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Research Paper

Determining conservation priority areas for Palearctic passerine migrant birds in sub-Saharan Africa

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ABSTRACT. Migratory bird species breeding in the Palearctic and overwintering in sub-Saharan Africa face multiple conservation challenges. As a result, many of these species have declined in recent decades, some dramatically. We therefore used the best available database for the distribution of 68 passerine migrants in sub-Saharan Africa to determine priority regions for their conservation. After modeling each species' distribution using BIOMOD software, we entered the resulting species distributions at a $1^\circ \times 1^\circ$ grid resolution into MARXAN software. We then used several different selection procedures that varied the boundary length modifier, species penalty factor, and the inclusion of grid cells with high human footprint and with protected areas. While results differed between selection procedures, four main regions were regularly selected: (1) one centered on southern Mali; (2) one including Eritrea, central Sudan, and northern Ethiopia; (3) one encompassing southwestern Kenya and much of Tanzania and Uganda; and (4) one including much of Zimbabwe and southwestern Zambia. We recommend that these four regions become priority regions for research and conservation efforts for the bird species considered in this study.

Détermination d'aires de conservation prioritaires pour les passereaux migrateurs du Paléarctique en Afrique subsaharienne

RÉSUMÉ. Les espèces d'oiseaux migrateurs nichant dans le Paléarctique et hivernant en Afrique subsaharienne font face à de nombreux défis de conservation. Par conséquent, beaucoup de ces espèces ont subi des baisses, parfois catastrophiques, dans les dernières décennies. Pour aborder ce problème, nous avons utilisé les meilleures bases de données disponibles sur la répartition de 68 passereaux migrateurs en Afrique subsaharienne, afin de déterminer quelles régions prioriser pour leur conservation. Après avoir modélisé la répartition de chaque espèce au moyen du logiciel BIOMOD, nous avons incorporé les répartitions obtenues dans le logiciel MARXAN, en utilisant une grille dont la résolution des cellules était de $1^\circ \times 1^\circ$. Nous avons ensuite testé diverses procédures de sélection en faisant varier le modificateur de longueur de bordure et le facteur de pénalité d'espèce, et en ajoutant des cellules présentant une emprise humaine élevée ou des aires protégées. Bien que les résultats aient différé selon les procédures de sélection testées, quatre régions principales sortaient régulièrement du lot : 1) une centrée sur le sud du Mali; 2) une englobant l'Érythrée, le centre du Soudan et le nord de l'Éthiopie; 3) une comprenant le sud-ouest du Kenya et la quasi-totalité de la Tanzanie et de l'Ouganda; et 4) une comprenant la majorité du Zimbabwe et le sud-ouest de la Zambie. Nous recommandons que ces quatre régions deviennent prioritaires pour y faire de la recherche et y mettre en place des mesures de conservation destinées aux espèces d'oiseaux considérées dans la présente étude.

Key Words: *area selection; BIOMOD; conservation priorities; Geographic Information Systems (GIS); MARXAN; niche modelling; Palearctic migrants; passerines; sub-Saharan Africa*

INTRODUCTION

The conservation of migratory bird species faces special problems associated with their annual movements because species survival is dependent on the conservation of not only breeding grounds but also stopover sites and wintering grounds (Biber and Salathé 1989, Crick 1992, Bibby 2003, Kirby et al. 2008). For the > 300 species of birds breeding in the Palearctic region that migrate to wintering grounds in Africa (Walther 2005), the breeding grounds and principal migration routes through Europe and the Mediterranean are reasonably well known (e.g., Glutz von Blotzheim 1966–1996, Cramp 1998). However, knowledge concerning the distribution of many of these migrants in Africa is still incomplete (Walther and Rahbek 2002).

In an effort to fill these data gaps, the sub-Saharan distributions of some of the nonpasserine migrants (e.g., Scott and Rose 1996, Delany et al. 2009, Walther et al. 2013) and all of the passerine migrants (Walther et al. 2010) have been mapped in the last two decades. These passerine distributions were also used to identify macroecological correlates of migrant species richness (Wiszniewski et al. 2007) and to model the effects of climate change on their future distributions (Barbet-Massin et al. 2009).

Given the recent population declines of many of these migratory passerines (summarized in Newton 2004, 2008, Walther et al. 2011, Walther 2016), conservation measures for breeding grounds, stopover sites, and wintering grounds need to be explored. Although many studies have suggested possible conservation measures for the breeding grounds (e.g., Arroyo et

al. 2002, Donald et al. 2007, