutto 2006), in which case they attract birds to a greater extent than other habitats do, even though they promote relatively poor survivorship for any of a number of reasons, including predators, pesticides, machinery, buildings, or other sources of mortality associated with human-altered environments. Indeed, the very origin of the ecological trap concept emerged from study of bird use of fields in an agricultural setting (Gates and Gysel 1978). I have no information on the overwinter survival or condition experienced by birds that were detected in this study, however, so the true conservation potential of heavily disturbed lands remains to be seen.

Conclusion

Any of the restricted habitat distribution patterns described here could be used to identify a vegetation type that deserves priority conservation attention. Unfortunately, the use of information from just 11 vegetation/condition categories does not provide nearly enough resolution to provide a sharp focus on the vegetation type/conditions we need to protect. To provide habitat-use information that can trigger meaningful conservation action, we must begin to include a larger number of disturbed vegetation categories in habitat-relationships studies. If I had, for example, conducted enough sampling in each of the various kinds of agricultural operations that exist on the land (e.g., pasturelands, plowed fields, fallow fields, corn fields, sorghum fields, understory crops, plantations, or border strips that usually surround each of these), I would not have had to combine the

different kinds of agricultural land types into a catch-all "low-elevation agriculture" category, and I would have been able to expose any differences in occurrence rates among each and to determine the relative importance of each as potential winter habitat. Thus, as forward thinking as the recent attempt is to provide habitat associations in association with eBird data (Fink et al. 2018), the spatial resolution of bird locations and the classification resolution of vegetation categories are probably still too crude to translate into meaningful conservation efforts. The relative abundance of birds in relation to the *combination* of vegetation type and condition is what exposes the effect of human activity on a given bird species. It is what we do as humans to the land and landscape that most affects other species, and those activities need to be included in our land classification schemes if we are to be successful at exposing unforeseen negative consequences of our land-use activities.

Concerning the resolution of vegetation information needed to inform management, all physically distinct land cover types ought to be included in the list of vegetation types available to birds. Unfortunately, even though the full range of vegetation types or existing land cover types can be easily discerned through remote sensing techniques, this level of resolution is generally missing from formal descriptions of habitat types used by land management agencies. For example, burned forest is not even included as a separate wildlife habitat category in the California Wildlife Habitat Relationships manual (Mayer and Laudenslayer 1988), which makes it impossible for land managers to know how important it is to maintain that particular vegetation type/condition. Even more problematic is the absence of information about human land-use practices associated with the different vegetation types. Land use that is incompatible with suitable occupancy by birds will probably affect demographic rates first, but will ultimately affect occurrence rates, which can be acquired most rapidly if we conduct surveys across a broad spectrum of not only vegetation types but also of land conditions within and surrounding those types.

Meaningful habitat relationships will also require large sample sizes across a necessarily large number of vegetation type/condition categories, which is impossible for any one scientist to attain,

but which is quite possible for a large number of citizen scientists to attain. The value of citizen-based programs like eBird (Sullivan et al. 2009, 2014) could, therefore, be enhanced immeasurably by the addition of the precise locations of bird detections and information on land condition associated with every bird observation. Fortunately, vegetation and land condition data layers are becoming more widely available through nongovernmental organizations and through state and federal land management agencies, so capturing the existing vegetation type and condition at the time and location where a bird is detected is well within reach. If observers were asked to record bird detections as they walk, the GPS location could then be automatically downloaded with each bird detection entry. To make bird locations even more precise, observers could even enter offset GPS locations of bird detections on a smartphone map screen as they record survey data. Precise bird locations do not have to be made available to the public, so sensitive bird location information could remain protected.

