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Integrating season-specific needs of migratory and resident birds in conservation planning

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ABSTRACT

Efforts to conserve migratory species have been challenged by a poor understanding of their temporally-dynamic distributions over large geographies. Consequently, most conservation plans have focused on the stationary periods despite the importance of migratory periods for overall population dynamics and fitness. Strategies that identify stopover sites for migratory species during migration and examine the potential for those sites to protect resident species may offer an efficient approach to enhance the conservation of both groups. Using crowdsourced data (i.e., eBird), we identified priority stopover sites (PSSs) that target protection of 30% of the seasonal average abundance of over 400 Nearctic-Neotropical migratory bird species in the Americas during spring and fall migratory periods. We then calculated the proportion of global abundance of 158 resident bird species including 27 imperiled species, that were captured on those sites, analysed the extent to which sites were protected, and forecast changes in land use. Around half or less of PSSs were shared between spring (52-54%) and fall (23-32%), indicating that planning efforts should be season-specific. Less than 10% of PSSs were protected, while 30-46% were in human modified landscapes. Even though our spatial algorithms targeted 30% of the abundance of migratory birds, comparable proportions of resident bird populations were also captured (36% of resident and 42% of imperiled bird populations in fall, 22% and 31% respectively in spring). Our findings demonstrate that protecting stopover sites for migrating species can provide co-benefits for resident and imperiled species.

1. Introduction

Evidence-based conservation has become standard among many natural resource management agencies and non-governmental organizations, in part due to growing availability of data and advances in computational methods, such as spatial optimization algorithms (Bower et al., 2018). Despite this progress, limited fiscal and human resources can still promote unfounded generalizations about the value of conservation efforts across taxa, space, and time. Critically-important sites for one species may contribute little to the conservation of other species, just as a site may be important during one stage in the annual cycle (e.g., breeding season) but not in others (e.g., migratory periods). Thus, no matter how sophisticated the methodology or how impressive a dataset, the effectiveness of systematic conservation planning depends upon the identification of appropriate targets (e.g., species), feature data, and spatiotemporal scales (Moilanen et al., 2009).

Defining the appropriate targets and spatiotemporal scales to identify the most important locations to protect for migratory species is challenging because they move across broad geographies (Wilcove, 2008; Wilcove and Wikelski, 2008). This is relevant to all migratory species but particularly challenging for long-distance migrants with diffuse migratory routes, such as many bird species (Wilcove and Wikelski, 2008). While habitat loss due to land use change is occurring throughout species' life cycle, most conservation efforts for migratory birds have focused on stationary periods used for breeding and overwintering with less emphasis on the protection of stopover sites during migratory periods (Faaborg et al., 2010). However, migratory birds often associate with different habitats across life stages (Zuckerberg

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Received 6 July 2020; Received in revised form 7 October 2020; Accepted 9 October 2020 Available online 6 November 2020 0006-3207/© 2020 Elsevier Ltd. All rights reserved. et al., 2016) or even during migration (Bayly et al., 2018), which makes it difficult to generalize needs during breeding periods to the full annual cycle. Because loss of critical stopover habitats due to land use change is thought to contribute to declines in migratory populations (Iwamura et al., 2013), conservation plans need to identify, prioritize, and protect locations used by migrants along their migration routes/corridors in order to secure the future of migratory species (Mehlman et al., 2005; Runge et al., 2014).

The protection of stopover habitats may also benefit resident species using the same location (Bayly et al., 2018; Faaborg et al., 2010; Johnson et al., 2011). For example, protecting habitats at mid elevations (700–1700 m) in the Neotropics could be beneficial for migratory and resident birds because the species richness and abundance of birds with different life histories peak within those regions (Gómez et al., 2015). Identifying and protecting locations used by both migrants and residents may increase the effectiveness of conservation planning by allowing for the allocation of limited resources to sites that maximize the protection of the taxonomic diversity of the broader avian community. Yet, we lack quantitative evidence on the extent of benefit resident species might receive due to the protection of stopover sites for migrants.

Traditionally, critical stopover sites for migratory birds have been identified using data from local surveys (Augusto and Rodrigues, 2007; Bayly et al., 2016; Mehlman et al., 2005), weather-surveillance radar images (Bonter et al., 2009), or telemetry tracking records (Xu et al., 2020). These approaches provide valuable information about the importance of local sites to a species during migration. However, prioritizing sites for the entire population requires a range-wide scale covering their full migratory journeys and needs to consider the proportion of a species/population using a given habitat among all sites (Bowlin et al., 2010; Runge et al., 2014; Wilcove and Wikelski, 2008) because species or individuals might use different routes and habitats during migration (Dokter et al., 2018; Gómez et al., 2013; La Sorte et al., 2014a). The development of large-scale crowd-sourced environmental monitoring projects provides opportunities to estimate the dynamic distribution and abundance of migratory species throughout their migration journeys (Fink et al., 2020a). Here we use data products from eBird, one of the world's largest biodiversity databases to which volunteers contribute bird observations and checklists from around the world. Data products from eBird Status and Trends provide weekly abundance estimates throughout the year for over 400 migratory and 150 resident bird species that breed in North America (Fink et al., 2020b). eBird data have been used previously to identify priority sites for migratory songbirds (Schuster et al., 2019) and shorebirds (Johnston et al., 2020) over the full annual cycle.

