Opportunities for the conservation of migratory birds to benefit threatened resident vertebrates in the Neotropics

Scott Wilson1,2,3 | Hsien-Yung Lin3 | Richard Schuster3 | Ana M. González1,4 | Camila Gómez4,5 | Esteban Botero-Delgadillo4 | Nicholas J. Bayly4 | Joseph R. Bennett3 | Amanda D. Rodewald5 | Patrick R. Roehrdanz6 | Viviana Ruiz Gutierrez5

1Wildlife Research Division, Environment and Climate Change Canada, Delta, BC, Canada; 2Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC, Canada; 3Department of Biology, Carleton University, Ottawa, ON, Canada; 4SELVA: Investigación para la Conservación en el Neotrópico, Bogotá, Colombia; 5Cornell Lab of Ornithology and Department of Natural Resources and the Environment, Cornell University, Ithaca, NY, USA and 6Moore Center for Science, Conservation International, Arlington, VA, USA

Abstract

1. Neotropical countries receive financing and effort from temperate nations to aid the conservation of migratory species that move between temperate and tropical regions. If allocated strategically, these resources could simultaneously contribute to other conservation initiatives. In this study, we use novel distribution maps to show how those resources could aid planning for the recovery of threatened resident vertebrates.

2. Using eBird-based relative abundance estimates, we first identified areas with high richness of Neotropical migrant landbirds of conservation concern (23 species) during the stationary non-breeding period. Within these areas, we then identified threatened species richness, projected forest loss and conducted a prioritization for 1,261 red-listed vertebrates using Terrestrial Area-of-Habitat maps.

3. Richness for migrants was greatest along a corridor from the Yucatan peninsula south to the northern Andes but also included south-west Mexico and Hispaniola. Protected areas account for 22% of this region while 21% is at risk of forest loss. Within this focal region for migrants, all four vertebrate groups showed hotspots of threatened species richness along the west and east Andean slopes. Taxa-specific hotspots included montane areas of southern Mexico and central Guatemala (amphibians/reptiles) and the entire east slope of the Colombian East Andes (mammals).

4. Our prioritization highlighted several areas of importance for conservation due to high threatened species richness and projected forest loss including (a) the Pacific dry forests of south-west Mexico, (b) montane regions of northern Central...
America and (c) the west Andean slope of Colombia and Ecuador. At a landscape scale in southern Colombia, we show how conservation efforts for six Neotropical migrants could benefit 56 threatened residents that share a similar elevational range.

5. Synthesis and applications. Funding and effort for migratory bird conservation also has potential to benefit threatened resident vertebrates in the Neotropics. Our study highlights how novel, high-resolution information on species distributions and risk of forest loss can be integrated to identify priority areas for the two groups at regional and landscape scales. The approach and data can be further modified for more specific goals, such as within-country initiatives.

KEYWORDS
amphibian, eBird, forest loss, Latin America, mammal, protected area, reptile, terrestrial area of habitat

1 | INTRODUCTION

Biodiversity conservation requires decisions about how to efficiently allocate limited resources among management strategies, locations and species (Margules & Pressey, 2000). These decisions will be influenced by the priorities and resources of different institutions that engage in conservation within the same region. However, even where institutional priorities differ, the actions necessary for a successful conservation outcome may be similar and therefore, by aligning multiple priorities among institutions, we have an opportunity to leverage and deploy resources to areas or initiatives that are likely to return shared benefits (Beger et al., 2015). In this article, we show how the allocation of resources towards the conservation of migratory birds can also benefit threatened resident vertebrates in the Neotropics.

Each year, resident faunal communities in the Neotropics are augmented by vast numbers of Nearctic-Neotropical migrant birds (hereafter ‘Neotropical migrants’) that move south after breeding to overwinter across Latin America and the Caribbean. Many countries in Latin America have provisions to protect Neotropical migrants (e.g. Naranjo & Amaya, 2009) in addition to other goals such as the protection of resident biodiversity (e.g. Langholz et al., 2000) and reforestation (e.g. Subak, 2000). There is growing recognition that population declines in some Neotropical migrants are influenced by habitat loss on the non-breeding grounds (Taylor & Stutchbury, 2016; Wilson et al., 2018). As a result, conservation efforts within Neotropical countries often receive financial and technical support from temperate nations that are subject to mandates to conserve migratory species that spend part of the annual cycle within the geopolitical boundaries of these countries (e.g. Canada’s Species-at-Risk Act, [SARA], 2002, United States Endangered Species Act [ESA], 1973). For example, since 2010, the US-based Neotropical Migratory Bird Conservation Act has provided over $30 million with an additional $130 million leveraged as match contribution for research and conservation, primarily in Central and South America. Although current financial and technical support from temperate nations is directed towards priority areas for migrants, alignment with other priorities within Neotropical countries provide an opportunity to leverage greater returns on conservation investments (Dallimer & Strange, 2015).

There has been little coordination to date on conservation efforts for non-breeding Neotropical migrants and tropical residents in part because of limited information on their fine-scale distributions or a limited capacity to access and utilize that information. However, recent advances in distribution modelling from the eBird Status and Trends project for Neotropical migrants (Fink et al., 2013, 2020) and Terrestrial Area of Habitat (AOH) mapping for residents (Brooks et al., 2019) now allow us to align estimates of the distribution of both groups at a high spatial resolution. With the integration of these databases, we can examine where areas of high conservation importance for resident taxa occur relative to areas receiving conservation investment for migrants. By further incorporating information on current protection and risk of habitat loss, we can also identify regions where conservation efforts are likely to benefit both groups.

We utilized this novel information to focus on three main objectives in this study. First, we identified areas of high overwintering Neotropical migrant richness across the western hemisphere with a focus on terrestrial landbird species that are listed federally in Canada or the United States (Endangered Species Act [ESA], 1973; Species At Risk Act [SARA], 2002) or by Partners in Flight (Rosenberg et al., 2016). We selected this group because they are the species most likely to receive conservation attention, funding and effort from Canada and the United States. Second, within priority areas of importance for listed migrants, we identified hotspots of high richness for threatened amphibians, birds, mammals and reptiles (IUCN, 2020). For both objectives, we examined where areas of importance are currently protected (UNEP-WCMC, 2020) and where they are at risk of forest loss based on shared socio-economic projections (O’Neill et al., 2017). Third, we conducted a systematic prioritization
with all resident species to identify areas that maximize conservation opportunities within the migrant focal area. For this objective, we asked what regions allow us to reach a 30% land area target within the focal area while maximizing the number of residents included within areas of projected forest loss. We also demonstrate how our approach can be used to identify areas of conservation importance for migrants and residents at landscape scales where on-the-ground conservation efforts are most likely to be implemented.

2 | MATERIALS AND METHODS

2.1 | Migrant focal area identification

Our geographic region focused on the Neotropics, including southern Mexico, Central and South America and the Caribbean (Holt et al., 2013). Neotropical migrants are defined as species that breed north of, and overwinter south of, the Tropic of Cancer (Hagan III & Johnson, 1992), which we defined as the northern boundary in this analysis. Our focus was on Neotropical migrant terrestrial landbirds and therefore, we excluded species whose wintering ranges are largely north of the Tropic of Cancer as well as seabirds, shorebirds and waterbirds as these species have differing land cover requirements that align poorly with goals to conserve terrestrial tropical forest species. Similarly, we also excluded one listed landbird, bobolink Dolichonyx oryzivorus, because of its preference for open grasslands.

We used species-specific weekly estimates of relative abundance from the eBird Status and Trends project to define the ranges of listed migratory landbirds (Fink et al., 2018). From this evaluation, we identified 23 species for which there was information from eBird on their non-breeding distributions (Table S1). The eBird relative abundance estimates are defined as the predicted number of individuals on a 1 hr, 1 km eBird checklist conducted at the ideal time of day for detection of the species in every week of the year, at a resolution of 2.96 km² (Fink et al., 2018). These relative abundance estimates are generated from an ensemble modelling strategy based on an Adaptive Spatio-Temporal Exploratory Model (AdaSTEM, Fink et al., 2013). The models include environmental predictors, temporal variation and observation-effort predictors to account for detectability (Fink et al., 2020). Weekly relative abundance estimates are assigned seasonally for migratory species with pre-breeding migration, breeding, post-breeding migration and non-breeding periods. We used the average values for all weeks that fall within the non-breeding period for each of the 23 species. The non-breeding period is estimated separately for each species depending on their migratory timing but ranged between 19 October and 15 March for the species in this analysis. Many migratory species have low abundances at range edges and we only selected the pixels that represented a cumulative 95% of total abundance of each species to emphasize their core non-breeding range.

The relative abundance rasters for all 23 migrant species were stacked using package RASTER (Hijmans, 2019) in R version 4.0.3 (R Core Team, 2020) and the stacked estimates for each pixel were then used to estimate richness per pixel. To focus our analysis on regions that provide benefit for multiple migratory species, we used the richness map to identify the upper 10% of pixels with the highest richness, corresponding to pixels with four or more species present. This approach of selecting a top percentage in a target category is similar to that used elsewhere (Hof et al., 2011; Li & Pimm, 2016; Wilson et al., 2019). This upper 10% of pixels was defined as our migrant focal area and was used for the remaining analyses with resident species. At 2.96 km², the eBird pixel resolution was larger than the 1 km² resolution for the Terrestrial AOH maps. Therefore, to match the resolutions, we disaggregated the eBird pixels to a 1 km² resolution using a nearest neighbour (ngb) method (Hijmans, 2019).

2.2 | Distribution and species richness of Neotropical residents

The distributions of Neotropical residents were based on Terrestrial AOH maps (Brooks et al., 2019). Species AOH ranges were produced previously for 10,774 species of birds, 5,219 mammals, 4,462 reptiles and 6,254 amphibians using available IUCN and Birdlife International polygon data (Bird Life International, 2019, IUCN, 2020) following the procedure outlined in Brooks et al. (2019). These polygons were first filtered for ‘extant’ range and then rasterized to a global 1 km grid. Individual species range rasters were then modified to only include land cover classes that match the habitat associations for each species. Habitat associations were obtained from the IUCN Red List species habitat classification scheme and were matched to ESA land cover classes for the year 2018 following Santini et al. (2019). ESA land cover classification data were aggregated from its native 300 m resolution to match the global 1 km grid using a majority rule. Species ranges were additionally filtered, so that only areas within a species accepted elevational range were included. Global elevation data derived from SRTM was obtained from WorldClim v. 2 (Fick & Hijmans, 2017).

Our selection of threatened Neotropical residents began with all species with Terrestrial AOH maps available and was then restricted to include only threatened taxa, that is, those categorized as Critically Endangered, Endangered, Vulnerable or Near Threatened on the IUCN Red List as of March 2020 (IUCN, 2020). The focal area for migrants was used as a mask layer to restrict the list to those resident species whose range fell within the focal area resulting in 1,261 species. To identify threatened resident hotspots within the focal area, we then stacked the species AOH maps individually for each taxa and identified sites where at least one species from each taxa overlapped the migrant focal area as well as the upper 5 and 10% of pixels representing the highest taxa-specific richness. For the migrant focal area and the upper 10% highest richness areas for each resident taxa, we also examined the proportional representation across countries (Table S2). With ongoing IUCN Red List assessments, the status of some species is expected to have changed over the course of this analysis. Moreover, some species that are now in the four categories above and fall within the focal area will
have been excluded if they were Least Concern at the beginning of this analysis.

2.3 | Protected area coverage and net forest loss

We used the IUCN Protected Areas database (WDPA, UNEP-WCMC, 2020) to identify whether 1 km² pixels were protected or unprotected for the analyses described above. The WDPA database includes different categories of protection but we combined all categories under a single protected area designation because some countries in our analysis do not report individual categories. We used a global land systems map for year 2000 (van Asselen & Verburg, 2012) and a global land systems change model (CLUMondo; van Asselen & Verburg, 2013) to examine where forest cover is projected to be lost and gained. The CLUMondo model projects land-use change at a 9.3 km² resolution based on regional demands for goods and resources dependent on the factors that promote or constrain land conversion. The land systems classification includes 17 categories, but we focused on areas where forest and mosaic forest is projected to be lost to open agricultural lands and where areas currently lacking forest cover are projected to gain forest and mosaic forest (Lin et al., 2020; Wilson et al., 2019). We focused on forest loss and gain because the vast majority of species in our analysis use forested landscapes to varying extents, but we acknowledge that a few species may benefit from the conversion of forest to open landscapes. The model can simulate a number of shared socio-economic pathways (SSPs; O’Neill et al., 2017) and we focused on a business-as-usual scenario (SSP2) in this analysis. Additional detail on the CLUMondo model and the SSPs is provided in Supporting Information Text 1.

2.4 | Spatial prioritization

We conducted a spatial prioritization to identify locations that had the potential to conserve the most residents within the migrant focal area. Our goal was a 30% land area target, which was selected for consistency with the commitments of world leaders at the 2020 One Planet Summit to protect 30% of land area by 2030. Existing protected areas were incorporated into the 30% target and therefore, the prioritization examined where we could focus on unprotected areas that allow us to reach the 30% target while maximizing the number of threatened resident species included. For this prioritization, we focused on unprotected areas at risk of forest loss but also present an alternative scenario in Supporting Information where we examine how prioritized areas change if we do not include projected forest loss.

We performed the prioritization using Integer Linear Programming (ILP) in the R prioritize package (Hanson et al., 2020) with the Gurobi optimizer (Gurobi Optimization & LCC, 2020). The prioritize package was based on Marxan (Ball et al., 2009), a systematic conservation program that offers different scenarios depending on the conservation planning objective. The problem function for the prioritization was based on a Maximum Utility goal, which aims to secure as many species as possible for a given budget (i.e. 30% land area). As a demonstration of our approach at a landscape scale, we focused on a small area of southern Colombia that includes sites that were selected in the prioritization. Within this area, we identified the migrant and resident species expected to overlap, the location of protected areas and the location of unprotected areas that are projected to lose forest cover. See Supporting Information Text 2 for additional detail on the prioritization.

3 | RESULTS

3.1 | Focal area for listed Neotropical migrants

Three general regions had a high richness for the 23 listed migrants (a) along a corridor extending from the Yucatan peninsula through the northern Andes, (b) Pacific coastal regions of south-west Mexico and (c) Hispaniola (Figure 1; Figure S1). The upper 10% of all pixels, representing locations with four or more species present was defined as the focal area and included 17 countries (Table S2). At the time of analysis, protected areas comprised 22.3% of the focal area. Based on a business-as-usual socio-economic projection (SSP2) for 2050, 22.7% and 2.0% of the focal area was predicted to lose and gain forest cover respectively (net loss = 20.7%). The areas of higher projected forest loss included the Pacific dry forests of Mexico, central Honduras, central Nicaragua and the western slope of the Colombian and Ecuadorian Andes (Figure 1).

3.2 | Threatened resident hotspots

The list of threatened residents with a distribution range that overlapped with the focal area included 1,261 vertebrates with an IUCN Red List status of near-threatened or higher (Table 1). Amphibians had the highest number of threatened species in our analysis (n = 643, 51.0% of species), followed by birds (n = 317, 25.1%), reptiles (n = 156, 12.4%) and mammals (n = 145, 11.5%). Amphibians also had a greater proportion of species in the critically endangered and endangered categories, smaller ranges and a higher average endemism to the focal area compared to the other three taxa (Table 1).

Within the migrant focal area, all four vertebrate groups showed hotspots of threatened species richness along the western and eastern Andean slopes of southern Colombia and northern Ecuador (Figure 2). Taxa-specific hotspots occurred elsewhere across the region. For example, areas of high threatened species richness for mammals occurred along the entire east Andean slope, in contrast to birds where the highest richness was concentrated on the west slope of the Andes and the southern extent of the east slope. For amphibians and reptiles, there was greater overlap with the focal area further north in Mexico, Central America and the Caribbean. Amphibian
threatened species hotspots included the Talamanca range of Costa Rica and Panama, the highlands of central Guatemala and western Honduras, and the Dominican Republic (Figure 2). Reptiles also had higher threatened species richness in central Guatemala, coastal areas of the Dominican Republic and western Mexico. Due to their smaller range sizes compared to birds and mammals (Table 1), there were far more areas without any threatened amphibians or reptiles despite the large number of amphibians in this analysis. Protected area coverage for the upper 10% of high richness areas for threatened residents ranged from 18.3% for reptiles to 34.2% for amphibians (Table 1, see also Table S3). Predicted net forest loss by 2050 for these upper 10% areas ranged from 8.9% for mammals to 18.4% for reptiles (Table 1; Table S3).

3.3 Spatial prioritization

For the spatial prioritization, we identified locations within the migrant focal area that are currently unprotected, projected to lose forest and maximize the number of threatened residents in reaching a 30% area target. All existing terrestrial protected areas were included (22.3%); thus, the prioritization for unprotected areas represented 7.7% of the migrant focal area. The results highlight several areas of importance including (a) the Pacific dry forests of south-west Mexico; (b) northern Central America, particularly northern Belize and western Honduras; and (c) the northern Andes, with emphasis on the western slope in Colombia and Ecuador (Figure 3). A similar prioritization focused on maximizing the number of threatened species would be useful for planning conservation efforts.

