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Comparing abundance distributions and range maps in spatial conservation planning for migratory species

A. Johnston,[1,2,7] T. Auer,[1] D. Fink,[1] M. Strimas-Mackey,[1] M. Iliff,[1] K. V. Rosenberg,[1,3] S. Brown,[4] R. Lanctot,[5] A. D. Rodewald,[1,6] and S. Kelling[1]

[1]*Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, New York 14850 USA*
[2]*Conservation Science Group, Department of Zoology, University of Cambridge, The David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ United Kingdom*
[3]*American Bird Conservancy, The Plains, Virginia 20198 USA*
[4]*Manomet Inc., P.O. Box 1770, Manomet, Massachusetts 02345 USA*
[5]*U.S. Fish and Wildlife Service, 1011 East Tudor Road, MS 201, Anchorage, Alaska 99503 USA*
[6]*Department of Natural Resources, Cornell University, Ithaca, New York 14853 USA*

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Abstract. Most spatial conservation planning for wide-ranging or migratory species is constrained by poor knowledge of species' spatiotemporal dynamics and is only based on static species' ranges. However, species have substantial variation in abundance across their range and migratory species have important spatiotemporal population dynamics. With growing ecological data and advancing analytics, both of these can be estimated and incorporated into spatial conservation planning. However, there is limited information on the degree to which including this information affects conservation planning. We compared the performance of systematic conservation prioritizations for different scenarios based on varying the input species' distributions by ecological metric (abundance distributions versus range maps) and temporal sampling resolution (weekly, monthly, or quarterly). We used the example of a community of 41 species of migratory shorebirds that breed in North America, and we used eBird data to produce weekly estimates of species' abundances and ranges. Abundance distributions at a monthly or weekly resolution led to prioritizations that most efficiently protected species throughout the full annual cycle. Conversely, spatial prioritizations based on species' ranges required more sites and left most species insufficiently protected for at least part of their annual cycle. Prioritizations with only quarterly species ranges were very inefficient as they needed to target 40% of species' ranges to include 10% of populations. We highlight the high value of abundance information for spatial conservation planning, which leads to more efficient and effective spatial prioritization for conservation. Overall, we provide evidence that spatial conservation planning for wide-ranging migratory species is most robust and efficient when informed by species' abundance information from the full annual cycle.

Key words: abundance; citizen science; conservation planning; eBird; full annual cycle; migration; spatial prioritization; species distribution models.

Introduction

Populations are seldom completely static, but are characterized by spatiotemporal dynamics that unfold at a variety of scales. Long-term changes in the distribution of populations may be caused by climate change or land-use change (Massimino et al. 2015, Le Louarn et al. 2018). Short-term fluctuations in distribution throughout the annual cycle can be driven by species shifting habitats, tracking ephemeral resources, or migrating between regions (Fahse et al. 1998, Skagen et al. 2005, Runge et al. 2016). These dynamic movements are a challenge for traditional conservation strategies and, for this reason, migratory species are under-protected relative to resident species (Runge et al. 2015). Correcting this shortfall is imperative to effectively conserve migratory species, and this requires novel approaches to conservation planning, ensuring resources are available across broad spatial and temporal regions and at all stages of the annual cycle (Lovejoy et al. 1987, Martin et al. 2007, Runge et al. 2014, 2016, Marra et al. 2015).

Traditionally, most spatial conservation plans use species' distributions, such as range maps, to identify networks of sites that meet stated objectives of species protection, subject to constraints such as cost or land area. However, even seasonal range maps fail to capture spatial or temporal variation in abundance, which is

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[7] E-mail: aj327@cornell.edu

particularly problematic for migratory species or species that have highly variable abundance across their range (Dallas et al. 2017). Populations are especially vulnerable if large numbers of individuals aggregate in unprotected sites (Buechley et al. 2018). Consequently, conservation should consider the relative abundance of species, because the value of any given site for conservation will usually increase as the number of individuals increase (Johnston et al. 2015, Veloz et al. 2015). In addition, conservation for dynamic species requires incorporation of their movements through space and time (Runge et al. 2014, 2016, Haupt et al. 2017). New data from large-scale citizen science projects, such as eBird, enable conservation prioritization to be informed by both relative abundance and seasonal dynamics (Reynolds et al. 2017, Schuster et al. 2019). However, little is known about the added benefits of this additional knowledge (Veloz et al. 2015, Tulloch et al. 2016).

The first challenge that must be addressed to improve conservation plans for migratory species is to acquire and use robust information on population dynamics and movement. Spatial conservation plans for migratory species typically consider only one stage of the annual life cycle (Lisson et al. 2017, Walther and Pirsig 2017) or treat seasons as static entities (Dias et al. 2017); although one study has incorporated monthly distributions (Runge et al. 2016). Others have developed population models that considered the explicit movement of migratory individuals among different "sites" or "regions" (Klaassen et al. 2008, Sheehy et al. 2011, Iwamura et al. 2013, Aharon-Rotman et al. 2016, Dhanjal-Adams et al. 2017, Oberhauser et al. 2017, Weeks 2017). This approach is suitable for species for which we have tracking data from a number of individuals, but it is otherwise difficult to parameterize individual-based models. Within the spatial prioritization literature, there are analytical methods to account for connectivity between sites (Beger et al. 2010*b*, Arponen et al. 2012), but their implementation for birds has been limited by lack of information on connectivity for most species.

The second challenge is that strategic conservation planning should identify networks of sites that capture high numbers of individual animals or large proportions of populations (Xia et al. 2017, Baker et al. 2018). Species ranges only show presence/absence and therefore do not allow us to identify sites with high abundance. Estimates of species occupancy (probability of occurrence 0–1) are often uncorrelated with species abundance and so will also not identify sites with high abundance (Johnston et al. 2015, Veloz et al. 2015, Acevedo et al. 2017). Even in cases where abundance estimates are available for individual sites, the importance of a site can seldom be sufficiently quantified without reference to a total population size. For this reason, we suggest that conservation efforts should aim to protect the greatest proportions of populations and should be based on seasonal estimates of density or relative abundance across the population.

In this paper, we address these two challenges by combining information on species' abundance and dynamic distributions to generate spatial prioritizations for land conservation. As an example community, we use migratory shorebirds that breed in North America, where they are among the most threatened community of birds (North American Bird Conservation Initiative 2016). Although shorebirds are the focus of an impressive internationally coordinated program of monitoring and conservation (Howe et al. 2000, Boere et al. 2006), information on the distribution and abundance of these species throughout their entire annual cycle has been difficult to obtain. To fill this gap, we use weekly estimates of shorebird relative abundance (hereafter, abundance) across the Americas, derived from eBird data (Sullivan et al. 2014). eBird data include curated and reviewed contributions from citizen scientists and some professional surveys, and have been used to derive species' distributions and inform conservation action (Kelling et al. 2015, Reynolds et al. 2017, Sullivan et al. 2017, Robinson et al. 2018). Weekly estimates of relative abundance enable prioritization to explicitly consider the dynamic nature of species' populations and to identify sites with high proportions of species' populations. We quantify the improvement in the proportion of populations that are protected under different planning scenarios, when including information on (1) dynamic distributions (using weekly distribution maps) and (2) abundance (using estimates of species' abundance). We demonstrate the ability for citizen science data to be used for conservation planning for a community of dynamic migratory species and across a large spatial domain.

Methods

Spatial conservation planning

Generally, spatial conservation planning aims to identify a set of sites that are efficient for conservation; this involves balancing the species that exist within each site, the cost of protecting those sites, and the desired level of species protection. Spatial conservation planning algorithms typically have a single layer for each species; these layers are overlaid and an optimal set of sites found that protect the greatest number of species within the selected set of sites. We used an algorithm that finds a minimum number of sites that together cover a minimum proportion of each species' range. Each species layer is referred to as a "feature" and the algorithm ensures that a given proportion of each feature is contained within the set of selected sites.