In conclusion, the most powerful conservation value of citizen-based bird survey data can emerge only if we match vegetation information with precise bird locations (to ensure that the birds detected are well within the vegetation type of interest), and only from the inclusion of land condition (e.g., level or occurrence of tree harvesting, cattle grazing, wind farming, mining, the kind of adjacent agricultural operation) as an integral part of well-defined vegetation type/condition categories. Coupling bird observations with satellite-based information on land type and condition surrounding those points, and then calculating the rates of change in areal coverage of those vegetation types and conditions would catapult conservation efforts ahead of where we are today by substantial amounts. Thus, although it is possible that "extensive research across the wintering range of Nearctic–Neotropical migrants will require a major investment of funds for research" (Faaborg et al. 2010:406), even without a major research investment, there may be a relatively inexpensive path toward being able to predict or anticipate conservation problems. All we need is information on habitat use to accompany citizen-based bird survey data that are now flowing in during all seasons from throughout North America. Precise bird locations coupled with high-resolution vegetation/land-use maps may be a powerful yet inexpensive avenue toward an understanding of basic bird–habitat relationships in all seasons.

Acknowledgments

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Appendix Table 1. The percentage of point counts on which each of 97 Nearctic–Neotropical migratory bird species was detected in each of 11 vegetation type/condition categories. A species was deemed to be a complete migrant (Status M) if all individuals leave Mexico to breed, or a partial migrant (Status P) if some individuals are known to breed in Mexico. Numbers in bold indicate percentages that were greater than expected due to chance (chi-square, $P < 0.05$). Point-count sample sizes for each vegetation type are provided with the footnoted descriptions.

Species	Status	n	M/TEF	TDF	L-AG	RIP	VILL	THOR	H-AG	OAK	POF	CLDF	PFF
Band-tailed Pigeon, *Patagioenas fasciata*	P	105	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**9.89**	**8.85**	0.00	0.59
Mourning Dove, *Zenaida macroura*	P	174	0.00	0.80	3.21	0.99	1.06	**13.36**	**6.57**	2.20	3.36	0.00	0.00
Rivoli's Hummingbird, *Eugenes fulgens*	P	72	0.00	0.00	0.00	0.00	0.00	0.00	0.79	0.00	3.54	1.41	**15.38**
Blue-throated Hummingbird, *Lampornis clemenciae*	P	16	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	**1.12**	0.00	**1.78**
Ruby-throated Hummingbird, *Archilochus colubris*	M	14	0.00	0.20	0.20	0.99	0.00	**1.08**	0.00	0.00	0.56	0.00	0.00
