Contributed Paper

Improving effectiveness of systematic conservation planning with density data

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Abstract: *Systematic conservation planning aims to design networks of protected areas that meet conservation goals across large landscapes. The optimal design of these conservation networks is most frequently based on the modeled habitat suitability or probability of occurrence of species, despite evidence that model predictions may not be highly correlated with species density. We hypothesized that conservation networks designed using species density distributions more efficiently conserve populations of all species considered than networks designed using probability of occurrence models. To test this hypothesis, we used the Zonation conservation prioritization algorithm to evaluate conservation network designs based on probability of occurrence versus density models for 26 land bird species in the U.S. Pacific Northwest. We assessed the efficacy of each conservation network based on predicted species densities and predicted species diversity. High-density model Zonation rankings protected more individuals per species when networks protected the highest priority 10-40% of the landscape. Compared with density-based models, the occurrence-based models protected more individuals in the lowest 50% priority areas of the landscape. The 2 approaches conserved species diversity in similar ways: predicted diversity was higher in higher priority locations in both conservation networks. We conclude that both density and probability of occurrence models can be useful for setting conservation priorities but that density-based models are best suited for identifying the highest priority areas. Developing methods to aggregate species count data from unrelated monitoring efforts and making these data widely available through ecoinformatics portals such as the Avian Knowledge Network will enable species count data to be more widely incorporated into systematic conservation planning efforts.*

Keywords: conservation prioritization, species distribution models, species diversity, systematic conservation planning, zonation

Mejoría de la Efectividad de la Planeación Sistemática de la Conservación con Datos de Densidad

Resumen: *La planeación sistemática de la conservación tiene como meta diseñar redes de áreas protegidas que cumplan con objetivos de conservación a lo largo de grandes paisajes. El diseño óptimo de estas redes de conservación se basa con mayor frecuencia en modelos de idoneidad de hábitat o probabilidad de ocurrencia de especies, a pesar de la evidencia existente de que las predicciones de esos modelos pueden no estar fuertemente correlacionadas con la densidad de especies. Hipotetizamos que las redes de conservación diseñadas con las distribuciones de la densidad de especies conservan con mayor eficiencia a las poblaciones de todas las especies consideradas que las redes diseñadas con modelos de probabilidad de occurencia. Para probar esta hipótesis usamos el algoritmo Zonation de planeación de la conservación para evaluar los diseños de redes de conservación basados en la probabilidad de ocurrencia versus los modelos de densidad para 26 especies de aves terrestres en el noroeste del Pacífico en los Estados Unidos. Evaluamos la efectividad de cada red de conservación con base en las densidades pronosticadas de cada especie y la diversidad de especies pronosticada. Las clasificaciones de Zonation de los modelos de alta densidad protegieron a más individuos por especie cuando las redes protegieron el 10-40% de la más alta prioridad del paisaje. Comparado con los modelos basados en la densidad, los modelos basados en la ocurrencia protegieron a más individuos en*

el 50% más bajo de las áreas prioritarias de los paisajes. Las dos estrategias conservaron la diversidad de especies de formas similares: la diversidad pronosticada fue más alta en las localidades de alta prioridad en ambas redes de conservación. Concluimos que tanto los modelos de densidad como los de probabilidad de ocurrencia pueden ser útiles para establecer prioridades de conservación, pero que los modelos basados en la densidad son más adecuados para identificar las áreas de más alta prioridad. Desarrollar métodos para agregar datos de conteos de especies a partir de esfuerzos de monitoreo no relacionados y hacer que estos datos estén disponibles en portales eco-informáticos como la Avian Knowledge Network permitirá que los datos de conteos de especies se incorporen más ampliamente en esfuerzos de planeación sistemática de la conservación.

Palabras Clave: diversidad de especies, modelos de distribución de especies, planeación sistemática de la conservación, priorización de la conservación, zonación

Introduction

Systematic conservation planning has arisen as an effective approach for designing conservation networks and setting spatial conservation priorities across large landscapes (Margules & Pressey 2000). The approach provides a transparent methodology for using existing biodiversity and environmental data to identify locations that are of high conservation priority based on biodiversity or other stakeholder priorities (Kukkala & Moilanen 2013). An important step in the systematic conservation planning process is to collect data on biodiversity features such as species and their habitats that occur within the planning area. Unfortunately, comprehensive biodiversity surveys are rarely conducted at large spatial scales (e.g., ecoregional).

To cope with this problem, systematic conservation planning typically relies on models to infer the distributions of species of interest in unsurveyed portions of the landscape (Ferrier et al. 2002). This approach provides a robust way to use existing and often eclectic collections of species data, such as from museum collections or citizen science programs, to predict distributions across large landscapes (Elith & Leathwick 2009). Although there are known limitations to the approach (Elith et al. 2010; Franklin 2010; Veloz et al. 2012), many studies show the high predictive accuracy of species distribution models (Elith et al. 2006; Dobrowski et al. 2009; Elith & Graham 2009).