The conventional approach to spatial conservation planning assumes each species has a single static distribution, which is usually a range map. The dynamic movement of migratory species can be incorporated into the standard framework by providing several distribution maps for each species. For example, rather than each species being represented by a single feature, they could each be represented by four features, each depicting the species' range at a given point in the year. The spatial prioritization algorithm that uses four features for each species would ensure that a fixed proportion of each species' range *within each time frame* is included in the set of selected sites. This approach ensures that species are protected at four times during their annual cycle. However, for many migratory species, movements throughout the annual cycle take place quickly. The temporal resolution of the spatial prioritization algorithm can be increased by including more features for each species, representing their ranges at finer temporal resolutions, for example, monthly or even weekly. Providing weekly species' ranges (52 features for each species) would ensure the algorithm selects sites that include a certain proportion of the range of the species within *each week* of the annual cycle. We compared the set of selected sites for a community of migratory birds using information on species' ranges from either weekly, monthly, or quarterly temporal resolutions of sampling.

The conventional approach to spatial conservation planning uses information on species' presence/absence from species' range maps. The spatial prioritization algorithms identify a set of sites that contain a given proportion of the species' range. By using species' ranges the implicit assumption is that the species is spread evenly throughout the range. Most species are not distributed evenly and conservation planning could be more efficient if it identified sites of highest abundance. Using estimated abundances of species as features, the spatial prioritization algorithm identifies a set of sites that contain a given proportion of the population. We compared the set of selected sites when using information on species' abundance or species' ranges. We use the term "distribution" to refer collectively to both species' abundance distributions and species' ranges.

Shorebird distribution models

We used a community of 41 migratory shorebirds to test the above comparisons of how spatial prioritizations vary with different input information on the temporal resolution and the species' distributions. Species' distributions across North, Central, and South America for each week of the annual cycle were estimated with bird count data from eBird and adaptive spatiotemporal exploratory models (AdaSTEM; Fink et al. 2010, 2013, *in press*, Johnston et al. 2015). These models were run separately for each species and estimated the relative abundance of each species within a 8.4 × 8.4 km grid cell for each week of the year. The abundance estimates for each grid cell were compiled from an ensemble of local models, each of which used data from a limited spatiotemporal block (Fink et al. 2013). Within each block, species' relative abundance was estimated with a zero-inflated boosted regression tree that included variables describing observer effort and the local environment (Johnston et al. 2015). The estimates of abundance are not absolute, because detectability was not estimated. But by accounting for heterogeneity in detectability this produces estimates of abundance that are relative across sites, within the given species and week. For example, a relative abundance estimate of 20 Whimbrel in the first week of May in one site may not reflect exactly 20 individuals, but can be assumed to be twice as many as another site with an estimated relative abundance of 10 Whimbrel in the first week of May. For further details of the data selected and the modeling, see Appendix S1. The output of the species' distribution models was an estimate of abundance for each species in each site (an 8.4 × 8.4 km grid cell in a uniform grid) for each week of the year. These distributions of relative abundance were converted to species' ranges, which defined the presence or absence of a species at each site.

The estimated species' abundance distributions for each week of the year were validated statistically using a portion of the data removed before analysis (Fink et al., *in press*) and had an ornithological review by an expert ornithologist (M. J. Iliff). In subsequent analyses, we included species results only during seasons in which they were judged by both validation methods to have sufficiently good estimates *and* in weeks in which they were judged to have at least 50% of the population in the prediction region, to facilitate the estimation of the proportion of total population (Appendix S1: Fig. S1). The 41 species each had between 9–52 weeks of estimated distributions included in the analysis (Appendix S1: Fig. S1). There are some regions in which limited data led to difficulties in estimating species' distributions, for example the Arctic breeding ranges of many shorebirds. We acknowledge that this prioritization will omit some of these sites, despite their importance, but the *comparisons* of different types of prioritizations are still robust (Appendix S1: Fig. S2).

Prioritization scenarios

The algorithm aimed to identify a set of planning units (hereafter "sites") that together would include 10% of the population of each species within each week. The input features of the prioritization algorithm were the weekly estimates of species' range or abundance across the Americas (Fig. 1). We randomized the order of the sites and then ran a prioritization algorithm that identified the minimum set of sites that together covered 10% of each feature, which is a target for red-listed species by the International Union for the Conservation of Nature (IUCN). The algorithm we used treated each site as independent, so randomizing the order did not affect the results. During weeks in which the species is more dispersed, a greater number of sites will be selected to meet the 10% criterion. For the prioritization, we used the "minimum set" algorithm within the *prioritizr* R package (Hanson et al. 2018) with the Gurobi optimizer (Gurobi Optimization and LLC 2018). The prioritizr package was based on the Marxan prioritization tool (Ball et al.

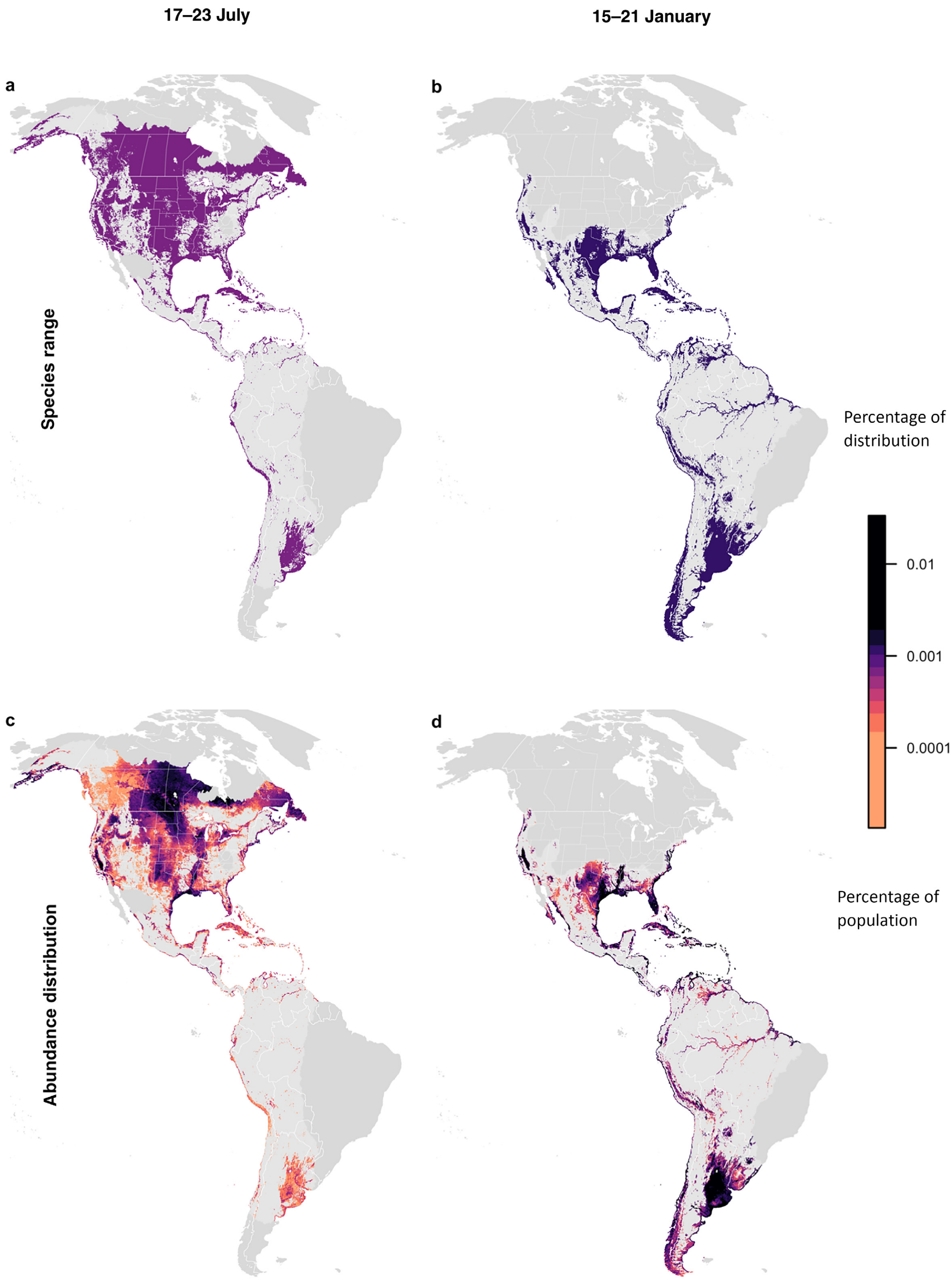

FIG. 1. Examples of weekly distributions of species range and abundance distributions used as features in the spatial prioritizations. The distributions shown are for Greater Yellowlegs *Tringa melanoleuca*. Estimated species ranges are depicted for (a) a single week in July and (b) a single week in January. As there is no information on relative abundance, percent of distribution is based on the number of sites in which the species occurs. The species is more dispersed during July, and so the average percent of distribution at each site is lower than in January. Estimated abundance distribution for (c) a single week in July and (d) a single week in January. The colors for the species ranges and abundance distributions represent the "percentage of population" within each site, and the total across all sites within each map is 100%.