Black-chinned Hummingbird, *Archilochus alexandri*	M	23	0.00	0.20	**1.31**	0.49	0.35	**1.81**	0.00	0.00	0.19	0.00	0.00
Broad-tailed Hummingbird, *Selasphorus platycercus*	P	28	0.00	0.00	0.00	1.48	0.00	0.00	0.11	**2.20**	**1.49**	0.00	**3.55**
Rufous Hummingbird, *Selasphorus rufus*	M	92	0.00	0.00	0.00	0.00	0.00	0.00	**7.25**	0.00	1.86	**11.27**	0.00
Calliope Hummingbird, *Selasphorus calliope*	M	8	0.00	0.00	0.00	0.49	0.00	0.00	0.00	0.00	**0.65**	0.00	0.00
Turkey Vulture, *Cathartes aura*	P	26	**3.77**	0.20	0.40	1.48	0.00	0.36	0.11	**2.20**	0.84	0.00	**1.78**
Elegant Trogon, *Trogon elegans*	P	10	**3.77**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.75**	0.00	0.00
Red-naped Sapsucker, *Sphyrapicus nuchalis*	M	44	0.00	0.00	0.00	0.49	0.00	0.00	0.23	0.00	**3.36**	0.00	**2.96**
American Kestrel, *Falco sparverius*	M	305	0.00	0.00	**10.94**	5.42	0.71	7.22	**13.93**	4.40	3.08	0.00	1.78
Rose-throated Becard, *Pachyramphus aglaiae*	P	30	**9.43**	**2.01**	0.40	0.49	0.00	0.00	0.00	0.00	0.65	**4.23**	0.00
Dusky-capped Flycatcher, *Myiarchus tuberculifer*	P	528	5.66	**57.34**	6.43	10.84	0.00	7.58	4.42	1.10	6.99	**23.94**	0.59
Ash-throated Flycatcher, *Myiarchus cinerascens*	M	624	1.89	**39.24**	**23.90**	11.33	1.41	**50.54**	1.36	2.20	0.84	0.00	0.00
Brown-crested Flycatcher, *Myiarchus tyrannulus*	P	172	0.00	**27.57**	1.91	1.48	0.00	3.61	0.34	0.00	0.00	0.00	0.00
Tropical Kingbird, *Tyrannus melancholicus*	P	416	13.21	0.20	**26.31**	**39.41**	**13.43**	9.75	0.11	0.00	0.00	0.00	0.00
Cassin's Kingbird, *Tyrannus vociferans*	P	276	0.00	0.20	0.20	0.00	1.41	**9.39**	**25.59**	0.00	1.58	0.00	0.00
Thick-billed Kingbird, *Tyrannus crassirostris*	P	270	0.00	**10.66**	**16.57**	**14.78**	0.71	4.33	0.79	0.00	0.09	0.00	0.00
Western Kingbird, *Tyrannus verticalis*	M	22	0.00	0.00	0.70	0.99	0.00	**4.69**	0.00	0.00	0.00	0.00	0.00
Greater Pewee, *Contopus pertinax*	P	243	0.00	0.00	0.00	0.49	0.00	0.00	5.10	**17.58**	**15.75**	5.63	4.73
Willow Flycatcher, *Empidonax traillii*	M	18	0.00	0.00	0.70	**5.42**	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Least Flycatcher, *Empidonax minimus*	M	13	0.00	0.40	**0.60**	0.49	0.00	**1.44**	0.00	0.00	0.00	0.00	0.00
Hammond's Flycatcher, *Empidonax hammondii*	M	10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.93**	0.00	0.00
Gray Flycatcher, *Empidonax wrightii*	M	7	0.00	0.20	0.10	**0.99**	0.00	**1.08**	0.00	0.00	0.00	0.00	0.00
Cordilleran Flycatcher, *Empidonax occidentalis*	P	288	**24.53**	**28.77**	5.92	**14.29**	0.35	2.53	2.04	1.10	1.30	4.23	0.00
Buff-breasted Flycatcher, *Empidonax fulvifrons*	P	49	0.00	0.00	0.00	0.00	0.00	0.00	**3.74**	**6.59**	0.93	0.00	0.00
Say's Phoebe, *Sayornis saya*	P	6	0.00	0.00	0.00	0.00	0.00	0.00	**0.68**	0.00	0.00	0.00	0.00