Relatively few studies use count data to model species density distributions. Although some models based on presence-absence data can identify the upper limit on species abundance (VanDerWal et al. 2009), other models show weak correlations between species probability of occurrence and species abundance, suggesting that substantially different processes may determine the distribution and abundance of species (Nielsen et al. 2005; Stewart-Koster et al. 2013). In particular, information loss from presence-absence data increases as pixel size increases, but this is not necessarily the case with count data (Aarts et al. 2012). Using areas estimated to have high suitability to predict areas of high abundance can result in overestimates of abundance

(Van Couwenberghe et al. 2013). Thus, reserve networks designed using models of habitat suitability or probability of occurrence may not optimally protect areas with the greatest number of individuals per species.

A lack of coordinated surveys that count individuals of species across large landscapes is probably the main limitation to development of species abundance or density models. Large-scale monitoring with standard-effort research techniques requires relatively large numbers of person hours of work. The alternative, an integration of multiple uncoordinated monitoring efforts, is hindered by the lack of proper curation of species monitoring data sets. Presence-absence modelers have been more successful at integrating data collected from different sources because more data are available thanks to large-scale citizen science projects (Greenwood 2007; Silvertown 2009; Hochachka et al. 2012) and because differences in data collection protocol matter less in determining presence or absence than in determining abundance (e.g., Thomas et al. 2001). Data from count surveys can be transformed to presence-absence data, but the converse is only possible under limited circumstances (e.g., Royle & Nichols 2003), resulting in greater availability of presence-absence data sets. Still, numerous smaller-scale surveys of species counts exist that may be aggregated into density estimates for large landscape models. As these data sets become increasingly available through the improvement of ecoinformatics databases and infrastructure (Michener & Jones 2012), we expect species density models will become more available for use in systematic conservation planning. Thus, we tested whether conservation networks designed based on count data are equivalent to networks designed based on presence-absence data to evaluate whether large investments in count surveys results in improved conservation outcomes.

We hypothesized that conservation networks designed using models constructed from count data provide more efficient protection of species populations than networks constructed using models of species probability of occurrence. Predictions from models of species probability of occurrence or suitability are likely to be positively correlated with predictions from models of species

density, but it is also possible that areas of high suitability may only support a few or no individuals of the target species because the realizations of those probabilities of occurrence may also include nonoccurrence. Thus, a conservation network designed using a suitability model may place undue weight on sites that support fewer numbers of individuals than if estimates of density were used to prioritize the network. We compared how well conservation networks designed using models of species probability of occurrence and using models of species density protect the largest proportions of the landscape-wide populations of 26 species of land birds in the U.S. Pacific Northwest. We used data from multiple, uncoordinated monitoring data sets aggregated and curated by the Avian Knowledge Network (AKN). We also evaluated the sensitivity of comparisons between the models as we altered the size of the conservation network and considered the differences in information content in occurrence versus density data and the consequences of using each type of data for conservation planning.

Methods

Avian Distribution and Density Data

We downloaded georeferenced point count data on the presence or absence and counts of 26 bird species in the states of California, Oregon, and Washington from the California Avian Data Center, a node of the AKN (http://data.prbo.org/multimap-v3/index.php). For each species, data from outside its breeding range or season were discarded. Breeding range was based on the Digital Distribution Maps of the Birds of the Western Hemisphere (version 3.0) (Ridgley et al. 2007). Breeding season window varied among species and ranged from a start date of 1 April to an end date of 15 August. These dates were based on information taken from the Birds of North America series and our expert opinions. We further filtered the avian data to those detections within 50 or 100 m of survey points. We produced individual estimates of density for both distance categories and multiplied the former by 4 to combine results with those of the latter. This ensured that all data were used, not just data conforming to either a 50- or 100-m cutoff distance. In all, we compiled 252,913 count records (i.e., with one or more individuals detected per count) from 96 different projects in which 38 variations of the basic point count protocol were used (Ralph et al. 1993). These were the result of 143,801 survey events sampling 19,407 points from 1992 to 2012.

Environmental Data

Our models of probability of occurrence and density were both based on climate and models of major vegetation types. We acquired contemporary climate data

to calibrate our vegetation and bird distribution models from the PRISM Climate Group (http://www.prism. oregonstate.edu/).

For models of vegetation (see below), we used bioclimatic variables frequently used in modeling exercises (Stralberg et al. 2009; Elith et al. 2011). We used the biovars function in the dismo package in R (Hijmans et al. 2012) to create 19 bioclimatic variables (http://www.worldclim.org/bioclim). We created a correlation matrix to examine the relationships between the bioclimatic variables. When variables were highly correlated with one another ($r \geq 0.8$), we retained the variable that was least correlated with the remaining layers, leaving us with 9 variables (Table 1). We also included a set of geophysical variables based on soil and topography (Table 1).

For our bird models, we selected climate covariates based on possible physiological tolerances. We hypothesized that 8 climate variables could constrain the distribution of birds during months when birds typically breed in the region (April–July). Variables were all summarized across the breeding season. After examining correlations between the predictor variables, we retained 3 variables to use in the bird models (Table 1). All environmental variables were resampled to a common spatial resolution of 0.00833 × 0.00833 decimal degrees (approximately 900 × 900 m within our study extent).

Vegetation Modeling

We modeled the potential distribution of 78 different vegetation types based on hybrid vegetation maps we created and current maps of climate, topographic, and soil characteristic variables. We created distribution models of vegetation types, rather than using the existing vegetation maps, because we needed to coarsen the spatial resolution of the vegetation map to match climate grids and to allow for multiple vegetation types to have a nonzero probability of occurring in each pixel. Furthermore, bird surveys were not conducted in all vegetation types, which required some adjustment to the vegetation maps to make predictions spatial (see below). We created a hybrid vegetation classification scheme derived from the GAP vegetation classification system (http://gapanalysis.usgs.gov/gaplandcover/). We initially considered all the vegetation classes that occur in Washington, Oregon, and California. When we had an adequate number of avian observation records in the finest GAP class (Ecological System), we modeled that class using current climate and geophysical variables. Otherwise, we used a lower resolution class in the classification hierarchy (lower classes based on the NVCS standards) (http://www.fgdc.gov/standards/projects/FGDC-standards-projects/vegetation/NVCS_V2_FINAL_2008-02.pdf/download [Supporting Information]).

To model the suitability of each vegetation class, we used boosted regression tree (BRT) models (Elith et al.

Table 1. Spatial covariate data used to construct vegetation and bird distribution models.

Vegetation models	Source
Geophysical variables	
sand fraction (5 cm)	USGS (U.S. Geological Survey) State Soil Geographic database (STATSGO)
silt fraction (5 cm)	STATSGO
clay fraction (5 cm)	STATSGO
soil porosity (5 cm)	STATSGO
soil ph (5 cm)	STATSGO
soil permeability (5 cm)	STATSGO
available water content (100 cm)	STATSGO
distance to perennial streams	USGS National hydrography data set
slope	USGS Global Multiresolution Terrain Elevation Data (2010)
solar radiation	USGS Global Multiresolution Terrain Elevation Data (2010)
Climate variables	
mean diurnal temperature range	PRISM Climate Group
temperature seasonality	PRISM Climate Group
mean temperature of the wettest quarter	PRISM Climate Group
mean temperature of the driest quarter	PRISM Climate Group
mean temperature of the coldest quarter	PRISM Climate Group
precipitation seasonality	PRISM Climate Group
precipitation of the wettest quarter	PRISM Climate Group
precipitation of the driest quarter	PRISM Climate Group
precipitation of the coldest quarter	PRISM Climate Group
Bird models	
vegetation (78 classes, individual layers)	USGS Gap Landcover database
mean monthly temperature (April–July)	PRISM Climate Group
temperature range (April–July)	PRISM Climate Group
total precipitation (April–July)	PRISM Climate Group

2008) and the climate and geophysical covariates (explained above) as predictors. We selected the optimal number of trees, tree complexity (TC), and learning rate (LR) following an optimization routine described in Elith et al. (2008). We standardized the results of the vegetation models by dividing the suitability for each class by the sum of the suitabilities for all vegetation classes in each pixel. In this way, the values for a given class at a pixel receive lower values if many classes have a high suitability. We did not attempt to determine which vegetation class would dominate a cell; rather, we retained the modeled suitability of all vegetation classes and thus allowed for multiple vegetation classes to give weight to the bird model prediction of each cell.

Bird Distribution Modeling

Using the bird data for our distribution and density models required that we estimate occupancy (Mackenzie et al. 2002) and determine the true density of bird species at survey points accounting for imperfect detection during field surveys (Supporting Information). Using the corrected presence-absence data from above, we fit an initial probability of occurrence BRT model (5000 trees, TC = 3, LR = 0.01) with a binomial (Bernoulli) link and all climate and vegetation variables. For each species, any variable with a relative influence <2% was removed as a possible predictor variable. We then subsampled the full data set to 5000 total records, matching the prevalence found in the total

data set (per species). We ran exploratory models with this subsample and the reduced set of variables. We tested a range of LRs (0.01, 0.005, 0.001) and TCs (1–5) and a maximum of 10,000 trees. Results were reviewed and optimal TC and LR were chosen for each species. Using all records, we ran final models with optimized settings and then projected the probability of occurrence model predictions across the study area landscape. We used a threshold based on the species prevalence in the survey data to convert the probability of occurrence maps to binary maps (0, absent; 1, present).

Density models were run using the vegetation variables, selected from the probability of occurrence models above, and all climate variables. We ran exploratory models with this subsample and the reduced set of variables in the same way as for the occurrence models, except that we used a Gaussian link to tune input BRT parameters. Results were reviewed and optimal TC and LR were chosen for each species. Using all records, final density models were run. Subsequently, we projected the density model predictions across the study area landscape and multiplied them by the binary probability of occurrence model, thereby converting to 0 those pixels where the species was not predicted to occur.

Prediction accuracy for both the probability of occurrence models and the density models were estimated using a 10-fold cross-validation. The data were partitioned into 10 groups and models were iteratively trained with data from 9 of the groups, and predictions were made to the 10th group of data withheld from model training.