2009). Our goal was to identify the sites that are most important for shorebirds, so we included a flat cost surface and we did not include current protected or designated areas. Although cost is an important factor in many prioritizations, here we were only identifying the most important shorebird sites, and the algorithm will select the smallest number of sites that meet the targets. The main focus of this analysis is the comparison between the different hypothetical scenarios, as buying the requisite number of sites at this hemispheric scale is not realistic.

We conducted separate spatial prioritizations with species' abundance distributions and with species' ranges. We converted the estimates of species' abundance to species' ranges, which had no distinction between sites of high or low abundance (Fig. 1). We conducted spatial prioritizations using species' ranges and abundance data with different temporal resolutions of the input data (Fig. 2). First, we ran prioritizations with weekly data (52 weeks), which resulted in 1,452 weekly features across the 41 species (Appendix S1: Fig. S1). Next, we ran prioritizations representing species data collected monthly (12 weeks), and quarterly (4 weeks), using a single weekly distribution to represent sampling at a given time point in the year (Fig. 2, Appendix S1: Fig. S1). These scenarios relate to the approaches outlined in the Comprehensive Monitoring Program for North American shorebirds that grew from long-term regional surveys that monitor birds during discrete periods rather than across the entire annual cycle (Howe et al. 2000). In total, we ran six prioritizations; three with species' ranges (quarterly, monthly, weekly) and three with abundance distributions (quarterly, monthly, weekly; Fig. 2). There is an important distinction between the prioritizations with ranges and abundance information; the sites selected from prioritizations with species' ranges will include 10% of the *distribution* of each species. The sites selected from prioritizations with abundance data will cover 10% of the *population* of each species (Fig. 1). In general, it is possible to set species-specific percentage targets or weights, however, in this case the algorithms targeted the same percentage for each species and were not weighted by species.

Comparing prioritizations

We compared the sites selected from the six prioritizations (species' ranges or abundance distributions, with quarterly, monthly, or weekly data). First, we examined the sites selected from each prioritization to understand whether they were in similar geographic areas. We wanted to understand how close the prioritizations with reduced information matched the prioritization with the maximum information (i.e., weekly abundance distributions). However, because nearby sites may be functionally similar for the shorebird community, even though the exact same site has not been selected, we aggregated the 8.4 km sites in the Americas into 100 × 100 km grid cells and calculated the proportion of sites selected within each larger grid cell. We used correlation coefficients to compare the proportions of sites selected within 100-km grid cells, between the prioritization with weekly abundance data and the other alternative prioritizations with reduced input information. These comparisons assessed the functional similarity of the prioritizations at a 100-km spatial scale.

Second, we assessed the estimated proportion of each population that would be protected, if the selected sites were all secured. Although this is an unrealistic outcome, it gives an indication of the potential efficacy of the prioritization methods. For example, a prioritization may be designed to include 10% of species' *ranges* with *monthly* distributions, and we assess how much of each *population* is included within those selected sites in each *week* of the year. Additionally, to compare how efficiently a set of selected sites would meet these targets for each species, we set the land area equal for each prioritization. The prioritization that used weekly abundance information included 10% of every population in each week and selected approximately 15,000 sites. For each alternative prioritization scenario, we rescaled the proportion of populations protected within each week, to the proportion that would be protected with 15,000 sites. We then examined the temporal patterns in coverage across the year and compared the prioritizations. When examining the patterns across all species, it is important to consider not only the average proportion of species protected, but also the variation amongst species and among weeks. A given prioritization may have a high average of populations protected, but this can obscure species or times of year that have particularly low proportions of their populations protected. To describe the temporal patterns of species' coverage, we modeled how the proportions protected varied throughout the year. The response variable was the proportion of each population included within the selected sites for each of 41 species within each week, so there was one data point for each species in each week. We used a Generalized Additive Model (GAM), and the predictor variable was a cyclic smooth on week of year with 12 degrees of freedom. This modeled how the proportion of populations included within selected sites varied throughout the year across all species. Rather than estimating the mean proportion, we wanted to understand the variation among species, so we modeled the 25th and 75th quantiles of the proportion of the population protected across all the species. The model therefore estimated the lower and upper quartiles of proportions of populations included in selected sites, enabling us to identify times of year where several species have particularly low or high estimates. We fitted these models in R package qgam (Fasiolo et al. 2018).

Third, we assessed species' temporal bottlenecks throughout the annual cycle. For each prioritization scenario, we estimated the week of the year in which the species had the minimum proportion of the population