In this study, we first identified the stopover sites most heavily used during spring and fall migration by birds. Next, we quantified the potential benefit for resident species by examining the abundance of resident and imperiled resident bird species occurring on the priority stopover sites. We then conducted a conservation gap analysis to examine the coverage of existing protected areas and assessed threats from current and future changes in land use.

2. Materials and methods

A summary figure of the workflow of this study is shown in Fig. 1 and the species list can be found in the supplementary material.

2.1. Species abundance data and study area

Species distribution and abundance data were accessed from the eBird database through the R package, ebirdst 0.2.0 (Auer et al., 2020). Among all species in the database (n = 610), we assigned species as migratory or resident based on the seasonality information: migratory species have separated seasons (i.e., breeding, non-breeding, prebreeding migration, and post-breeding migration) while resident species have a year-round distribution (supplementary species list). Next, we extracted the distribution and abundance data for migratory species during pre- (n = 432) and post-breeding migration (n = 424) seasons which are defined in the eBird database for each species. Overall, there were 433 migratory species belonging to 55 families. The top five families with the highest number of species were Parulidae (10.9%), Anatidae (8.8%), Scolopacidae (7.6%), Passerellidae (7.4%), and Tyrannidae (7.4%). In the database, most migratory species such as migratory landbirds (both Neotropical and temperate migrants), shorebirds, and waterfowl breed in North America and move south during the nonbreeding period. eBird data were available for one austral migrant, Fork-tailed Flycatcher (Tyrannus savana), which moves northward after breeding in the tropics but we removed this species from the analysis because its strategy differed from all others. For resident species, we performed separate analyses for all resident birds (n = 158) and imperiled birds (n = 27). Among 47 families, the top five families with the highest number of resident bird species were Corvidae (9.5%), Picidae (9.5%), Paridae (7.0), Phasianidae (6.3%), and Passerellidae (5.7%). Species were defined as imperiled when they were either



Fig. 1. Workflow of data processes and analyses. Numbers within parentheses are the number of bird species analysed. For migratory birds, 432 species had data available for identifying priority stopover sites for spring migration while 424 species had data available for fall migration. Among 158 resident bird species, 27 were listed as imperiled species by international (IUCN Red list) or national/federal (Canada, US, and Mexico) entities. We used *prioritizr* (Hanson et al., 2020) to select areas containing at least 30% of the population of each species.

included in international (IUCN Red list: Vulnerable, Endangered, and Critically Endangered) or national/federal (Canada: Species at Risk; US: Fish and Wildlife Endangered Species; Mexico: Secretaria de Medio Ambiente y Recursos Naturales species list) lists of species of conservation concern. In some cases, subspecies were recognized as imperiled but in these cases we only included an imperiled status at the species level if all subspecies in the same country were recognized as imperiled. For example, Western Screech-Owl (*Megascops kennicottii*) was treated as imperiled in this study because all subspecies in Canada (*M. kennicottii kennicottii and M. kennicottii macfarlanei*) were listed under the Species at Risk Act. In contrast, Northern Cardinal (*Cardinalis cardinalis*) was not considered as imperiled here because only one subspecies on Tres Marías Islands (*C. cardinalis mariae*) was listed on the Secretaria de Medio Ambiente y Recursos Naturales species list among 15 subspecies in Mexico.

The data downloaded from the eBird database represent the weekly and seasonal (for migrants) or year-round (for residents) relative abundance at a 2.96 \times 2.96 km spatial resolution for each species (Fink et al., 2020b), which were estimated by observed bird counts and adaptive spatiotemporal exploratory models (AdaSTEMs) (Fink et al., 2020a, 2010). The observation data used to run the AdaSTEMs was a subset of eBird data (i.e., checklists) recorded by eBird users across the Americas. Only complete checklists (i.e., observers recorded the number of individuals of all bird species detected and identified during the survey) collected with the "stationary", "traveling", or "area search" protocols from 1 January 2014 to 15 January 2019 were used. In addition, checklists must contain information related to survey effort such as search duration, distance travelled, protocol, and number of observers in order to model and control potential bias caused by different sampling effort and thus detection rates (Fink et al., 2020a). The relative abundance of each species was estimated with zero-inflated boosted regression trees that included variables accounting for local environment and observer effort (details see Fink et al. (2020a)). This approach results in an abundance per pixel that is the expected number of birds of a given species by a typical eBird participant on a search starting from the center of the pixel from 7:00 to 8:00 AM while traveling 1 km. The seasonal and year-round relative abundance were based on the average of weekly data over a specific season (timing and duration vary with species) and the whole year (52 weeks), respectively. We defined stopover site in this study using a broad sense, which includes various types of habitats that birds use along their journey between breeding and wintering grounds for different purposes, such as refuelling, roosting, or avoiding adverse conditions (Bayly et al., 2018; Mehlman et al., 2005). Nevertheless, seasonal average abundance estimates will be higher at sites where birds stay longer (temporally crowded) or those that are used by a large number of individuals (spatially crowded), which are comparable to the bottleneck, stopover, and staging sites described in Bayly et al. (2018). The average duration for the fall migration season was 102 days with a standard deviation of 32 days, and 76 days for the spring migration with a standard deviation of 24 days. Detailed descriptions about the seasons can be found on the eBird website (https://ebird.org/science/status-and-trends/faq).

The full range of both migratory periods were used to identify priority stopover sites for all migratory species, and thus may have included Central and South America for long-distance migrants. However, our analyses with resident species only focused on the three North American countries (i.e., Canada, US, and Mexico) because the eBird data available for resident species was most comprehensive in these countries, especially Canada and the US (Fink et al., 2020b).

2.2. Spatial prioritization

We used the minimum set objective function concept in systematic conservation planning to identify a set of priority sites that collectively achieve a defined conservation goal while minimizing the overall cost (Ball et al., 2009). While the cost could be the price required to acquire a

piece of land or conduct specific conservation actions on selected sites, we set a flat cost layer for all sites because our goal was to identify important stopover sites during different migration seasons. Therefore, our objective was to identify sites that together would include at least 30% of the relative abundance of each species (similar to Schuster et al., 2019) within each migration season while minimizing the number of sites selected. The data were considered to be a relative estimate of species abundance because eBird data only provide an index and not true abundance; nonetheless, hereafter we refer to this index as 'abundance'. It is important to note that although a 30% objective was set for optimization, the 30% value was set for seasonal average (instead of daily or weekly) abundance distributions and there was no information of the connectivity among sites. Using a similar approach with migratory shorebirds, Johnston et al. (2020) previously identified a high concordance between stopover areas prioritized using quarterly, monthly, and weekly data. However, their quarterly prioritizations, which most closely approximate the time windows used in our analysis, were most likely to produce temporal bottlenecks (i.e., the time of the year when the species have the minimum proportion of the population covered within selected sites) and leave populations vulnerable at particular times. Therefore, the PSSs identified in this study may not be enough to secure 30% of the abundance of all species continuously through the migratory period, but would identify those sites with the highest abundance and thus likely to be priorities for conservation planning. We performed the optimization using the Integer linear programming (ILP) algorithm in the R package, prioritizr (Hanson et al., 2020; Schuster et al., 2020) with the Gurobi optimizer (Gurobi Optimization and LCC, 2020). The prioritizr package was based on a widely used systematic conservation program, Marxan (Ball et al., 2009). After we identified priority stopover sites (PSSs hereafter) for spring (before breeding) and fall (following breeding) migrations, the outputs were overlaid to reveal sites that were selected for both migration seasons (Fig. 1).

2.3. Benefit for resident species

To quantify the benefits for resident species of protecting migratory stopover sites, we calculated the proportion of the abundance of all resident species and all imperiled resident species that were included within PSSs. We examined the abundance of resident birds occurring on priority sites prioritized for migrants because our primary interest was focused on identifying stopover sites for migratory species, and then examining the potential of those sites for resident species protection. To account for cases where a species was only listed in one country but present in more than one, we conducted an additional analysis where we restricted the calculation of abundance of country-level imperiled species only to the country they were listed in. For example, Western Screech-Owl (M. kennicottii) was listed in Canada but not in the US nor Mexico, and thus, we used the abundance of Canadian Western Screech-Owl and the PSSs in Canada to calculate the country level PSSs coverage. Species only listed in the international list (i.e., IUCN Red list) but not in any national/federal list were excluded from this analysis.

2.4. Protected area coverage

We estimated protected area coverage within PSSs in North American countries by combining the protected areas from the WDPA database (UNEP-WCMC, 2018) with the PSSs for all migrants during spring or fall migrations, and the overlapped sites between seasons (Fig. 1). A site was considered to be protected if the center of the grid cell intersected with the WDPA layer. We further identified the category of protection area each priority site was located in, based on the IUCN Protected Areas Management Categories. The original seven categories were aggregated into three categories representing high (Ia: strict nature reserve, Ib: wilderness area), medium (II: national park, III: national monument), and low (IV: habitat/species management, V: protected landscape/seascape, VI: managed resource protected area) protection

status (Wilson et al., 2019).

In order to compare the potential benefit of PSSs with the effectiveness of existing protected areas for resident species, we further calculated the proportion of the abundance of all resident and imperiled resident birds included within protected areas.

2.5. Land use change

A global land systems map (van Asselen and Verburg, 2012) and the output from global land system change model (CLUMondo) (van Asselen and Verburg, 2013) were used to represent land use patterns for the year 2000 and 2050. The land system map and the model use the combination of land cover percentage (i.e., tree, bare, cropland, and build-up area), livestock density, and land use intensity to classify land cover into several types at an approximately 9.25×9.25 km spatial resolution (van Asselen and Verburg, 2012). We used the 8 main land system types (Fig. 1 in van Asselen and Verburg (2012)), which includes two anthropogenic dominated landscapes (1. cropland and 2. settlement), two mosaic anthropogenic and natural systems (3. mosaic cropland and grassland, and 4. mosaic cropland and forest), and three natural dominated landscapes (5. forest, 6. mosaic grassland, 7. grassland, and 8. bare) to represent the land use patterns in our study area. The CLU-Mondo model projects land use change based on regional demands for goods and services influenced by factors that may constrain or promote land system conversion. Empirical relationships between the land system types, biophysical and socio-economic factors, and land availability in the surrounding area are used to estimate the changes of land system types in each grid cell (van Asselen and Verburg, 2013).

We used three shared socioeconomic pathway scenarios (SSP1, 2, 3) to explore different land use changes between year 2000 and 2050 (details see Riahi et al. (2017)). SSP1 represented a global sustainability scenario, in which the investments in education and health accelerate the demographic transition, the emphasis on economic growth shifts toward improving human wellbeing, the inequality both among and within countries is reduced, and the consumption changes toward low

material growth and lower resource intensity (Best-Case scenario). SSP2 was an intermediate scenario that the economy, society, and technology mainly follow the historical trends with the population grows moderately and levels off in the mid-century (Business-as-Usual). In other words, this scenario reflected efforts by countries to improve sustainability and income inequality, but had yet to make meaningful progress. In SSP3, environmental issues were low in the international priority and countries focus on domestic and national security issues because of the increase of nationalism and concerns about competitiveness and regional conflicts. Population growth was considered high in developing countries but low in industrialized countries (Worst-Case scenario).

Similar to protected areas, the land use on a specific priority stopover site was based on the location of the center of the priority site and the overlapped land use type. We examined the patterns and proportion of land use types throughout priority sites in year 2000 and 2050 under SSP1, 2, and 3. We note that the coverage of the land use dataset we used do not project well in high latitude areas (above 70 degree north). Nevertheless, the influence of this may be minor because the majority of the priority sites were located further south (97.3% of the fall and 96.8% of the spring PSSs) and the effect of land use change is relatively low in high latitude areas (Jetz et al., 2007; Newbold, 2018).

3. Results

3.1. Priority sites for migrants

Priority stopover sites (PSSs) in fall were more geographically spread across the Americas whereas most priority sites during spring were concentrated in North and Central America (Fig. S1). Among the North American countries (Fig. 2), the overall area selected to protect 30% of the seasonal average abundance of 424 migratory species for fall migration was 4.76 million km² and the area for 432 migratory species during spring migration was 2.91 million km². The overlapped area was 1.51 million km², which equals 31.6% of the fall migration priority sites or 51.7% of the spring migration priority sites. Across the Americas, the



Fig. 2. Sites selected to protect 30% of the populations for migratory birds during fall migration, spring migration, and the overlapped areas between both migration seasons. The turquoise color represents protected areas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

size of PSSs was 7.96 million km^2 for fall migration, 3.31 million km^2 for spring migration, and 1.80 million km^2 for the overlapped area (22.6% of the fall migration sites or 54.4% of the spring migration sites).

3.2. Potential benefit for resident species

In the North American countries, the average potential benefits for resident birds were similar to the conservation objective we set for migratory birds (i.e., 30% of the population) but depended on the season (Fig. 3). Among 158 resident birds species, the average proportion of abundance included in fall migration PSSs was 35.6% (SD = 15.9%) and in spring migration PSSs was 22.3% (SD = 17.2%). The proportion of resident birds included in the overlapped priority sites was lower at 14.2% (SD = 12.6%). The proportion of residents protected was higher when we focused on the 27 imperiled resident species, where on average, 42.5% (SD = 19.2%) of the abundance was included in fall migration PSSs, 31.2% (SD = 21.0%) in spring migration PSSs, and 19.5% (SD = 13.7%) where fall and spring PSSs overlapped. When we restricted analyses only to the country where imperiled residents were listed, the average proportion of abundance protected increased to 45.0% (SD = 24.6%) in fall migration PSSs, 39.1% (SD = 23.9%) in spring migration PSSs, and 28.0% (SD = 17.8%) in overlapped sites (Fig. S2). The PSSs in the south (e.g., Florida, Texas, and Mexico) held more resident or imperiled resident bird species than those in the north (Fig. S4).