**TABLE 1** Summaries of threatened resident taxa whose distributions fall within the migrant focal area. CR, EN, VU and NT refer to the number of species in the Critically Endangered (CR), Endangered (EN), Vulnerable (VU) and Near Threatened (NT) IUCN Red List Categories. Range size is the median and interquartile range size (in brackets) while endemism is the mean and SE percentage of the global range that falls within the focal area. For the upper 10% areas of highest richness of each taxa within the focal area, % protected area is the per cent of that area currently protected while % projected net forest loss is the per cent of that area predicted to lose forest by 2050.

| Taxa          | CR | EN | VU | NT | Range size (km²) | Endemism       | % protected area | % projected net forest loss |
|---------------|----|----|----|----|------------------|----------------|------------------|--------------------------|
| Birds (317)   | 13 | 55 | 110| 139| 11,086 (2,810–73,849) | 40.7 ± 2.0 | 20.6             | 9.1                      |
| Mammals (145) | 12 | 33 | 59 | 41 | 20,366 (3,205–118,375) | 40.8 ± 2.7 | 27.3             | 8.9                      |
| Amphibians (643) | 147 | 249 | 157 | 90 | 742 (144–3,109) | 67.0 ± 1.4 | 34.2             | 12.9                     |
| Reptiles (156) | 13 | 58 | 50 | 35 | 1,228 (228–4,179) | 50.5 ± 3.2 | 18.3             | 18.4                     |
**FIGURE 2** Areas of overlap for threatened residents within the focal area for listed migrants. Percentages show the pixels within the focal area containing the highest number of threatened resident species, areas with at least one threatened species and no threatened species. Grey pixels are those outside the focal area as shown in Figure 1.

**FIGURE 3** Prioritization scenario to maximize threatened residents on unprotected lands at risk of forest loss within the migrant focal area. For this scenario, our target was a 30% land area including existing protected areas and prioritized areas. Sites in orange are those that are currently unprotected, projected to lose forest and maximize the number of threatened resident species. See Figure S2 for a scenario that did not incorporate forest loss projections.
residents but without considering the risk of forest loss was entirely focused in the Andes of southern Colombia and northern Ecuador (Figure S2).

As a local example of our approach, we highlight an area in and around Parque Nacional Natural la Serranía de los Churumbelos in south-west Colombia (Figure 4). This landscape encompassed 306 km$^2$ within the migrant focal area including a National Park and unprotected lands west of the park that were selected by the prioritization due to high threatened resident richness and projected forest loss. This 306 km$^2$ area overlapped the distribution of six Neotropical migrants and 56 threatened residents that share a similar elevational range (37 birds, 17 mammals and two amphibians, Figure 4; Table S4) indicating high potential for migrant conservation to benefit a range of other threatened residents.

4 | DISCUSSION

We demonstrate how the use of high-resolution species distributional data allow us to strategically identify where conservation efforts can jointly benefit threatened migrants and residents in the Neotropics at regional and landscape scales. Our analysis necessarily begins broadly with areas of importance for overwintering migrants of concern, as the funding and effort from bird conservation programs in temperate nations will be directed towards regions and actions that benefit these species. Most Neotropical migrants in our analysis are of concern because of long-term population declines and habitat loss on the overwintering grounds is thought to be a principal cause of declines for several of these species (Buehler et al., 2020; Kramer et al., 2018; Taylor & Stutchbury, 2016; Wilson et al., 2018). Key regions and ecosystems with a higher richness of listed migrants included the Pacific dry forests of south-west Mexico, Hispaniola, montane forests of central Guatemala and western Honduras, the Talamanca region of Costa Rica and Panama, and the western and eastern slopes of the Andes of Colombia and Ecuador.

Within the focal area for migrants, all four resident groups had high threatened species richness along the western slope of the Andes of southern Colombia and northern Ecuador. This region is recognized for high biodiversity and endemism (Hof et al., 2011; Pimm et al., 2014) but has also experienced extensive impact in some areas (Correa Ayram et al., 2020); this combination of high biodiversity and impact underlies why this region featured so prominently in our analysis. Some regions of the Western Andes in Colombia receive de facto protection through the presence of indigenous reserves and Afro-Colombian territories, as well as the Reserva Forestal del Pacífico, but since the signing of a peace deal in 2016 between the Colombian government and the FARC, the region has been increasingly threatened by unregulated economic activities that result in deforestation (Prem et al., 2020). As such, we highlighted many unprotected locations that are projected to lose forest and would be high priority sites for conservation efforts.

Our analyses also identified several more northern sites in Mexico, Central America and the Caribbean that were a priority for specific resident taxa due to high species richness and projections of forest loss. For example, the montane forest ecosystems of southern Mexico, central Guatemala and the Talamanca region of Costa Rica.

---

**FIGURE 4** Local-scale prioritization for migrants and residents in the southern Colombian Andes. Solid square in the centre figure shows the area selected to examine the overlap of migrants and residents (306 km$^2$) within and adjacent to Parque Nacional Natural la Serranía de los Churumbelos. Sites in green are protected areas, sites in orange were selected in the prioritization based on high resident species richness and projected forest loss, sites in blue fall within the migrant focal area but were neither protected nor selected by the prioritization. Right image shows a sample of species that overlap migrants within the solid black square: *Aotus lemurinus* (1), *Hemiphractus bubalus* (2), *Ateles belzebuth* (3), *Chloropipo flavicapilla* (4), *Grallaricula cucullata* (5) and *Campylopterus villaviscensio* (6). See Table S4 for the full species list and Supporting Information Text 3 for photograph credits.
and Panama were key areas for threatened amphibians. Amphibians were the resident taxa of highest conservation concern in this analysis representing 51% of all species and 79% of critically endangered species. Global amphibian declines have been the subject of much recent attention due to a range of threats including infectious disease, climate change and habitat loss (Beebee & Griffiths, 2005; Hof et al., 2011). The impacts of chytrid fungi may be the most serious risk to amphibians within the montane ecosystems of Central America and northern South America (Fisher & Garner, 2020) where there is also considerable attention directed towards Neotropical migrants given their use of mid-elevation montane forests (Blake & Loiselle, 2000; Céspedes-Arias et al., 2021). Although reducing the impact of chytrid and other diseases on amphibians requires a multifaceted approach, protecting, restoring and managing habitat is still expected to benefit amphibian populations at serious risk of extinction. As another example, south-west Mexico contained small pockets of high richness for threatened reptiles and is an important overwintering region for listed migrants such as black-capped vireo *Vireo atricapilla* and rufous hummingbird *Selasphorus rufus*. This region includes both dry deciduous and pine–oak forest and contains high endemism but much of it is unprotected and at risk (Portillo-Quintero & Sánchez-Azofeifa, 2010, Figure 1). Targeted planning to minimize forest loss would have important benefits for both threatened residents and Neotropical migrants.

### 4.1 Caveats and future study

We acknowledge five important caveats in this study. First, the choice of a conservation goal will have a strong influence on which geographic regions to focus. Our emphasis was on Neotropical migrant landbirds of conservation concern that use forested landscapes and therefore excluded other important regions for migratory bird conservation. For example, Cuba contains high overwintering migrant diversity (Hagan III & Johnson, 1992; Wilson et al., 2019) but relatively few of these species appear on SAR, ESA or Partners in Flight lists. Consequently, this region was not included within our migrant focal area and we did not assess richness or priority areas for threatened residents within Cuba. Similar analyses conducted within countries could be done to aid national initiatives for ecotourism, restoration and conservation. Second, our migratory species group included species with varying degrees of conservation concern even though they all occurred on at least one of the SAR, ESA or PIF lists. Finer scale analyses focused on particular species or species groups could be done to target migratory species of high concern. Third, given that many funding sources from temperate nations are directed to migratory birds, we constrained prioritizations to areas that were important for migrants. As such, our prioritization will overlook areas that are important exclusively for resident fauna (i.e. areas with few migrants would not be considered in prioritizations). Fourth, our prioritization was based on areas of expected forest loss based on a business-as-usual shared socio-economic projection but we acknowledge that these are only predictions and that extent of forest loss differs in other scenarios (O’Neill et al., 2017). Nevertheless, several of the areas projected to lose forest in our analysis have already experienced deforestation and are considered conservation priorities in other assessments (e.g. dry forests of Mexico, Miles et al., 2006; western Andes, Prem et al., 2020). Finally, despite the fine-scale distribution mapping in this analysis, it is still likely that we overestimated the extent of overlap for migrant and resident priority areas in some cases. This possibility may be most likely in areas of strong elevational change where the 1 km² pixels cover a broad elevational gradient but species only occupy narrow elevational bands within that gradient. In such cases, finer scale evaluation of distributional overlap is needed prior to assessing which resident species could benefit from conservation actions directed towards Neotropical migrants.

### 4.2 Application

Our approach and results have application at regional and landscape scales. At a regional scale, we identify locations where conservation funding and efforts can benefit multiple migratory species of conservation concern and where those areas may be most at risk. These locations may be used to guide decision-making by governmental and non-governmental funding organizations in Canada and the United States that annually provide millions of dollars to domestic and international groups for the conservation of Neotropical migrants in Latin America and the Caribbean. While the overall region of importance for Neotropical migrants is broad, we show that a strategic focus in particular areas has the potential to benefit multiple resident taxa, whereas most plans for the conservation of Neotropical migrants in Latin America do not consider co-benefits for other Neotropical species.