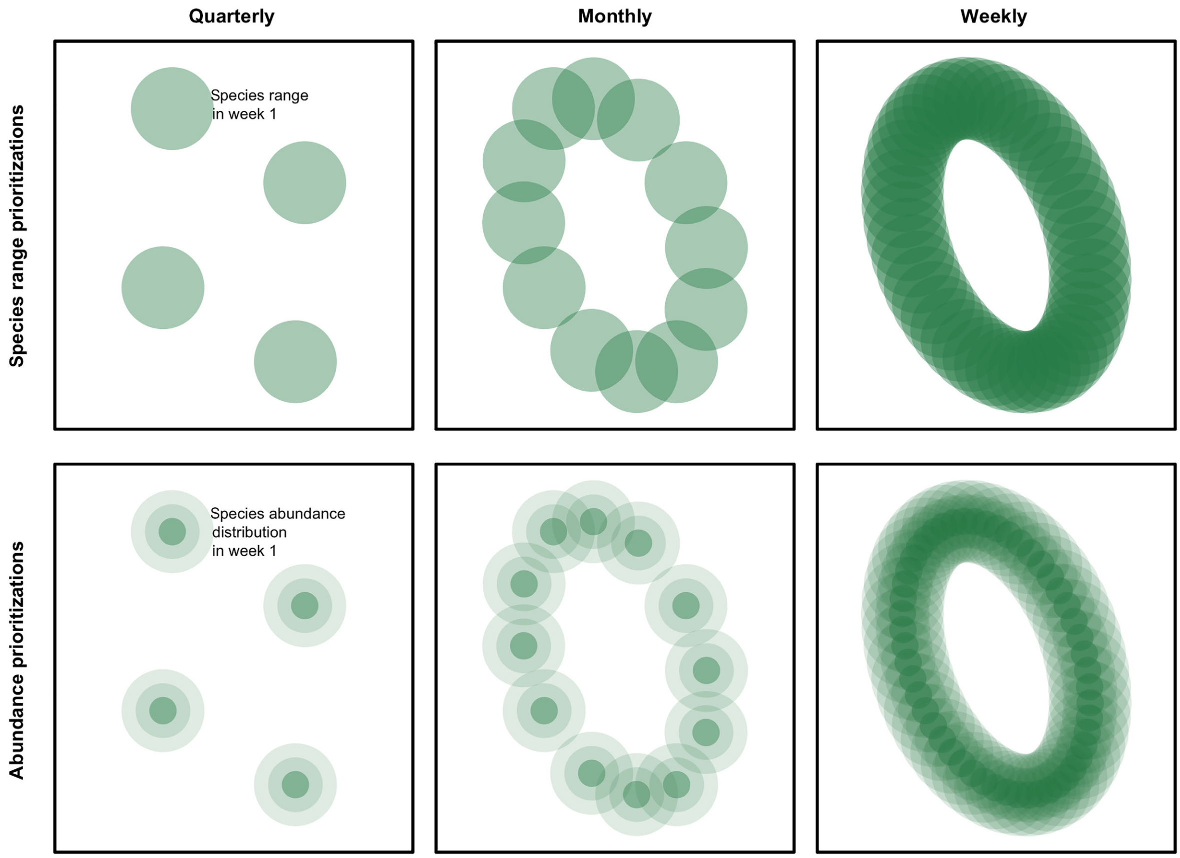

Fig. 2. Schematic diagram of the information in each of the six prioritizations for a single species. Each circle represents a species range or relative abundance distribution within a single week. The ellipse represents an annual migration of a population (taking different routes in pre-breeding and post-breeding migrations). Prioritizations with species ranges (top row) assume an even distribution of the population within each week. Prioritizations with relative abundance (lower row) contain information on variable abundance within the range. Prioritizations with 52 weeks (third column) require 10% of the range/population within each of the 52 weeks to be within the selected sites. Prioritizations with only four weeks (first column) generally select fewer sites as they only require 10% of the range/population within the four weeks to be within selected sites. This is a hypothetical example for a single species, but the real prioritizations include distribution information for all 41 shorebird species.

protected within selected sites. We compared these between prioritization scenarios. The prioritizations above targeted 10% of species' ranges or populations. We re-ran each of the six prioritization scenarios with different targets for each species: 5%, 15%, 20%, 30%, 40%, and 50%. We then estimated the proportion of the population that would be covered for each of these targets and with different input information.

Results

We modeled data from approximately 14 million eBird checklists and produced estimates of weekly abundance across the Americas for 41 shorebird species (Fig. 1). The prioritizations based on species' ranges required approximately twice as many sites and were more dispersed than abundance prioritizations (Fig. 3, Appendix S1: Fig. S3). Species were distributed unevenly throughout their range (Fig. 1), so covering 10% of the population required fewer sites than covering 10% of the range.

Prioritizations based on species' ranges identified divergent solutions depending on the temporal resolution of the data included (Figs. 3 and 4). At a 100-km scale, the species' range prioritizations had low agreement with the weekly abundance prioritization (all $r < 0.5$). A number of 100-km grid cells, which were identified as important with the abundance data prioritization (due to many 8.4-km sites selected within the 100-km grid cell), were "missed" using only the species' ranges (Fig. 4). Therefore, even at a large spatial scale, species' ranges did not identify important geographic areas with large proportions of populations.

Conversely, prioritizations with abundance data were more consistent, and importance values at the 100-km scale aligned particularly well between the monthly and weekly resolutions (Figs. 3 and 4). In other words, spatial prioritizations that used monthly abundance data selected geographically similar sites to those selected using weekly abundance data. Even with only quarterly abundance data, the landscape-scale prioritization was

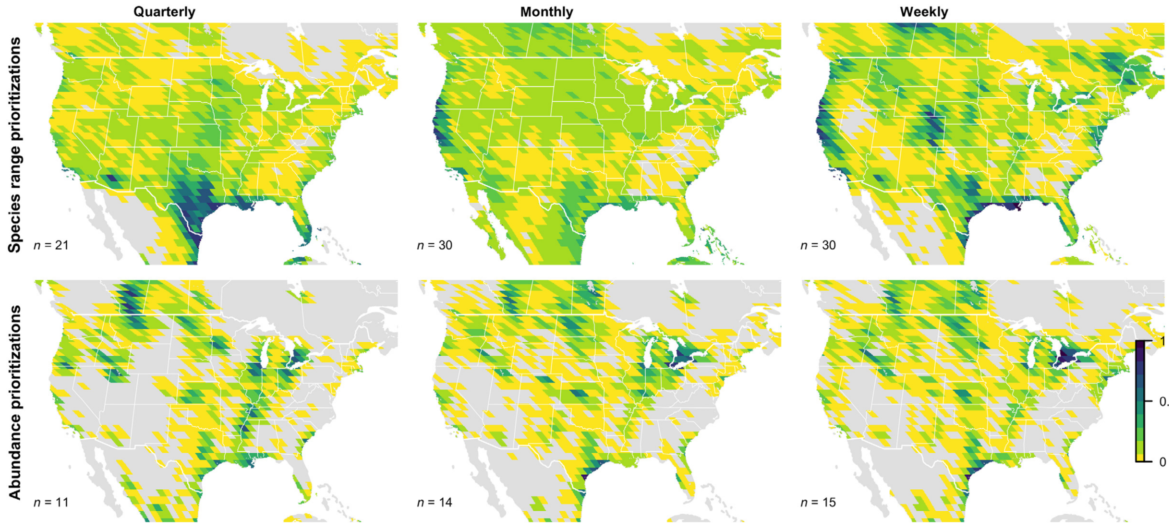

Fig. 3. Proportion of sites within 100 × 100 km squares that were selected for each of the six prioritizations. Sites were identified as a minimum set to protect 10% of each of 41 species of shorebirds, using distributions from different temporal resolutions: quarterly (left column), monthly (middle column), or weekly (right column). The *n* value indicates the number of 8.4 × 8.4 km sites (in thousands) that were selected for each prioritization. Species' range prioritizations were generally more dispersed and used approximately twice the number of sites compared with abundance prioritizations to achieve the 10% goal. We show the region that has the best coverage of species distributions and larger maps are shown in Fig. S3.

closer to weekly abundance prioritization than when using weekly species' ranges (Fig. 3). Therefore, even when temporal coverage is poor, solutions based on abundance outperformed those derived from species' ranges with high temporal resolution.

Prioritizations based on abundance data most consistently protected similar proportions of populations across time and among species (Fig. 5). In contrast, prioritizations based on species' ranges were highly variable in the proportions of populations protected and often failed to achieve the 10% target. The prioritizations with only quarterly data protected the smallest proportions of populations, potentially resulting in temporal bottlenecks during the breeding season (Fig. 5). Monthly abundance data met 98% of the targets met by weekly abundance data, with 1,420 of the 1,452 weekly species' features meeting the 10% protection target. Overall, abundance data at high temporal resolution produced solutions that were most consistent in protecting at least 10% of populations, across the multiple axes of species, space, and time.

The minimum proportion of a population protected throughout the year, is an indication of any temporal bottlenecks that might be experienced by a species. The prioritization that used only quarterly species' ranges (which most closely aligns with the conventional data inputs for spatial conservation planning) would need to select sites that cover more than 40% of species' ranges, in order to protect just 10% of each population throughout the full annual cycle (Fig. 6). Furthermore, these prioritizations would require at least seven times more sites than a prioritization based on weekly abundance distributions. Overall, prioritizations based on species' ranges may leave populations vulnerable at some times in their annual cycle.

Discussion

Effective conservation relies on the ability to make informed decisions about when and where to invest limited resources, but for many taxa we lack sufficient information about population dynamics throughout the full annual cycle. In this example, spatial conservation plans performed best when based on estimates of species' abundance at a high temporal resolution. Indeed, the most robust and consistent solutions for protecting 10% of the populations in this community were achieved when prioritization algorithms used abundance data at a monthly or weekly resolution. Our assessment showed that in the absence of this ideal information, abundance information at lower temporal resolution was more valuable than species' ranges at high temporal resolution.