Appendix Table 1. Continued.

Species	Status	*n*	M/TEF	TDF	L-AG	RIP	VILL	THOR	H-AG	OAK	POF	CLDF	PFF
								Vegetation type[a]					
Vermilion Flycatcher, *Pyrocephalus rubinus*	P	336	7.55	0.20	7.83	6.90	3.89	3.25	**24.35**	2.20	0.19	0.00	0.00
Loggerhead Shrike, *Lanius ludovicianus*	P	111	0.00	0.20	1.61	0.49	0.00	**7.58**	**8.15**	0.00	0.00	0.00	0.00
Bell's Vireo, *Vireo bellii*	M	105	3.77	0.20	**6.63**	**10.34**	1.06	2.89	0.45	0.00	0.00	0.00	0.00
Cassin's Vireo, *Vireo cassinii*	M	153	7.55	**6.04**	1.00	2.46	0.71	0.36	0.91	**13.19**	**6.62**	**11.27**	1.18
Warbling Vireo, *Vireo gilvus*	M	365	13.21	**14.29**	8.73	11.82	1.77	7.94	7.36	4.40	7.08	5.63	0.00
Horned Lark, *Eremophila alpestris*	P	25	0.00	0.00	0.00	0.00	0.00	0.00	**2.83**	0.00	0.00	0.00	0.00
House Wren, *Troglodytes aedon*	M	463	0.00	0.20	3.92	3.94	2.83	9.39	**24.58**	2.20	11.09	4.23	**23.67**
Blue-gray Gnatcatcher, *Polioptila caerulea*	P	1609	35.85	**58.55**	**63.45**	**65.52**	23.32	**61.73**	26.39	8.79	4.01	18.31	0.00
Ruby-crowned Kinglet, *Regulus calendula*	M	746	0.00	0.00	0.10	2.96	3.53	1.81	12.23	**51.65**	**45.29**	18.31	**41.42**
Eastern Bluebird, *Sialia sialis*	P	79	0.00	0.00	0.00	0.00	0.00	0.00	**5.55**	2.20	**2.42**	0.00	1.18
Western Bluebird, *Sialia mexicana*	P	146	0.00	0.00	0.00	0.00	1.06	0.00	0.45	**26.37**	**8.20**	0.00	**15.98**
Swainson's Thrush, *Catharus ustulatus*	M	15	0.00	**1.61**	0.00	0.49	0.00	0.00	0.00	**2.20**	0.09	1.41	**1.18**
Hermit Thrush, *Catharus guttatus*	M	75	0.00	0.00	0.00	0.00	0.35	0.00	0.23	0.00	**5.31**	**8.45**	**5.33**
American Robin, *Turdus migratorius*	P	436	0.00	0.00	0.10	0.49	2.12	0.00	14.27	**20.88**	**21.99**	1.41	**27.22**
Northern Mockingbird, *Mimus polyglottos*	P	131	1.89	0.20	**6.12**	3.45	2.12	**13.72**	1.81	0.00	0.09	0.00	0.00
Cedar Waxwing, *Bombycilla cedrorum*	M	17	0.00	0.00	0.20	0.00	0.00	0.00	0.45	0.00	**0.84**	0.00	1.18
Phainopepla, *Phainopepla nitens*	P	40	0.00	0.00	0.00	0.00	0.00	0.00	7.69	**3.08**	0.00	0.00	0.00