In southern Colombia, we also use an example to demonstrate how our approach could be applied at a finer landscape scale and show how within a small area of 306 km², resources for migrant conservation have an opportunity to benefit 56 species of threatened residents that share the same elevational range. This approach applied locally could aid planning elsewhere, for example within the numerous endemic bird areas across the Neotropics (Stattersfield et al., 1998). It is noteworthy that in our landscape example, there was far higher representation of resident birds (37 species) and mammals (17 spp.) than amphibians (2 spp.) and reptiles (0 spp.) despite the high overall number of amphibians in our analysis at the regional scale. This difference in representation may be true for many finer scale analyses owing to the average differences in range size among taxa. With much smaller ranges on average, a local area may contain fewer threatened amphibians compared to birds but may often include a greater proportion of the range of those amphibians and greater species turnover among local sites.

The types of conservation actions most needed to support migrants and residents will vary depending on the socio-economic and political context, as well as varying degrees of investment in current
conservation efforts. In some cases, unprotected sites with current forest cover may be candidates for protected area designation. However, much of the region highlighted in our study contains working landscapes where protected area goals are not feasible. While our prioritization was area based, it does not necessarily mean that formal protection of those areas is the most suitable conservation action. Within working landscapes, implementing strategies that both conserve biodiversity and support rural livelihoods and communities remains essential. For example, where native forest restoration is not possible, agroforestry systems such as shade-grown coffee can benefit migratory and resident species (Bakermans et al., 2009; Caudill & Rice, 2016; González et al., 2020) and be an economically productive option for landowners (Hernandez-Aguilera et al., 2019). While we demonstrated opportunities to align conservation efforts for migratory and resident species, the approach we used could also be aligned with other initiatives such as forest restoration and sustainable development programs to benefit people and biodiversity.

ACKNOWLEDGEMENTS
The authors thank Stuart Pimm for valuable comments on an earlier draft of this manuscript and the many eBird participants for their contributions to the eBird database. The eBird outputs used in this work were funded by The Leon Levy Foundation, The Wolf Creek Charitable Foundation, NASA (NNH12ZDA001N-ECOF), Microsoft Azure Research Award (CRM: 0518680) and the National Science Foundation (ABI sustaining: DBI-1939187; computing support from CNS-1059284 and CCF-1522054). No ethical approval was required for this research.

CONFLICT OF INTEREST
The authors have no conflict of interest to report.

AUTHORS’ CONTRIBUTIONS
All authors contributed to the ideas and design of the study; H.-Y.L., S.W. and R.S. conducted analyses; S.W. led writing of the manuscript. All authors contributed to the drafts and gave final approval for publication. Our study brought together scientists and conservationists from temperate and tropical nations in the Americas, thus providing contributions to both project development and the implementation of these results into conservation planning.

DATA AVAILABILITY STATEMENT
Publicly available R code and datasets are provided on GitHub to detail the steps used throughout this process (https://github.com/wilsonscottd/Migrant-Resident). Data are also provided in the Dryad Digital Repository https://doi.org/10.5061/dryad.vt4b8gtt2 (Wilson et al., 2021).

ORCID
Scott Wilson https://orcid.org/0000-0002-1210-8727
Hsien-Yung Lin https://orcid.org/0000-0002-2564-3593
Ana M. González https://orcid.org/0000-0002-9291-5560
Camila Gómez https://orcid.org/0000-0002-2770-5794

Esteban Botero-Delgadillo https://orcid.org/0000-0003-4653-7551
Nicholas J. Bayly https://orcid.org/0000-0001-9326-1936
Patrick R. Roehrdanz https://orcid.org/0000-0003-4047-5011
Viviana Ruiz Gutierrez https://orcid.org/0000-0001-7116-1168