Previously Runge et al. (2016) found that single static distributions did not provide a good representation of the movements of nomadic species. Our results demonstrate that, when using abundance data, a monthly temporal resolution hit 98% of the weekly targets and therefore provided almost as efficient a conservation strategy as the weekly temporal resolution. In contrast, species' protection across the full annual cycle is likely to be compromised when using a temporal resolution with four or fewer estimated distributions a year. These results provide empirical evidence for the intuitive assertion that effective conservation of migratory species

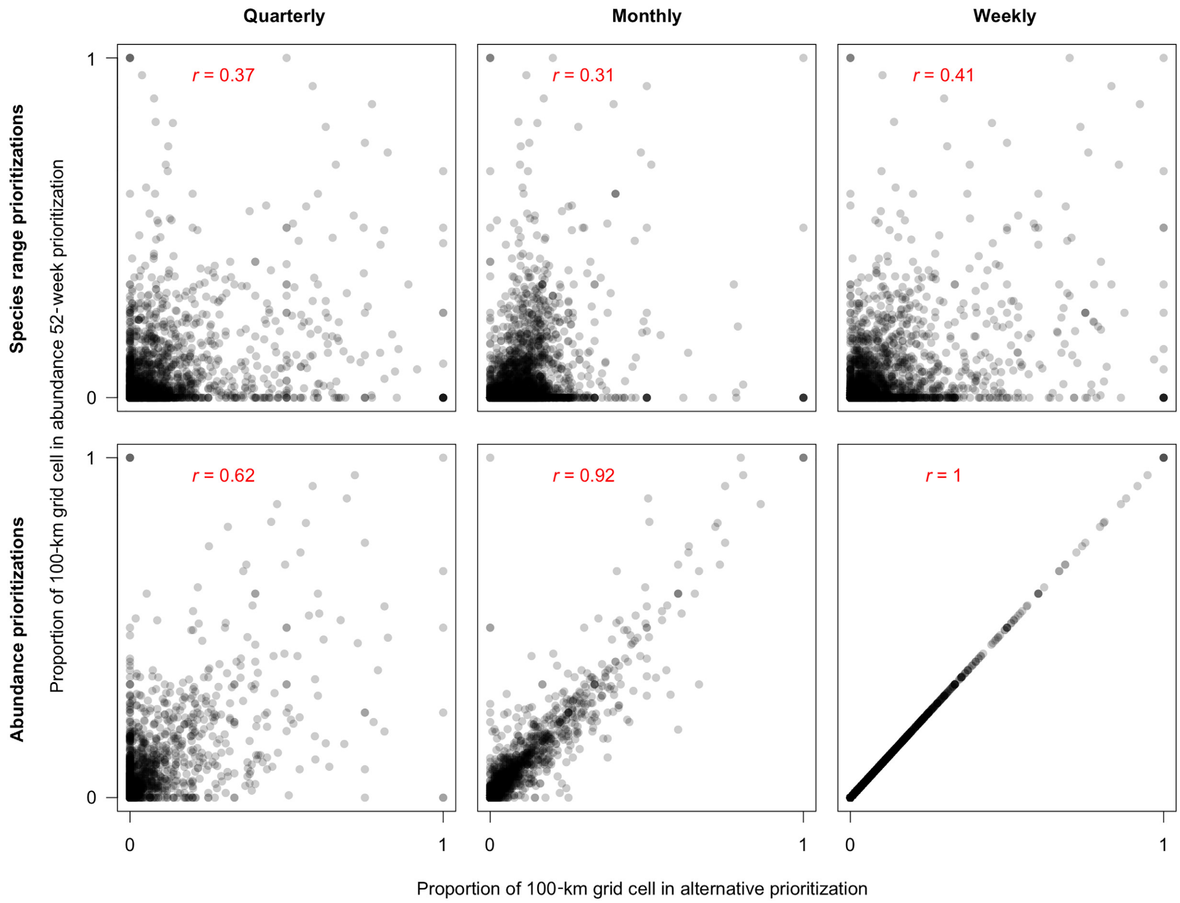

Fig. 4. Correlations between the proportion of selected sites within 100-km grid cells for the abundance prioritizations with 52 weeks and all other prioritizations across the Americas. A stronger correlation value indicates that a given prioritization (on the *x*-axis) is functionally more similar to the prioritization based on with 52 weeks of abundance data. Pearson correlation coefficients are shown in red. There are n = 3,274 points within each panel, each representing a single 100-km grid cell that has a non-zero proportion of the grid cell selected in at least one of the six prioritizations.

needs to be informed by data on their spatial and temporal population dynamics throughout the annual cycle (Martin et al. 2007, Sheehy et al. 2011, Runge et al. 2014, Schuster et al. 2019).

Compared to plans that incorporated species' abundance, those using species' ranges alone gave rise to population protection that was more variable among species and across time, and importantly, had a much greater spatial footprint. Abundance information enabled the prioritization to target sites that have a high number of individuals, making the selected sites more efficient for conservation. Previous studies at smaller scales have found that probability of occurrence does not identify sites of highest abundance (Johnston et al. 2015, Veloz et al. 2015, Acevedo et al. 2017). In addition to higher efficacy, prioritization using abundance data was more robust to lower temporal resolution of monthly distributions throughout the annual cycle. Our results therefore demonstrate the value of broad-scale information on species' abundance for spatial conservation planning.

Despite the high value of abundance information for conservation, few species have sufficient data from formal surveys to estimate their relative abundance across large spatial and temporal domains. Here, we demonstrate the use of eBird to estimate relative abundance for a large number of species at high spatial and temporal resolutions. The advantages of these data are that they are available across large extents and for the entire year. Citizen science data can be highly variable, although analytical methods can account for much of this variation (Johnston et al. 2018, 2019, Kelling et al. 2019). Although citizen science data may be spatially biased and or data deficient for particular places (e.g., the Arctic for breeding shorebirds), in some cases, this shortfall could be addressed by combining citizen science data with more formal surveys (Skagen et al. 2003). More generally, we expect that the accuracy of the estimated distributions will vary spatially and temporally, due to volume of data and changing environmental requirements of populations. Citizen science data are also