3.3. Protected stopover sites

Among all PSSs in North American countries, less than 10% were covered by existing public protected areas (6–9%: Table 1; Fig. 2). Half of the protected PSSs were under low protection status while around a quarter of the protected sites were under high or medium protection status. The coverage of protected areas was higher for fall migration PSSs than spring migration and overlapped sites regardless of protected status. The overall area of PSSs under protection was 0.45 million km² for fall migration.

For all resident birds, the average proportion of abundance covered by protected areas was 8.2% (SD = 6.8%), which was slightly higher

Table 1

Proportion of PSSs in protected areas with high (strict nature reserve, wilderness area), medium (national park, national monument, habitat/species management), low (protected landscape/seascape, managed resource protected area), or any protection status.

PSSs	High	Medium	Low	Any
Fall migration	3.50%	2.57%	4.34%	9.53%
Spring migration	1.55%	1.20%	3.50%	6.04%
Overlapped sites between both migration periods	1.42%	1.65%	3.13%	6.12%

than that for imperiled resident birds (average 7.8% and SD 6.8%) (Fig. S3).

3.4. Land use change

We presented the results of land use patterns and change for year 2000 and 2050 under the SSP2 (Business-as-Usual) scenario here while the results for SSP1 (Best-Case scenario) and SSP3 (Worst-Case scenario) can be found in the supplementary information (Fig. S5 and Table S2). Based on land-use patterns in 2000, a higher proportion (46.4%) of the PSSs for spring migration was located on anthropogenic modified landscapes (i.e., settlement, cropland, and mosaic cropland) than fall migration PSSs (<30%; Fig. 4, Table S1), which had a higher proportion of forest and mosaic grassland.

Across scenarios and migration periods, the proportion of PSSs in settlements and grasslands increased around 100% or more from year 2000 to 2050 (Fig. 4, Tables S1 and S2). The proportions of PSSs on mosaic cropland and grassland, mosaic cropland and forest, and bare land decreased by about half while the proportion of sites on cropland decreased slightly (Fig. 4, Tables S1 and S2). The expansion of settlement was most obvious in Eastern North America (e.g., New England, St Lawrence River, northern Florida) and several metropolitan areas (e.g., Vancouver to Seattle, San Francisco to Sacramento, Denver, Phoenix, Mexico City, and Culiacán), where expansion primarily resulted in the loss of forested and grassland stopover sites in Canada and the US, although in some cases the expansion of settlements resulted in the loss of agricultural landscapes (e.g., croplands in Mexico) (Figs. 5 and S4).



Priority stopover sites selected for different migration seasons

Fig. 3. Proportion of the abundance of resident (a) and imperiled (b) birds included in the priority stopover sites for fall (fall), spring (spring), or the overlap between both migrations (both). Solid horizontal line represents target of 30% of global abundance of migratory birds.



Fig. 4. Proportion of eight land use types on priority stopover sites for fall migration (fall_), spring migration (spr_), and the overlapped sites between migrations (over_) in year 2000 or 2050 (SSP2 Business-as-Usual scenario). Numbers for this figure could be found in Table S1.



Fig. 5. Land use patterns on priority stopover sites for fall migration (a, d), spring migration (b, e), or overlapped sites between both migrations (c, f) across North American countries in year 2000 (a, b, c) or 2050 under SSP2 scenario Business-as-Usual (d, e, f).

Many PSSs changed from cropland to grassland in the center of North America, such as northern Texas, Oklahoma, Kansas, northern North Dakota, southern Manitoba and Saskatchewan. However, in the lower part of the Mississippi River basin and several East Coast States (Virginia to Florida), sites with mosaic anthropogenic and natural landscapes were changed to cropland (Figs. 5 and S4). The land use pattern was relatively stable in the north (Alaska and northern Canada).