For the probability of occurrence models, we calculated the area under the receiver operating characteristic curve (AUC) as an estimate of how well the model discriminates presence from absence. An AUC value of one equaled perfect discrimination and values of 0.5 equaled discrimination of presence from absence no better than random. For the density models we calculated R^2 based on observed versus predicted values.

Conservation Prioritization

We used the core-area Zonation algorithm in Zonation 3.10 (Moilanen et al. 2005) to prioritize the landscape for conservation protection. Zonation iteratively removes pixels from the landscape; at each iteration the pixels with the lowest values are removed. Value is based on the cell's contribution to the population or distribution of the species. Cells selected for removal contribute the least to a species remaining population or distribution. During each iteration, the algorithm seeks to maintain core areas for all species; thus, pixels are ranked by how important the pixel is for all species rather than by species richness (Moilanen 2007). The final output includes a map of the order of cell removal scaled from 0 to 1 representing the proportion of the landscape removed at the point the pixel was selected for removal. The model is hierarchical in that cell values of 0.8 and above represent the top 20% of the landscape, which includes cells that are ≥0.9 that represent the top 10% of the landscape. We ran 2 iterations of the Zonation algorithm, the first with the probability of occurrence models as inputs and the second with the density models as inputs. We selected the core-area algorithm because we were interested in conserving each of the species in the analysis and not as concerned with maximizing the diversity of each pixel in the landscape. We did not use species weightings or distribution smoothing.

The effectiveness of the 2 Zonation classifications was evaluated by estimating the total abundance of each species and the diversity of species protected in different Zonation classification rankings. For our comparisons, we assumed that the abundance models represented the true number of individuals for each species per pixel in the landscape. We also assumed that pixels with higher numbers of individuals for a species were of higher conservation value for that species. We evaluated each version of the Zonation analyses by summing the total number of individuals of each species predicted by the density models protected in all bins covering each 10% Zonation ranking (i.e., 0–0.09, bottom 10%; 0.9–1.0, top 10%). We also assessed the mean and SD of Shannon-Wiener diversity (*H*) of all the pixels in each Zonation rank bin to estimate average site-level diversity protected by the Zonation rankings. Additionally, we calculated a single value of *H* for each bin to represent the regional diversity protected in each Zonation rank bin. Regional diversity represented the diversity of all 26 species in the

entire Zonation rank bin, not just at a pixel level and would be the landscape diversity protected if all pixels in the bin were protected in a conservation network.

Results

Bird Distribution Models

Both the probability of occurrence and density models demonstrated relatively high predictive accuracy. We achieved excellent predictive accuracy with our probability of occurrence models; mean AUC was 0.987 (min 0.973, max 0.999) (Table 2). The mean R^2 from the density models was 0.527, but there was considerable variability in R^2 among species (range 0.176–0.785) (Table 2).

Zonation Models

Spatial ranking of the landscape differed substantially depending on whether probability of occurrence or density models were used for the Zonation analysis or whether density models were used (Fig. 1). The probability-of-occurrence-based Zonation analysis prioritized the Olympic National Park (coniferous forests in the northwest of the study extent) and the Willamette Ecoregion (north central portion of the study region) as of much higher conservation priority than the abundance-based Zonation analysis (Fig. 1). The highest rankings in the density-based analyses were more spatially dispersed (Fig. 1b), whereas 3 large clumps of high-priority cells were identified in the models based on probability of occurrence. Areas where the density-based Zonation analysis produced high rankings and the probability of occurrence Zonation analysis produced low rankings were distributed throughout the study region but were somewhat concentrated in the southwest (Fig. 1c) in the Klamath-Siskiyou Bioregion.

The difference in the number of individuals protected under the 2 Zonation ranking schemes was sensitive to the amount of the total landscape protected when individual Zonation rank bins were considered. For a majority of species, the density-based Zonation rankings protected more individuals in each of the 4 highest ranked bins (Fig. 2) than occurrence-based rankings. The number of individuals of each species protected in the 2 Zonation classifications differed the least in the 40–49% and 50–59% Zonation rank bins (Fig. 2). For most species, the probability-of-occurrence-based Zonation classification protected more individuals in the 4 lowest ranked bins (Fig. 2) than the density-based Zonation. In contrast to when individual Zonation rank bins were considered, differences in the performance of the 2 Zonation models were not sensitive to the total proportion of the landscape protected (Fig. 3). The probability-of-occurrence-based Zonation results consistently protected smaller

Table 2. Estimates of accuracy of landscape model prediction of probability of occurrence and density for 26 breeding bird species.