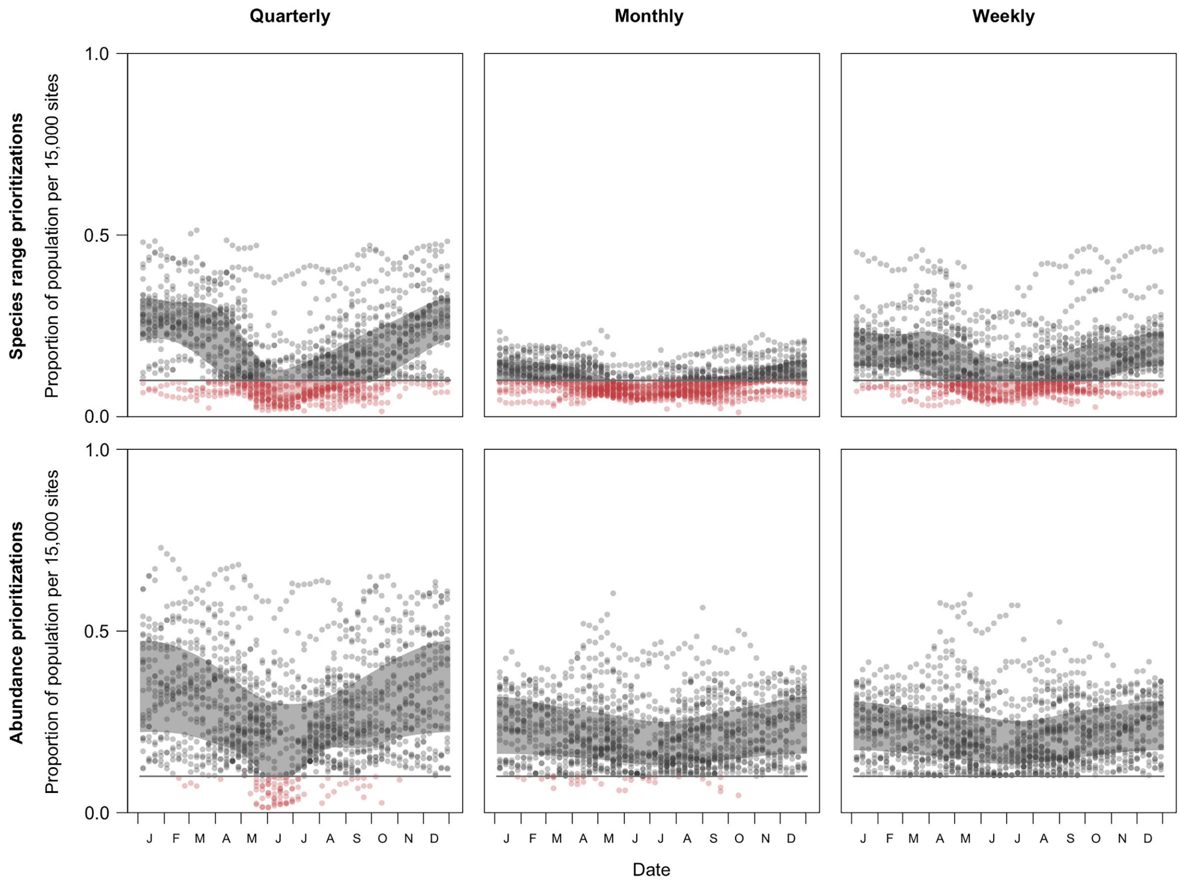

FIG. 5. Proportion of weekly shorebird populations within sites identified in each prioritization, averaged per 15,000 sites. Each dot represents the estimated proportion of a given species that is within the prioritized sites, for a given week. Dots are gray when at least 0.1 of the population is protected and red otherwise. Species–week combinations with poor coverage of the population are eliminated. The gray-shaded regions denote the area between the modeled 25th and 75th quantiles. The thin gray horizontal lines show the threshold for 0.10 of the populations. There are 1,452 data points on each panel, each point representing the estimated proportion of population covered within prioritized sites for a single species in a single week.

taxonomically biased and currently birds are likely the only taxon with sufficient data to provide robust, estimates of relative abundance across large spatial scales and for many species (Sullivan et al. 2014, Fink et al., *in press*). Overall citizen science data provide untapped opportunities to generate estimates of relative abundance and improve spatial conservation planning for many terrestrial bird species.

There are several assumptions inherent in the analyses presented here and we highlight the lack of information on connectivity or cost in these prioritizations. First, we did not consider connectivity between sites or different parts of the population, which can be an important aspect of spatial conservation planning for migratory species (Moilanen and Moilanen 2005, Martin et al. 2007, Linke et al. 2012, Iwamura et al. 2013, Runge et al. 2014, Hewson et al. 2016, Brown et al. 2017, D'Aloia et al. 2017, Dhanjal-Adams et al. 2017). There are quantitative strategies for incorporating connectivity into spatial prioritizations (Beger et al. 2010*a*, *b*, Daigle et al. 2018), and these strategies have been used in some marine and freshwater prioritizations (Hermoso et al. 2011, Linke et al. 2012, Magris et al. 2014, 2018, Schill et al. 2015). However, for most bird species, information on connectivity is not available, so the analysis presented here aligns with the level of information most often used for conservation planning. The increasing volume of tagging data will likely transform this knowledge gap in the future, but for a large suite of species, connectivity is currently not known, although it can be approximated by spatial clustering (Schuster et al. 2019). Second, though we recognize that cost can profoundly affect implementation, our assessment used land area as the principle cost and instead focused on ecological inputs. Variability in the cost of protecting different sites and the presence of existing protected areas can be included in future prioritizations.

Here, we adapted conventional spatial conservation planning, which identifies a static network of sites, to accommodate highly dynamic populations throughout

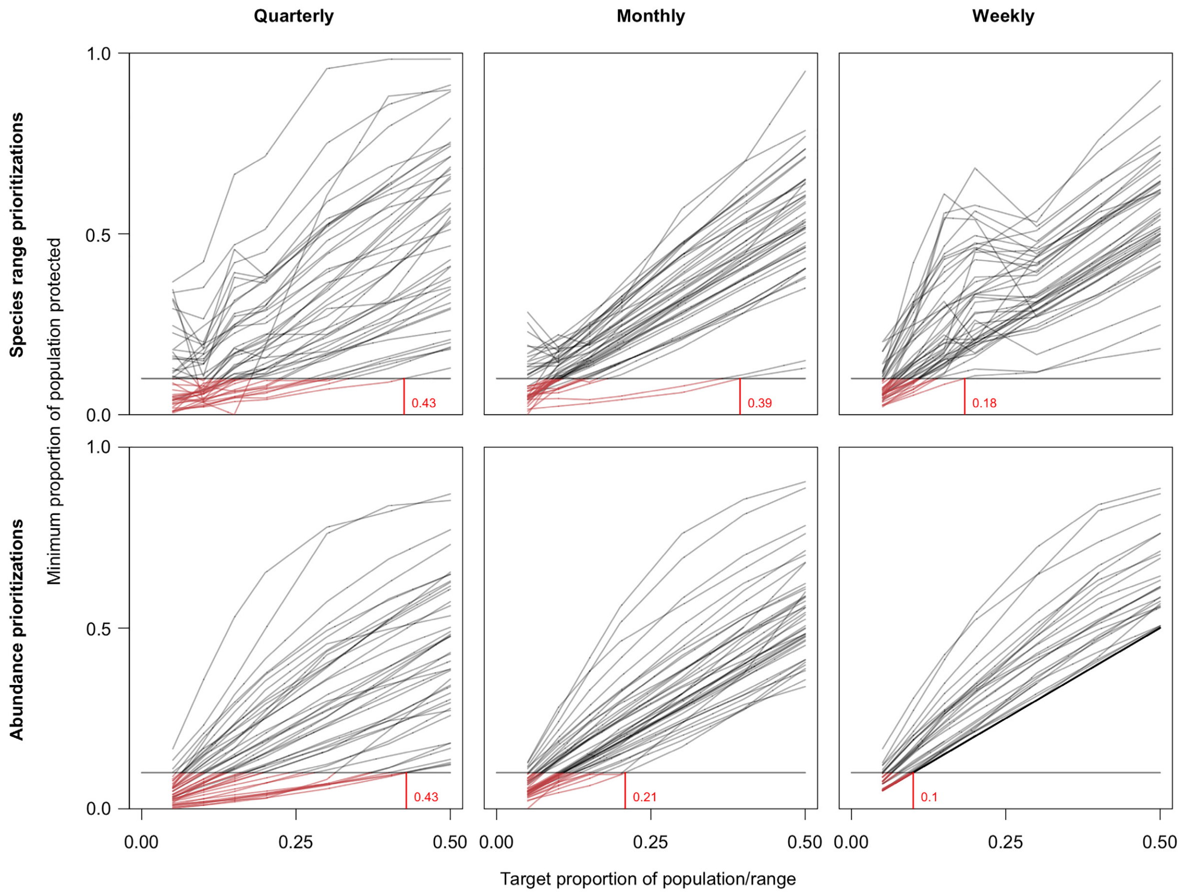

FIG. 6. The estimated minimum proportion of each species protected throughout the full annual cycle. Each species is represented by a line that indicates how the minimum proportion of the population protected changes as the targets for the prioritizations increase from 0.1 to 0.5. Red parts of the lines indicate where less than 0.1 of a species is protected for part of the year and indicates temporal bottlenecks for each species. The lines indicate how the proportion of that species protected increases with a prioritization based on increasing proportion of the range or proportion of the population (abundance). The horizontal gray line is the target of 0.1 of each species. The vertical red line shows the point at which at least 0.1 of all species are protected, and the red number shows the target proportion required in the prioritization to protect all species at this level.

their full annual cycle. Our approach also contributes to the emerging field of dynamic conservation planning, which is based on the premise that some aspects of conservation can be achieved by protecting areas for limited periods of the year without the need to permanently protect specific sites (Johnston et al. 2015, Haupt et al. 2017, Reynolds et al. 2017, Hazen et al. 2018). This approach is most effective for species and populations that follow highly repeatable migratory journeys each year. However, many species are likely to have populations that adapt their spatiotemporal dynamics to local conditions and this can present additional challenges for traditional conservation strategies (Skagen et al. 2005, Runge and Tulloch 2017). For species that track ephemeral resources, data can be aggregated across several years to capture the range of sites used over time (Runge and Tulloch 2017).