Olive Warbler, *Peucedramus taeniatus*	P	246	0.00	0.00	0.00	0.00	0.00	0.00	0.11	1.10	**14.35**	5.63	**50.89**
American Pipit, *Anthus rubescens*	M	6	0.00	0.00	0.00	0.00	0.00	0.00	**0.68**	0.00	0.00	0.00	0.00
Pine Siskin, *Spinus pinus*	P	75	0.00	0.00	0.00	0.00	1.06	0.00	1.36	**16.48**	2.61	0.00	**10.06**
Green-tailed Towhee, *Pipilo chlorurus*	M	23	0.00	0.20	0.40	0.49	0.00	**4.33**	0.57	0.00	0.00	0.00	0.00
Chipping Sparrow, *Spizella passerina*	P	366	0.00	0.00	0.40	1.48	0.35	**12.64**	**30.46**	**15.38**	3.54	0.00	1.18
Clay-colored Sparrow, *Spizella pallida*	M	13	0.00	0.20	0.10	0.00	0.00	**1.44**	**0.68**	0.00	0.09	0.00	0.00
Brewer's Sparrow, *Spizella breweri*	M	7	0.00	0.00	0.10	0.00	0.00	**0.72**	0.34	**1.10**	0.00	0.00	0.00
Black-chinned Sparrow, *Spizella atrogularis*	P	6	0.00	0.00	0.10	0.49	0.00	0.36	0.34	0.00	0.00	0.00	0.00
Vesper Sparrow, *Pooecetes gramineus*	M	37	0.00	0.00	0.10	0.00	0.00	1.81	**3.40**	0.00	0.09	0.00	0.00
Lark Sparrow, *Chondestes grammacus*	M	200	0.00	0.00	**9.64**	2.46	0.35	7.22	**8.72**	0.00	0.09	0.00	0.00
Savannah Sparrow, *Passerculus sandwichensis*	M	66	0.00	0.00	0.10	0.00	0.00	0.00	**7.25**	0.00	0.09	0.00	0.00
Grasshopper Sparrow, *Ammodramus savannarum*	M	95	0.00	0.00	2.11	0.00	0.00	3.25	**7.36**	0.00	0.00	0.00	0.00
Song Sparrow, *Melospiza melodia*	P	21	0.00	0.00	0.10	0.99	0.00	0.00	**2.04**	0.00	0.00	0.00	0.00
Lincoln's Sparrow, *Melospiza lincolnii*	M	295	0.00	0.20	5.62	6.90	1.06	4.33	**22.88**	0.00	0.56	0.00	0.59
Yellow-breasted Chat, *Icteria virens*	M	100	**9.43**	0.40	**5.42**	**15.27**	0.00	0.00	0.91	0.00	0.00	0.00	0.00
Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*	M	6	0.00	0.00	0.00	0.00	0.00	0.00	**0.68**	0.00	0.00	0.00	0.00
Eastern Meadowlark, *Sturnella magna*	P	111	0.00	0.00	2.41	0.00	0.00	1.08	**9.29**	0.00	0.00	0.00	1.18
Orchard Oriole, *Icterus spurius*	M	64	0.00	0.00	**3.41**	**5.42**	**5.65**	0.00	0.23	0.00	0.09	0.00	0.00
Hooded Oriole, *Icterus cucullatus*	M	47	0.00	1.41	**1.91**	0.99	1.77	0.72	0.57	1.10	0.56	0.00	0.00