Scientific name	Common name	AUC[a]	R^{2b}	Cor[c]
Aphelocoma californica	Scrub Jay	0.996	0.448	0.823
Carpodacus purpureus	Purple Finch	0.992	0.630	0.684
Catharus ustulatus	Swainson's Thrush	0.991	0.592	0.693
Certhia americana	Brown Creeper	0.973	0.603	0.777
Contopus cooperi	Olive-Sided Flycatcher	0.983	0.573	0.814
Contopus sordidulus	Western Wood-Pewee	0.975	0.378	0.792
Setophaga occidentalis	Hermit Warbler	0.992	0.515	0.764
Setophaga petechia	Yellow Warbler	0.984	0.374	0.708
Setophaga townsendi	Townsend's Warbler	0.987	0.785	0.755
Empidonax difficilis	Pacific-slope Flycatcher	0.995	0.619	0.742
Empidonax traillii	Willow Flycatcher	0.991	0.458	0.702
Eremophila alpestris strigata	Streaked Horned Lark	0.992	0.373	0.583
Ixoreus naevius	Varied Thrush	0.998	0.676	0.720
Passerculus sandwichensis	Savannah Sparrow	0.999	0.176	0.762
Picoides pubescens	Downy Woodpecker	0.986	0.539	0.870
Picoides villosus	Hairy Woodpecker	0.987	0.642	0.798
Pooecetes gramineus affinis	Oregon Vesper Sparrow	0.996	0.527	0.711
Selasphorus rufus	Rufous Hummingbird	0.982	0.768	0.724
Sitta carolinensis	White-breasted Nuthatch	0.985	0.417	0.804
Spizella passerina	Chipping Sparrow	0.990	0.581	0.680
Sturnella neglecta	Western Meadowlark	0.994	0.357	0.623
Troglodytes aedon	House Wren	0.986	0.387	0.837
Troglodytes hiemalis	Winter Wren	0.991	0.560	0.774
Oreothlypis celata	Orange-Crowned Warbler	0.978	0.615	0.777
Vireo gilvus	Warbling Vireo	0.973	0.470	0.814
Cardellina pusilla	Wilson's Warbler	0.976	0.639	0.786

[a]*Area under the receiver operator characteristic curve. It measures how well probability of occurrence models discriminate observed presence from absence (1, perfect discrimination; 0.5, discrimination no better than random).*
[b]*Square of Pearson correlation coefficient. Provides relative goodness of fit.*
[c]*Pearson correlation coefficient between the predicted probability of occurrence and predicted density for each species.*

proportions of the populations of the 26 species modeled than the density-based Zonation results (Fig. 3).

Differences in *H* protected between the 2 Zonation rankings depended on whether diversity was measured at the pixel or across all pixels in each Zonation rank bin. Mean site-level (pixel) *H* was highest in the density-based Zonation in each of the top 2 Zonation rank bins (Fig. 4a). In contrast, mean *H* was highest in the probability-of-occurrence-based Zonation results in rank bins less than or equal to the 0.6–0.69 bin (Fig. 4a). Mean site-level differences in *H* were smallest in bins from 0.2 to 0.59 (Fig. 4). Variability in site-level *H* was high in all Zonation bins (Fig. 4a). Mean *H* from the probability-of-occurrence Zonation was less than the mean *H*-1 SD from the density-based Zonation approach in the top Zonation rank bin (Fig. 4a). In contrast to mean site-level *H*, regional *H* was consistently higher in each bin selected by probability-of-occurrence-based Zonation (Fig. 4b). Differences in regional *H* between the 2 Zonation approaches were greatest in the highest and lowest rank bins (Fig. 4b).

In general, diversity (both site-level and regional) increased from low to high Zonation rank bins in both Zonation approaches (Fig. 4). However, changes in mean site-level diversity between adjacent rank bins decreased between the 0.3–0.39 and the 0.8–0.89 rank bins (Fig. 4a). We found a marked decline in mean site-level

H between the second highest and highest site-level rank bin for the probability-of-occurrence Zonation approach (Fig. 4a).