4. Discussion

Effective conservation of migratory species requires protecting critical sites across the full annual cycle (Singh and Milner-Gulland, 2011), but to date these have been poorly described outside of stationary breeding periods (but see Schuster et al., 2019). Biologists also lack a sound understanding of the extent to which the needs of other species, such as residents, can be accommodated at those same locations. Our study demonstrates how crowd-sourced data can be used to identify and prioritize important stopover locations that support one-third of the populations of >400 species of migratory birds in North America and to evaluate co-benefits for resident and imperiled bird species. Only 32% of fall priority sites and 52% of spring priority sites overlapped between seasons, which points to the need to separately consider each migratory period. Although our spatial prioritization algorithm targeted migratory birds, solutions benefited resident species as well. Specifically, the priority sites we identified supported 22.3–35.6% of the populations of 158 resident species and 31.2–42.5% of the populations of 27 imperiled residents, depending upon the season. The relatively high average proportion of imperiled species' abundance included in PSSs is the result of many imperiled species in this study that were also found in locations used by migrants during stopover (e.g., Florida Peninsula, California Central Valley, and Gulf Coast). Fewer than 10% of priority sites were formally protected and most occurred within anthropogenic and mosaic anthropogenic and natural landscapes.

4.1. Comparison between spring and fall migration

Several of the PSSs we identified are also know based on earlier studies at smaller scales, such as the stopover areas along the Gulf Coast and the northern part of South America (Bayly et al., 2018; Dokter et al., 2018). Our results also revealed differences and similarities between migration seasons. For example, sites along the East Coast (Virginia to Georgia) were selected to protect fall migration while further inland sites were selected for spring migration, which matches the different routes migrants are known to use during the two migration periods (La Sorte et al., 2014b). In northwestern Mexico, PSSs for spring migration, likely because migrants in this region tend to track the emerging productivity in low elevation areas during spring migration (La Sorte et al., 2014a). In contrast, sites in southern Florida and southern Texas were used by birds during both migration seasons (Dokter et al., 2018; La Sorte et al., 2014b).

In this study, the area required to meet abundance targets for fall stopover sites was more than double that required for spring, which might reflect different migratory strategies. For many migratory birds, spring migration is more time constrained than in fall, thus, birds tend to migrate more rapidly, use fewer stopover sites, and move longer distances between stopovers (La Sorte et al., 2016; Zhao et al., 2017). Indeed, data we extracted from eBird indicated a shorter migration period for spring (average 76 days) than fall migration (average 102 days). In addition, locations for molt migration and some resident populations of migratory species might be included in the fall migration sites (https://ebird.org/science/status-and-trends/faq).

4.2. Resident and imperiled species

The fact that the proportions of resident and imperiled resident birds included in PSSs were similar or even greater than the abundance objective for migrants (i.e., 30%) and much higher than the proportions of resident birds covered in existing protected areas highlights the opportunity to design conservation strategies for both migratory and resident species. Higher proportions of resident birds' abundance in PSSs for fall than spring migration may be the result of the larger area (see previous section) and higher proportion of natural landscapes (see next section) for fall migration PSSs. Our PSSs for fall migration also included many sites with high endemic bird species richness across the Atlantic coast of the US (Jenkins et al., 2015). Conserving natural habitats or conducting wildlife-friendly practices in those locations could benefit both migrants and residents (Leveau et al., 2019; Wilcoxen et al., 2018).

However, our results also indicated some differences between protecting PSSs for migrants and key habitats for residents. Several smallranged endemic resident species were not included or included with relatively low proportions in PSSs for migratory birds. For example, zero proportion of the abundance of Island Scrub-Jay (*Aphelocoma insularis*), a species only found on Santa Cruz Island was included in the PSSs. Furthermore, the Pinyon Jay (*Gymnorhinus cyanocephalus*), an IUCN Vulnerable species that distributes in the Pinyon-Juniper woodlands in Nevada, Utah, and Arizona, was not well represented in the PSSs (16.18% and 4.59% were included in fall and spring PSSs, respectively).

At local scales, migratory and resident species may use different habitats across the annual cycle. For example, while Neotropical migratory birds mainly used ephemeral streams as stopover habitats in deserts, most resident birds used both ephemeral streams and uplands similarly (Kozma et al., 2012). The resolution $(2.96 \times 2.96 \text{ km})$ we used may not be able to detect this difference, especially on a highly diverse landscape. Large protected areas or conservation plans incorporating multiple habitat types may be a beneficial approach when the objective is to protect species with different life histories and that utilize different habitats within a landscape as a result.

4.3. Protected area, land use change, and conservation strategies

Among PSSs, the low percentage in protected areas and substantial proportion in anthropogenic landscapes may be one of the reasons that migratory populations are declining in North America (Bayly et al., 2018; La Sorte et al., 2017). Our results were comparable to the coverage of protected areas for 24 forest passerine species over their annual migrations (La Sorte et al., 2017) and slightly lower than the protected area coverage for wintering grounds of 112 Neotropical migratory passerines (Wilson et al., 2019). Our results could be used to support existing policies and programs (examples in Fig. 6), such as locations for migratory bird sanctuaries (Canada; Panel b in Fig. 6), USDA Farm Bill incentive programs (US; croplands on Panel d in Fig. 6), Urban Bird Treaty programs (US; settlements on Panel d in Fig. 6), North American Bird Conservation Initiative programs (Canada, US, Mexico; sites shared among multiple bird species, Panel c in Fig. 6), and Neotropical Migratory Bird Conservation Act projects (across Americas). Among international programs, the Partners in Flight Landbird Conservation Plan (Canada and US) suggests the use of eBird data to identify critical non-breeding areas for migratory bird conservation (Rosenberg et al., 2016; Wilson et al., 2019).