Spatial conservation planning for migratory species is a major challenge, given the highly dynamic nature of their populations across space and time. Abundance data are highly valuable for spatial conservation planning, enabling more efficient prioritizations that target sites with more individuals. Abundance data enable prioritizations that have more consistent coverage across species and throughout the full annual cycle, reducing temporal bottlenecks in species' protection. Our results highlight that abundance information is critical for efficient spatial prioritization strategies to conserve migratory species' populations. Conversely, we also demonstrate that spatial conservation planning with seasonal species' ranges may select sites that are inefficient or ineffective at conserving populations. Conservation decisions should be informed by the best information available in order to invest limited resources in the places where they will have the biggest impact. However, all data and models that contribute to conservation planning have assumptions and uncertainty associated with them, and it is important to understand and acknowledge the limitations of each source of information. Understanding the value of full annual cycle abundance data can guide future data collection, analysis, and interpretation of conservation plans derived from this information, leading to more efficient conservation strategies for migratory species.

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Literature Cited

Acevedo, P., J. Ferreres, M. A. Escudero, J. Jimenez, M. Boadella, and J. Marco. 2017. Population dynamics affect the capacity of species distribution models to predict species abundance on a local scale. Diversity & Distributions 23:1008–1017.

Aharon-Rotman, Y., S. Bauer, and M. Klaassen. 2016. A chain is as strong as its weakest link: assessing the consequences of habitat loss and degradation in a long-distance migratory shorebird. EMU—Austral Ornithology 116:199–207.

Arponen, A., J. Lehtomäki, J. Leppänen, E. Tomppo, and A. Moilanen. 2012. Effects of connectivity and spatial resolution of analyses on conservation prioritization across large extents. Conservation Biology 26:294–304.

Auer, T., D. Fink, and M. Strimas-Mackey. 2019. ebirdst: Tools for loading, plotting, mapping and analysis of eBird Status and Trends data products. https://cornelllabofornithology.github.io/ebirdst/reference/ebirdst.html

Baker, D. J., S. T. Garnett, J. O'Connor, G. Ehmke, R. H. Clarke, J. C. Z. Woinarski, and M. A. McGeoch. 2018. Conserving the abundance of nonthreatened species. Conservation Biology 33:319–328.

Ball, I. R., H. P. Possingham, and M. Watts. 2009. Marxan and relatives: software for spatial conservation prioritisation. Pages 185–195 *in* A. Moilanen, K. A. Wilson, and H. P. Possingham, editors. Spatial conservation prioritisation: quantitative methods and computational tools Oxford University Press, New York, New York, USA.

Beger, M., H. S. Grantham, R. L. Pressey, K. A. Wilson, E. L. Peterson, D. Dorfman, P. J. Mumby, R. Lourival, D. R. Brumbaugh, and H. P. Possingham. 2010*a*. Conservation planning for connectivity across marine, freshwater, and terrestrial realms. Biological Conservation 143:565–575.

Beger, M., S. Linke, M. Watts, E. Game, E. Treml, I. Ball, and H. P. Possingham. 2010*b*. Incorporating asymmetric connectivity into spatial decision making for conservation. Conservation Letters 3:359–368.

Boere, G. C., C. A. Galbraith, and D. A. Stroud. 2006. Waterbirds around the world: a global overview of the conservation, management and research of the world's waterbird flyways. The Stationery Office, Edinburgh, UK.

Brown, S., et al. 2017. Migratory connectivity of semipalmated sandpipers and implications for conservation. Condor 119:207–224.

Buechley, E. R., et al. 2018. Identifying critical migratory bottlenecks and high-use areas for an endangered migratory soaring bird across three continents. Journal of Avian Biology 49:e01629.

Daigle, R. M., A. Metaxas, A. Balbar, J. McGowan, E. A. Treml, C. D. Kuempel, H. P. Possingham, and M. Beger. 2018. Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect. BioRxiv 315424.

Dallas, T., R. R. Decker, and A. Hastings. 2017. Species are not most abundant in the centre of their geographic range or climatic niche. Ecology Letters 20:1526–1533.

D'Aloia, C. C., R. M. Daigle, I. M. Côté, J. M. R. Curtis, F. Guichard, and M.-J. Fortin. 2017. A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas. Biological Conservation 216:93–100.

Dhanjal-Adams, K. L., M. Klaassen, S. Nicol, H. P. Possingham, I. Chadès, and R. A. Fuller. 2017. Setting conservation priorities for migratory networks under uncertainty. Conservation Biology 31:646–656.

Dias, M. P., et al. 2017. Using globally threatened pelagic birds to identify priority sites for marine conservation in the South Atlantic Ocean. Biological Conservation 211:76–84.

Fahse, L., W. R. J. Dean, and C. Wissel. 1998. Modelling the size and distribution of protected areas for nomadic birds: Alaudidae in the Nama-Karoo, South Africa. Biological Conservation 85:105–112.

Fasiolo, M., Y. Goude, R. Nedellec, and S. N. Wood. 2018. Fast calibrated additive quantile regression. arXiv:1707.03307.

Fink, D., W. M. Hochachka, B. Zuckerberg, D. W. Winkler, B. Shaby, M. A. Munson, G. J. Hooker, M. Riedewald, D. Sheldon, and S. Kelling. 2010. Spatiotemporal exploratory models for large-scale survey data. Ecological Applications 20:2131–2147.

Fink, D., T. Damoulas, and J. Dave. 2013. Adaptive spatio-temporal exploratory models: hemisphere-wide distributions from massively crowdsourced eBird data. In: TwentySeventh AAAI Conference on Artificial Intelligence (AAAI-13) July 14–18. Bellevue, Washington, USA.

Fink, D., M. T. Auer, A. Johnston, V. Ruiz-Gutierrez, W. M. Hochachka, and S. Kelling. *In press*. Modeling avian full annual cycle distribution and population trends with citizen science data. Ecological Applications. https://doi.org/10.1002/eap.2056

Gurobi Optimization and LLC. 2018. gurobi: Gurobi Optimizer 8.0 interface. R package version 8.0-1. http://www.gurobi.com

Hanson, J. O., R. Schuster, N. Morrell, M. Strimas-Mackay, M. E. Watts, P. Arcese, J. Bennett, and H. P. Possingham. 2018. prioritizr: Systematic conservation prioritization in R. https://CRAN.R-project.org/package=prioritizr

Haupt, P. W., A. T. Lombard, P. S. Goodman, and J. M. Harris. 2017. Accounting for spatiotemporal dynamics in conservation planning for coastal fish in KwaZulu-Natal, South Africa. Biological Conservation 209:289–303.

Hazen, E. L., et al. 2018. A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. Science Advances 4:eaar3001.

Hermoso, V., S. Linke, J. Prenda, and H. P. Possingham. 2011. Addressing longitudinal connectivity in the systematic conservation planning of fresh waters. Freshwater Biology 56:57–70.

Hewson, C. M., K. Thorup, J. W. Pearce-Higgins, and P. W. Atkinson. 2016. Population decline is linked to migration route in the Common Cuckoo. Nature Communications 7:12296.

Howe, M., J. Bart, S. Brown, C. Elphick, R. Gill, B. Harrington, C. Hickey, G. Morrison, S. Skagen, and N. Warnock. 2000. A comprehensive monitoring program for North American shorebirds. Manomet Center for Conservation Sciences. http://www.Manomet.org/USSCP/files.htm

Iwamura, T., H. P. Possingham, I. Chadès, C. Minton, N. J. Murray, D. I. Rogers, E. A. Treml, and R. A. Fuller. 2013. Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. Proceedings of the Royal Society B 280:20130325.

Johnston, A., D. Fink, M. D. Reynolds, W. M. Hochachka, B. L. Sullivan, N. E. Bruns, E. Hallstein, M. Merrifield, S. Matsumoto, and S. Kelling. 2015. Abundance models improve spatial and temporal prioritization of conservation resources. Ecological Applications 225:1749–1756.