Discussion

Systematic conservation planning will be most efficient at protecting populations when the most precise and accurate data are used to prioritize conservation efforts. Thus, the density-based Zonation prioritization protected more individuals of each species in the highest ranked portion of the landscape than the probability-of-occurrence-based Zonation because the density-based analysis had more detailed data on the core areas of species. In an ideal world, systematic conservation planning would entail monitoring efforts designed to inform optimal conservation planning across large landscapes. In reality, constraints on time, funding, and accessibility often prevent the implementation of optimal monitoring efforts. Thus, landscape-level conservation planning will need to continue to rely on data collected from multiple sources. Our results demonstrate that conservation networks can be designed with the intent to protect more individuals when count data are available. Thus, our results show the high value of species count data and how that value can
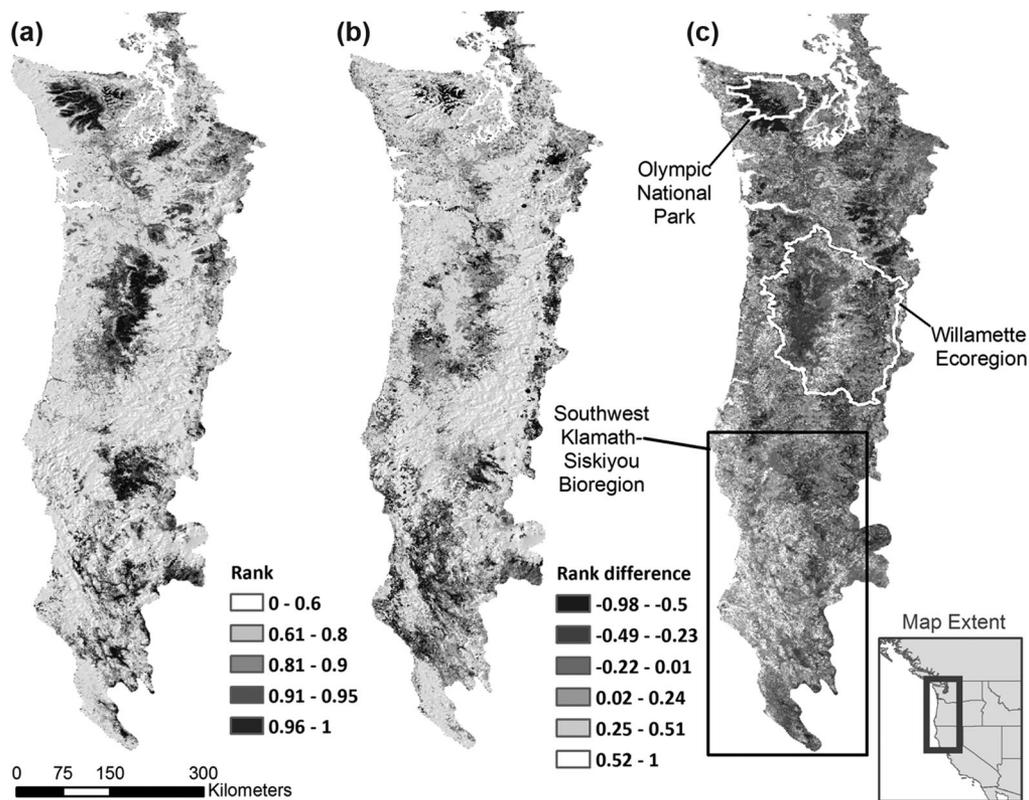
Figure 1. Results from Zonation conservation ranking of the landscape based on probability of (a) occurrence, (b) density of breeding birds, and (c) the priority ranking difference between the two. Dark areas in (c) indicate where the probability-of-occurrence-based Zonation rankings are high and density-based Zonation rankings are low (zonation rank class: range 0–0.09 [lowest 10 % rank of the landscape] to 0.9–1.0 [top 10% of the landscape]).

be leveraged to support broad conservation goals when data are made available through ecoinformatics systems (Michener & Jones 2012).

Although more individuals were protected when we incorporated count data in the network design, regional diversity was consistently highest (generally only by a narrow margin) in all the probability-of-occurrence-based Zonation ranking bins. This result suggests that probability-of-occurrence-based Zonation rankings can be effective when diversity is the goal rather than specific population targets. However, it may be unrealistic to protect all the land within each of the 10% Zonation rank bins in this study. The availability of land for protection and costs often dictate what areas can be protected; thus, it is more likely that a subset of the areas within each of our conservation ranking bins could realistically be protected for conservation. In that case, mean site-level diversity was highest in the top rank bins of the density-based Zonation, again illustrating the benefits of using count-based data for systematic conservation planning.

Systematic conservation planning is most frequently used to identify areas of high priority for protection, but recent studies also suggest the approach can be used to identify areas where development or other nonconserva-

tion activities would be most appropriate. For example, Moilanen (2013) showed how Zonation could be used for development impact avoidance based on the lowest rankings from a Zonation analysis. However, we found that the probability-of-occurrence-based Zonation approach classified cells in the lowest ranking that had higher numbers of individuals of many species (Fig. 2) and higher mean site-level diversity (Fig. 4a) than the density-based Zonation. This could lead to higher-quality areas for biodiversity being lost if probability-of-occurrence-based Zonation models are used rather than density-based models for impact avoidance. The limited money available for conservation has led to calls for a more careful and systematic allocation of conservation resources to ensure they are used most effectively (Bottrill et al. 2008). Our results suggest that an investment in relatively costly monitoring data could result in a substantially more efficient allocation of resources when utilized through systematic conservation planning.