REFERENCES
Bakermans, M. H., Vitz, A. C., Rodewald, A. D., & Rengifo, C. G. (2009). Migratory songbird use of shade coffee in the Venezuelan Andes with implications for conservation of Cerulean Warbler. *Biological Conservation*, 142, 2476–2483. https://doi.org/10.1016/j.biocon.2009.05.018
Ball, I. R., Possingham, H. P., & Watts, M. E. (2009). Maxran and relatives: Software for spatial conservation prioritization. In A. Mollanen, K. A. Wilson, & H. P. Possingham (Eds.), *Spatial conservation prioritization* (pp. 185–195). Oxford University Press.
Beebee, T. J. C., & Griffiths, R. A. (2005). The amphibian decline crisis: A watershed moment for conservation biology. *Biological Conservation*, 125, 271–285.
Beger, M., McGowan, J., Treml, E. A., Green, A. L., White, A. T., Wolff, N. H., Klein, C. J., Mummy, P. J., & Possingham, H. P. (2015). Integrating regional conservation priorities for multiple objectives into national policy. *Nature Communications*, 6, 8208. https://doi.org/10.1038/ncomms9208
Bird Life International. (2019). *Bird life international data zone*. http://datazone.birdlife.org/home
Blake, J. G., & Loiselle, B. A. (2000). Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. *The Auk*, 117, 663–686. https://doi.org/10.1093/auk/117.3.663
Brooks, T. M., Pimm, S. L., Akçakaya, H. R., Buchanan, G. M., Butchart, S. H. M., Foden, W., Hilton-Taylor, C., Hoffmann, M., Jenkins, C. N., Joppa, L., Li, B. V., Menon, V., Ocampo- Peñuela, N., & Rondinini, C. (2019). Measuring Terrestrial Area of Habitat (AOH) and its utility for the IUCN Red List. *Trends in Ecology & Evolution*, 34, 977–986. https://doi.org/10.1016/j.tree.2019.06.009
Buehler, D. A., Hamel, P. B., & Boves, T. (2020). *Cerulean Warbler (Setophaga cerulea)*, version 1.0. In A. F. Poole (Ed.), *Birds of the world*. Cornell Lab of Ornithology.
Caudill, S. A., & Rice, R. A. (2016). Do Bird Friendly coffee criteria benefit mammals? Assessment of mammal diversity in Chiapas, Mexico. *PLoS One*, 11, e0165662. https://doi.org/10.1371/journal.pone.0165662
Céspedes-Arias, L., Wilson, S., & Bayly, N. J. (2021). Community modeling reveals the importance of elevation and land cover in shaping migratory bird abundance in the Andes. *Ecological Applications*, in press. https://doi.org/10.1002/eap.2481
Correa Ayram, C. A., Etter, A., Díaz-Timoté, J., Rodríguez Buriticá, S., Ramírez, W., & Corzo, G. (2020). Spatiotemporal evaluation of the human footprint in Colombia: Four decades of anthropic impact in highly biodiverse ecosystems. *Ecological Indicators*, 117, 106630.
Dallimer, M., & Strange, N. (2015). Why socio-political borders and boundaries matter in conservation. *Trends in Ecology and Evolution*, 30, 135–139. https://doi.org/10.1016/j.tree.2014.12.004
Endangered Species Act [ESA] (1973). Pub. L. No. 93–205, 87 Stat. 884.
Fick, S. E., & Hijmans, R. J. (2017). *WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas*. *International Journal of Climatology*, 37, 4302–4315. https://doi.org/10.1002/joc.5086
Fink, D., Auer, T., Johnston, A., Strimas-Mackey, M., Iliff, M., & Kelling, S. (2018). *eBird Status and Trends, Version November 2018*. Cornell Lab of Ornithology. https://ebird.org/science/status-and-trends/
Fink, D., Auer, T., Ruiz-Gutierrez, V., Hochachka, W. M., Johnston, A., La Sorte, F. A., & Kelling, S. (2020). Modeling avian full annual cycle distribution and population trends with citizen science data. *Ecological Applications*, 30, e02056. https://doi.org/10.1002/eap.2056
Wilson, S., Schuster, R., Rodewald, A. D., Bennett, J. R., Smith, A. C., La Sorte, F. A., Verburg, P. H., & Arcese, P. (2019). Prioritize diversity or declining species? Trade-offs and synergies in spatial planning for the conservation of migratory species in the face of land cover change. *Biological Conservation, 239*, 108285. https://doi.org/10.1016/j.biocon.2019.108285

**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of the article at the publisher’s website.

**How to cite this article:** Wilson, S., Lin, H.-Y., Schuster, R., González, A. M., Gómez, C., Botero-Delgadillo, E., Bayly, N. J., Bennett, J. R., Rodewald, A. D., Roehrdanz, P. R., & Ruiz Gutierrez, V. (2022). Opportunities for the conservation of migratory birds to benefit threatened resident vertebrates in the Neotropics. *Journal of Applied Ecology, 59*, 653–663. https://doi.org/10.1111/1365-2664.14077