Johnston, A., D. Fink, W. M. Hochachka, and S. Kelling. 2018. Estimates of observer expertise improve species distributions from citizen science data. Methods in Ecology and Evolution/British Ecological Society 9:88–97.

Johnston, A., W. M. Hochachka, M. E. Strimas-Mackey, V. Ruiz Gutierrez, O. J. Robinson, E. T. Miller, T. Auer, S. T. Kelling, and D. Fink. 2019. Best practices for making reliable inferences from citizen science data: case study using eBird to estimate species distributions. bioRxiv 574392.

Kelling, S., D. Fink, F. A. La Sorte, A. Johnston, N. E. Bruns, and W. M. Hochachka. 2015. Taking a “Big Data” approach to data quality in a citizen science project. Ambio 44:601–611.

Kelling, S., et al. 2019. Using semistructured surveys to improve citizen science data for monitoring biodiversity. BioScience 69:170–179.

Klaassen, M., S. Bauer, J. Madsen, and H. Possingham. 2008. Optimal management of a goose flyway: migrant management at minimum cost. Journal of Applied Ecology 45:1446–1452.

Le Louarn, M., P. Clergeau, D. Strubbe, and M. Deschamps-Cottin. 2018. Dynamic species distribution models reveal spatiotemporal habitat shifts in native range-expanding versus non-native invasive birds in an urban area. Journal of Avian Biology 49:jav–01527.

Linke, S., M. J. Kennard, V. Hermoso, J. D. Olden, J. Stein, and B. J. Pusey. 2012. Merging connectivity rules and large-scale condition assessment improves conservation adequacy in river systems. Journal of Applied Ecology 49:1036–1045.

Lisson, A., K. H. Taffs, and L. Christidis. 2017. Mapping foraging habitat for migratory shorebirds in their Australian nonbreeding grounds and prioritising sites for conservation and management. Pacific Conservation Biology 23:32–42.

Lovejoy, T. E., M. Sallaberry, S. E. Senner, and A. Tarak. 1987. Conservation strategy for migratory species. American Scientist 75:1926.

Magris, R. A., R. L. Pressey, R. Weeks, and N. C. Ban. 2014. Integrating connectivity and climate change into marine conservation planning. Biological Conservation 170:207–221.

Magris, R. A., M. Andrello, R. L. Pressey, D. Mouillot, A. Dalongeville, M. N. Jacobi and S. Manel. 2018. Biologically representative and well-connected marine reserves enhance biodiversity persistence in conservation planning. Conservation Letters 11:e12439.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. A call for full annual cycle research in animal ecology. Biology Letters 11:20150552.

Martin, T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham, and D. R. Norris. 2007. Optimal conservation of migratory species. PLoS ONE 2:e751.

Massimino, D., A. Johnston, and J. W. Pearce-Higgins. 2015. The geographical range of British birds expands during 15 years of warming. Bird Study 62:523–534.

Moilanen, A. 2005. Reserve selection using nonlinear species distribution models. American Naturalist 165:695–706.

North American Bird Conservation Initiative. 2016. The state of North America’s Birds 2016. Environment and Climate Change Canada, Ottawa, Ontario, Canada.

Oberhauser, K., R. Wiederholt, J. E. Diffendorfer, D. Semmens, L. Ries, W. E. Thogmartin, L. Lopez-Hoffman, and B. Semmens. 2017. A trans-national monarch butterfly population model and implications for regional conservation priorities. Ecological Entomology 42:51–60.

Reynolds, M. D., et al. 2017. Dynamic conservation for migratory species. Science Advances 3:e1700707.

Robinson, O. J., V. Ruiz-Gutierrez, D. Fink, R. J. Meese, M. Holyoak, and E. G. Cooch. 2018. Using citizen science data in integrated population models to inform conservation decision-making. Biological Conservation 227:361–368.

Runge, C., and A. I. T. Tulloch. 2017. Solving problems of conservation inadequacy for nomadic birds. Australian Zoologist 39:280–295.

Runge, C. A., T. G. Martin, H. P. Possingham, S. G. Willis, and R. A. Fuller. 2014. Conserving mobile species. Frontiers in Ecology and the Environment 12:395–402.

Runge, C. A., J. E. M. Watson, S. H. M. Butchart, J. O. Hanson, H. P. Possingham, and R. A. Fuller. 2015. Protected areas and global conservation of migratory birds. Science 350:1255–1258.

Runge, C. A., A. I. T. Tulloch, H. P. Possingham, V. J. D. Tulloch, and R. A. Fuller. 2016. Incorporating dynamic distributions into spatial prioritization. Diversity and Distributions 22:332–343.

Schill, S. R., G. T. Raber, J. J. Roberts, E. A. Treml, J. Brenner, and P. N. Halpin. 2015. No reef is an island: integrating coral reef connectivity data into the design of regional-scale marine protected area networks. PLoS ONE 10:e0144199.

Schuster, R., S. Wilson, A. D. Rodewald, P. Arcese, D. Fink, T. Auer, and J. R. Bennett. 2019. Optimizing the conservation of migratory species over their full annual cycle. Nature Communications 10:1754.

Sheehy, J., C. M. Taylor, and D. R. Norris. 2011. The importance of stopover habitat for developing effective conservation strategies for migratory animals. Journal of Ornithology/DO-G 152:161–168.

Skagen, S. K., J. Bart, B. Andres, S. Brown, G. Donaldson, B. Harrington, V. Johnston, S. L. Jones, and R. I. G. Morrison. 2003. Monitoring the shorebirds of North America: towards a unified approach. Bulletin-Wader Study Group 100:102–104.

Skagen, S. K., S. Brown, and R. Johnson. 2005. Implications of different shorebird migration strategies for habitat conservation. Pages 680–683 *in* C. J. Ralph, and T. D. Rich, editors. Bird conservation implementation and integration in the Americas: Proceedings of the Third International Partners in Flight Conference. General Technical Report PSW-GTR-191. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Sullivan, B. L., et al. 2014. The eBird enterprise: an integrated approach to development and application of citizen science. Biological Conservation 169:31–40.

Sullivan, B. L., et al. 2017. Using open access observational data for conservation action: a case study for birds. Biological Conservation 208:5–14.

Tulloch, A. I. T., P. Sutcliffe, I. Naujokaitis-Lewis, R. Tingley, L. Brotons, K. M. P. M. B. Ferraz, H. P. Possingham, A. Guisan, and J. R. Rhodes. 2016. Conservation planners tend to ignore improved accuracy of modelled species distributions to focus on multiple threats and ecological processes. Biological Conservation 199:157–171.

Veloz, S., L. Salas, B. Altman, J. Alexander, D. Jongsomjit, N. Elliott, and G. Ballard. 2015. Improving effectiveness of systematic conservation planning with density data. Conservation Biology 29:1217–1227.

Walther, B., and L. Pirsig. 2017. Determining conservation priority areas for Palearctic passerine migrant birds in sub-Saharan Africa. Avian Conservation and Ecology 12:2.

Weeks, R. 2017. Incorporating seascape connectivity in conservation prioritisation. PLoS ONE 12:e0182396.

Xia, S., X. Yu, S. Millington, Y. Liu, Y. Jia, L. Wang, X. Hou, and L. Jiang. 2017. Identifying priority sites and gaps for the conservation of migratory waterbirds in China's coastal wetlands. Biological Conservation 210:72–82.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2058/full

Data Availability

The data used to conduct the study are freely available on the eBird website https://ebird.org/science/download-ebird-data-products; the data version used in this study was the eBird Reference Dataset from 2016, using checklists within the Western Hemisphere from 1 January 2004 to 31 December 2016. Further details of checklists used for the analysis are provided in Appendix S1. Visualizations of weekly species' relative abundance are available to view on the eBird website: https://ebird.org/science/status-and-trends. Raster files of weekly species' relative abundance are available for download with the R package *ebirdst* (Auer et al. 2019).