We acknowledge that basing systematic conservation planning on density models could have limitations beyond the added costs and difficulties of monitoring abundance across large landscapes. Primarily because of the widespread availability of presence-absence and presence-only data, a much greater emphasis on
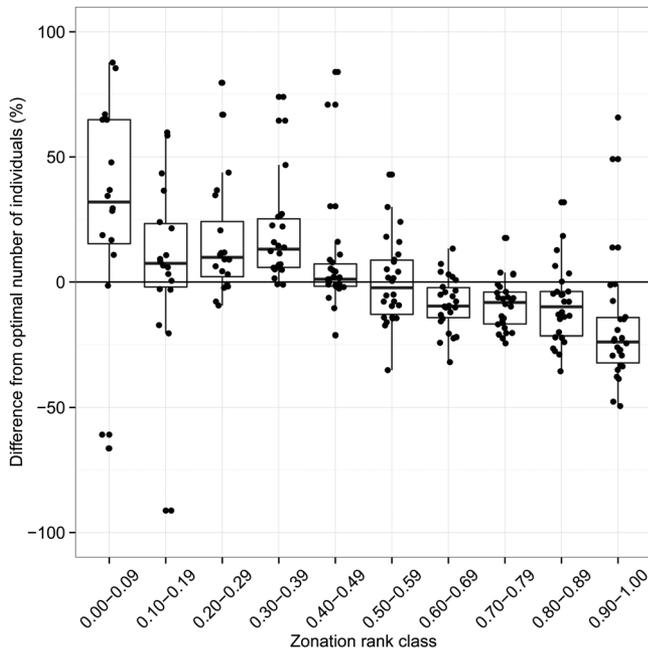
Figure 2. Percent difference between birds protected by the density-based Zonation rankings and by the probability-of- occurrence-based Zonation rankings for different levels of the landscape protected (black horizontal line, no difference in the number of birds protected in either prioritization; values above black line, probability-of-occurrence-based Zonation ranks protect more individuals per species than the abundance-based Zonation; values below black line, abundance-based Zonation ranks protect more individuals per species than probability-of-occurrence-based Zonation; boxplot hinges, first and third quartile; whiskers, extend to the most extreme values in the data that are within 1.5 times the interquartile range; points, value for each species [n=26]; location of points jittered horizontally for clarity).
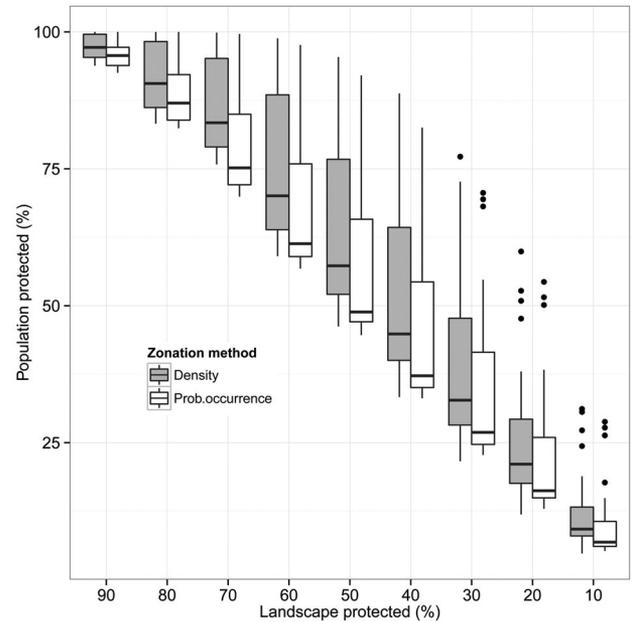

Figure 3. Percentage of the population of 26 bird species protected by different percentages of protected area (boxplot hinges, first and third quartile; whiskers, extend to the most extreme values in the data within 1.5 times the interquartile range; points, displayed when data are beyond the range of the whiskers).

improving these models is evident in the ecological and conservation literature. Still, there are an increasing number of studies that explore different methods for species abundance distribution modeling (e.g., Potts & Elith 2006). Recent work also suggests that using abundance data can improve the accuracy of species distribution models relative to models calibrated with presence-absence data (Howard et al. 2014). There are cases where isolated local populations of a species might have high conservation value but be ranked relatively low in a conservation prioritization based on density. For example, conservation value may be high due to the presence of unique genotypes or the need to maintain high neutral or adaptive genetic variation (Kohn et al. 2006). Similar to our results demonstrating the benefit of incorporating additional information on species density, we expect that incorporating information on population

genetics may improve conservation outcomes (Kark et al. 1999). However, for most species there are currently no maps of the genetic diversity within populations that can be used in systematic conservation planning, although this may change in the future (but see Ruegg 2008). Moreover, there is no reason to expect that a probability-of-occurrence-based conservation prioritization would be more efficient at protecting within-population genetic diversity than a density-based Zonation.

We also acknowledge that species densities can have large interannual variability, variability that may be greater than the variation in species ranges across time. Our density models were constrained to areas predicted to be within each species range and to areas where environmental conditions were suitable for occupancy; thus, the density data provided more information for ranking suitability among sites. Future work could explicitly test how temporal variability in species presence or density could be most effectively incorporated into systematic conservation planning.