Two large-scale land use changes were consistently predicted among scenarios in North America: the expansion of settlement and the reduction of cropland. However, the resolutions we used for birds (2.96 \times 2.96 km) and land use (9.25 \times 9.25 km) are much larger than the observed size of stopover sites used by some Nearctic-Neotropical migratory birds (0.5-50 ha: Amaya-Espinel and Hostetler, 2019; Archer et al., 2019; Partridge and Clark, 2018). This could underrepresent the importance of small stopover habitats (e.g., $<1 \text{ km}^2$) within human-modified landscapes like settlement. Strategies that can incorporate small stopover habitats for birds into planning for urban or agricultural areas could be vital for these species (e.g., Urban Bird Treaty, U.S. Fish and Wildlife Service, 2020). Conservation strategies that are amenable to human-dominated landscapes include protecting and/or restoring natural habitats, green spaces, and riparian corridors, promoting sustainable building elements like green roofs, facilitating conservation easements, and encouraging wildlife-friendly farming practices (Amaya-Espinel and Hostetler, 2019; Archer et al., 2019; Greco and Airola, 2018; Johnson et al., 2011; Partridge and Clark, 2018; Stodola et al., 2014; Wilcoxen et al., 2018). In some cases, conservation strategies may focus on time-specific restrictions related to human disturbance, such as construction activities, off-leash pet activity, noise, and light during migration seasons (U.S. Fish and Wildlife Service, 2020). Some croplands in the center of North America may convert to grassland because of abandonment (Johnson et al., 2011; van Asselen and Verburg, 2013). Abandoned farms and pastures might benefit some bird species due to the reduced human disturbances and increased habitat complexity (Johnson et al., 2011) and studies have revealed that some forest breeding migratory birds use early successional habitats during the post breeding season (Burke et al., 2017). However, further studies are needed to examine the response of both migratory and resident birds to this conversion. Potential conservation strategies to restore grassland species on farmlands include removing invasive grasses, and restoring native vegetation and natural disturbance regimes such as fire and grazing (Keyser et al., 2019).

One of the most critical next steps requiring study is to identify the spatial connectivity (i.e., distances and barriers) and functional connectivity (i.e., animal movement) among priority sites identified in the analysis and between these sites and the breeding and wintering grounds. For migratory species using multiple stopover sites, a loss of small proportion of those sites could result in disproportionately large population losses because of the connectivity among sites (see Fig. 2 in Runge et al., 2014). Incorporating connectivity (e.g., the number/proportion of birds moving from stopover site A to B or from stopover site C to wintering site D) into protected area selection is crucial for migratory birds because different subpopulations or individuals could use multiple



Fig. 6. Examples for identifying possible conservation strategies on different PSSs (see Fig. 6). Panel (a) shows the locations of (b), (c), and (d) in North America where different conservation strategies were suggested. Panel (b) shows potential locations for permanent protection with sites that are priorities for spring migration and outside existing protected areas, have no imperiled resident species, and are dominated by natural landscapes such as grassland (1) or forest (2). Panel (c) shows potential locations for permanent or other forms of long-term protection with sites that are priorities for both migration seasons with relatively high imperiled species richness. Panel (d) shows potential locations for seasonal protection with sites that are priorities for fall migration, outside protected areas, dominated by mosaic or anthropogenic landscapes, such as (1) cropland, (2) settlement, and (3) mosaic cropland and forest.

and different set of stopover sites during the migration season (Bayly et al., 2018). While eBird data have been used to identify priority habitats in breeding and wintering areas (Johnston et al., 2020; Schuster et al., 2019; Wilson et al., 2019), information on connectivity among priority sites during migration is lacking for most bird species (Johnston et al., 2015). Telemetry and isotope studies combined with crowd-sourced data offer a promising way to address this information gap (Fournier et al., 2017; Xu et al., 2020) but can also be done by incorporating spatial clustering into analyses, as in Schuster et al. (2019).