Appendix Table 1. Continued.

Species	Status	*n*	M/TEF	TDF	L-AG	RIP	VILL	THOR	H-AG	OAK	POF	CLDF	PFF
								Vegetation type[a]					
Bullock's Oriole, *Icterus bullockii*	M	222	0.00	0.20	1.61	1.48	**11.31**	1.81	**11.66**	2.20	5.31	4.23	0.00
Scott's Oriole, *Icterus parisorum*	P	41	0.00	0.00	0.00	0.00	0.00	2.17	1.02	0.00	**2.33**	0.00	0.59
Red-winged Blackbird, *Agelaius phoeniceus*	P	6	0.00	0.00	**0.60**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brown-headed Cowbird, *Molothrus ater*	M	55	0.00	0.00	1.41	0.99	**4.95**	0.00	**2.83**	0.00	0.00	0.00	0.00
Northern Waterthrush, *Parkesia noveboracensis*	M	26	**33.96**	0.00	0.20	0.99	0.00	0.00	0.45	0.00	0.00	0.00	0.00
Black-and-white Warbler, *Mniotilta varia*	M	180	3.77	**8.05**	3.41	**10.84**	1.06	0.72	0.57	**12.09**	4.57	**14.08**	1.18
Orange-crowned Warbler, *Oreothlypis celata*	M	508	7.55	2.41	**13.55**	**22.17**	6.01	10.11	**17.89**	4.40	7.74	5.63	10.65
Lucy's Warbler, *Oreothlypis luciae*	M	123	0.00	0.40	**9.64**	**5.42**	1.41	1.44	0.57	0.00	0.09	0.00	0.00
Nashville Warbler, *Oreothlypis ruficapilla*	M	902	15.09	**35.81**	**36.55**	**34.48**	14.49	14.80	13.59	2.20	4.75	**29.58**	3.55
Virginia's Warbler, *Oreothlypis virginiae*	M	27	0.00	0.40	0.00	0.00	0.00	**7.58**	0.00	1.10	0.28	0.00	0.00
MacGillivray's Warbler, *Geothlypis tolmiei*	M	417	24.53	1.01	**13.05**	**39.90**	0.35	3.97	**12.00**	6.59	4.38	**22.54**	0.59
Common Yellowthroat, *Geothlypis trichas*	P	77	**30.19**	0.20	1.71	**11.33**	0.35	0.00	2.15	0.00	0.00	0.00	0.00
American Redstart, *Setophaga ruticilla*	M	59	**64.15**	0.80	0.60	**5.91**	0.35	0.00	0.23	0.00	0.00	0.00	0.00
Yellow Warbler, *Setophaga petechia*	M	411	**33.96**	1.21	**21.49**	**41.87**	**25.80**	0.36	1.59	0.00	0.00	0.00	0.00
Yellow-rumped Warbler, *Setophaga coronata*	M	1224	0.00	1.61	20.18	22.66	19.08	22.74	**50.17**	31.87	**30.38**	2.82	30.77
Grace's Warbler, *Setophaga graciae*	P	194	0.00	0.00	0.00	0.00	0.00	0.00	0.34	0.00	**15.84**	21.13	3.55
Black-throated Gray Warbler, *Setophaga nigrescens*	M	276	**15.09**	7.85	3.31	7.88	0.71	2.17	5.66	**19.78**	9.69	0.00	0.00
Townsend's Warbler, *Setophaga townsendi*	M	229	0.00	0.00	0.00	0.99	2.47	0.36	4.08	4.40	**13.70**	25.35	8.28
Hermit Warbler, *Setophaga occidentalis*	M	133	0.00	0.00	0.00	0.00	0.00	0.00	0.45	1.10	9.13	14.08	11.83
Black-throated Green Warbler, *Setophaga virens*	M	10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.47**	7.04	0.00
Wilson's Warbler, *Cardellina pusilla*	M	605	**60.38**	21.33	8.03	**22.66**	3.89	4.69	**18.91**	2.20	9.32	**61.97**	2.37
Red-faced Warbler, *Cardellina rubrifrons*	M	87	0.00	0.00	0.00	0.00	0.00	0.00	1.13	0.00	**6.34**	9.86	1.18
Painted Redstart, *Myioborus pictus*	P	210	0.00	0.00	0.00	1.97	0.00	0.00	0.68	**13.19**	17.15	2.82	1.18
Hepatic Tanager, *Piranga flava*	P	213	0.00	0.00	0.00	0.99	0.71	0.00	4.53	**15.38**	12.95	12.68	4.14
Summer Tanager, *Piranga rubra*	M	66	0.00	**9.05**	1.31	1.48	0.35	0.72	0.23	0.00	0.00	0.00	0.00
Western Tanager, *Piranga ludoviciana*	M	213	0.00	5.23	**7.83**	**11.33**	5.30	1.81	2.94	0.00	2.05	**25.35**	0.00
Black-headed Grosbeak, *Pheucticus melanocephalus*	P	162	0.00	0.60	1.31	0.99	1.41	2.53	**8.15**	6.59	4.38	5.63	2.37
Blue Grosbeak, *Passerina caerulea*	P	202	1.89	0.20	**9.64**	4.43	2.47	1.08	**9.63**	0.00	0.00	0.00	0.00
Lazuli Bunting, *Passerina amoena*	M	12	0.00	0.00	0.50	0.00	0.00	0.36	0.34	0.00	0.28	0.00	0.00
Indigo Bunting, *Passerina cyanea*	M	11	0.00	0.00	**0.80**	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00
Varied Bunting, *Passerina versicolor*	P	185	5.66	**9.46**	7.33	7.39	0.35	5.05	2.72	1.10	0.65	0.00	0.00
Painted Bunting, *Passerina ciris*	M	151	5.66	1.21	**11.04**	**11.82**	0.35	1.08	0.45	0.00	0.00	0.00	0.00

[a] Vegetation types and sample sizes are as follows: M/TEF = Mangrove/Tropical evergreen forest (*n* = 53), TDF = Tropical deciduous forest (*n* = 497), L-AG = Low-elevation agriculture (*n* = 996), RIP = Riparian (*n* = 203), VILL = Village (*n* = 283), THOR = Thornforest (*n* = 277), H-AG = High-elevation agriculture (*n* = 883), OAK = Oak woodland (*n* = 91), POF = Pine-oak forest (*n* = 1,073), CLDF = Cloudforest (*n* = 71), PFF = Pine-for forest (*n* = 169).