Increasing the use of count data in systematic conservation planning requires the development and refinement of best practices for integrating count data from multiple sources. We used information from repeated sampling both within and across years (when available) and applied this information to generate estimates of probability of detection where repeated sampling was not conducted.
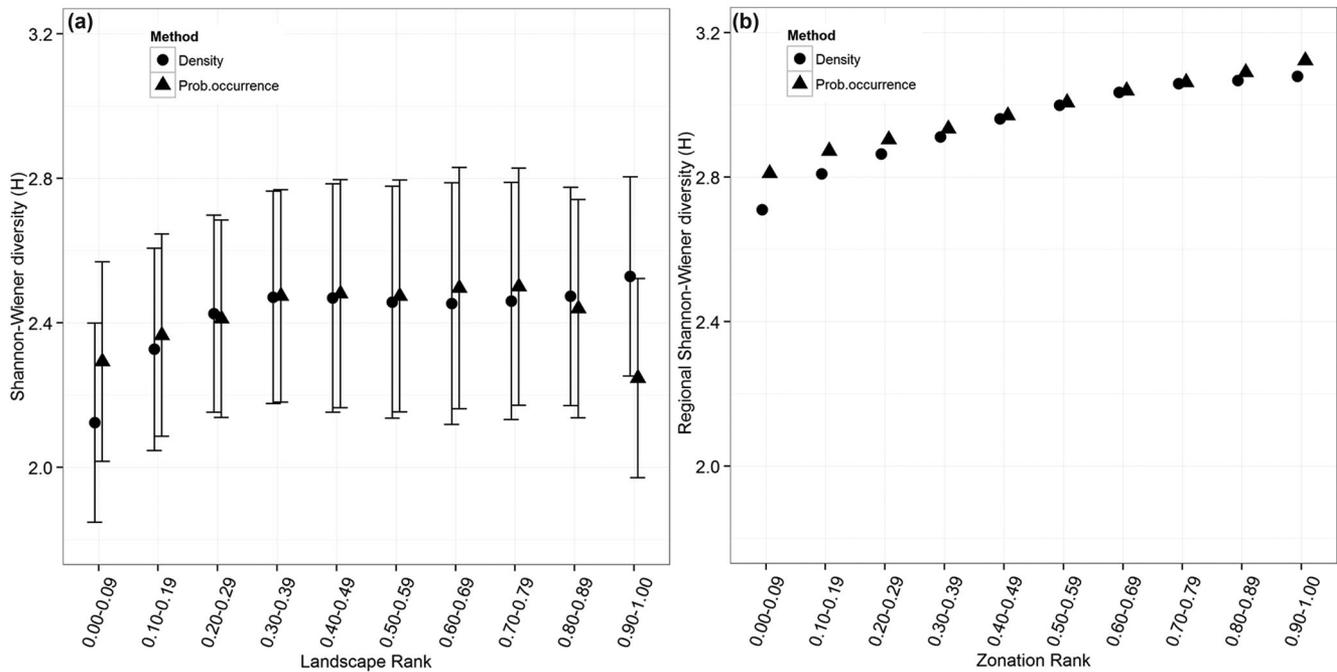
Figure 4. Site-level and regional Shannon-Weiner diversity (H) protected within each 10% Zonation conservation ranking bin for Zonation classifications based on the modeled abundance of individuals and probability of occurrence and density of individuals of 26 bird species (a) site-level diversity estimated using the mean (SD 1) H per pixel within each conservation ranking bin and (b) regional H calculated using the sum of all individuals per species across all pixels within the Zonation rank.

Our approach thus made the greatest use of available data while controlling for variable survey quality to correct for imperfect detection and other sources of sampling error. We illustrated the utility of our approach with terrestrial breeding birds, which are good indicators of ecosystem quality and conservation need (Blair 1999; Aslan et al. 2014). However, we recommend researchers test our approach with other taxa and investigate whether the approach can be refined. Expanding the types of monitoring data collected and sharing the data within coordinated monitoring networks in countries with little funding available for monitoring may be difficult but worthwhile given the increased efficacy of the resulting conservation networks.

We found that count data improved results of the application of presence-absence and presence-only data in systematic conservation planning. Additional improvements could ensure that conservation efforts effectively reduce or eliminate vulnerabilities of species populations. Our models of bird density provide a refined and more precise estimate of the areas of importance to the regional populations of the 26 species we modeled. However, true population vulnerabilities could be better assessed by including information on the demography and dispersal abilities and constraints of the species being modeled. This would better identify local populations vulnerable to extirpation and management actions that

could reduce these vulnerabilities (Nur et al. 2012). As with count data, demographic data are often unavailable for species at large spatial scales, but it is possible that the approach we used to aggregate count data across studies could be transferred to aggregating demographic data from disparate efforts. Many species are likely to shift their spatial distributions in response to climate (Stralberg et al. 2009) and land use change (Jongsomjit et al. 2013); thus, an optimal spatial conservation prioritization of the landscape may be sensitive to different future scenarios (Veloz et al. 2013). Therefore, future systematic conservation planning efforts ought to include multiple future scenarios in addition to current conditions in the prioritization process.

Future systematic conservation planning efforts will be improved by using the best available data on species distribution and density. We encourage researchers to share their data through ecoinformatics networks so that individual monitoring efforts can be repurposed to support large-scale conservation efforts, thereby reducing the limitations of a lack of data availability. To that end, we have made all the models for this study available for viewing and downloading (http://data.prbo.org/apps/nplcc/aknw.php). Additionally, all the bird observation data are available through the AKN and viewable through the Avian Knowledge Northwest Web site (http://data.prbo.org/cadc/tools/multimap/aknw.php).

Acknowledgments

Supporting Information

A table of hybrid vegetation classes (Appendix S1) and methods for imperfect detection occupancy and density models (Appendix S2) are available as part of the online article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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