4.4. Limitations and caveats

There are several limitations and caveats with our methodological approach. First, rather than use weekly abundance estimates from eBird (Johnston et al., 2020; Schuster et al., 2019), we relied upon seasonal averages that provide less temporal resolution. Our intent in using seasonal average was to avoid prioritizing habitats occupied by birds for very brief or highly variable periods (e.g., rest-roost sites sensu Bayly et al. (2018)) and instead focus on stopover and staging sites used by large numbers of birds and/or for longer periods that are more consistent across seasons and years (Schuster et al., 2019). Using seasonal averages also provides a way to treat every species equally and enable us to include all species in one optimization process because the migration window (e.g., when and how long) varies among species. However, species-specific seasonal data limit our ability to select specific timing (weeks) when calculating the abundance of resident species. The use of seasonal averages may also overrepresent locations in Central America, where birds concentrate as they pass from north to south (or the opposite), while underrepresenting locations near the breeding grounds in North America given the hourglass shape of the continents.

Nevertheless, there is a substantial proportion of fall (60%) and spring (88%) PSSs identified in this study located in all three North American countries. Furthermore, a previous study suggests that prioritizations using quarterly or monthly abundance estimates could produce results having medium to high correlations (r = 0.62-0.92) with prioritizations using weekly estimates (Johnston et al., 2020).

Second, although distributions of resident birds were assumed to be static for the purposes of this analysis, we recognize that some species move seasonally over smaller spatial scales. An alternative way is to define specific temporal periods to represent a season based on a biological understanding of when most species are sedentary, as in Wilson et al. (2019). However, for the purposes of this study, we decided to align the temporal periods of our analysis for both resident and migrants, in order to generate comparable abundance estimates.

Third, while crowd-sourced data provide unparalleled spatial and temporal information about avian abundance, certain geographies are under-sampled. Such spatially-biased sampling effort is partly resolved by using adaptive spatiotemporal exploratory models (AdaSTEMs) (Fink et al., 2010), but there remain gaps in our knowledge, especially outside of North America. Integrating resident species into stopover site conservation may be more important for the Neotropics due to the high diversity of resident birds there (Somveille et al., 2013). Incorporating the abundance of resident birds or other taxa (e.g., mammals, reptiles, plants) can improve the effectiveness of conservation plans to cover different species using areas that are also important stopover habitats for migrants. One way to address this issue is to integrate data from multiple sources like community science projects, government and NGO databases, and formal surveys (Roy-Dufresne et al., 2019). Increasing the popularity of crowd-sourced science projects to Neotropical regions and accumulating scientific database could benefit future conservation

planning.

Finally, we assumed the PSSs remain relatively constant through time (2000 to 2050); however, this assumption may be incorrect given that changing climate and land uses may alter the locations of breeding and wintering grounds for migratory birds (Clairbaux et al., 2019; Curley et al., 2020; Reese and Skagen, 2017). Furthermore, migratory and resident birds might respond to these changes differently (Lindenmayer et al., 2018; Wittwer et al., 2015). Nevertheless, land use change alone might not affect the spatial pattern of large-scale migration routes/corridors because of the influence of other large-scale factors like weather conditions (Moore et al., 2005). For example, many migrants still used the Mississippi Flyway in spite of agricultural activities (Fig. 5). Further studies are required to examine and predict the individual and combined influences of climate and land use changes on the distribution and abundance of migratory and resident species.

5. Conclusion

Large-scale databases like eBird have proven to be enormously useful in identifying the locations that are important for conserving migratory species (e.g., Johnston et al., 2020; Schuster et al., 2019). Not only did we identify the priority stopover locations in spring (pre-breeding) and fall (post-breeding) migratory periods, but we expanded the lens to include resident and imperiled species. Doing so provides opportunity to evaluate where conservation interventions may have added value for non-migratory species and to optimize accordingly. In cases where sites are used primarily by migrants and for brief periods, managers may consider using dynamic conservation strategies (e.g., agreements that restrict certain activities for a brief time) that are likely more practical and cost-effective than acquiring lands for permanent protection on private lands (Reynolds et al., 2017). By integrating information about protection status and current/future land uses, we are also able to anticipate which priority sites will be most threatened and, consequently, are in most need of attention. Although our paper is focused on North American birds, our approach is translatable to other taxa, geographies, and ecosystems (e.g., aquatic). Given the important role of migratory species in coupling biodiversity and ecosystem function across diverse scales (Bauer and Hoye, 2014), there is great urgency to develop conservation strategies that protect habitats and migratory routes/corridors used by migratory wildlife (Runge et al., 2014).

CRediT authorship contribution statement

Hsien-Yung Lin: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Writing - Original Draft.

Richard Schuster: Conceptualization, Formal analysis, Writing -Review & Editing.

Scott Wilson: Conceptualization, Investigation, Writing - Review & Editing.

Steven J. Cooke: Supervision, Writing - Review & Editing.

Amanda D. Rodewald: Conceptualization, Writing - Review & Editing.

Joseph R. Bennett: Conceptualization, Resources, Writing - Review & Editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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H.-Y. Lin et al.

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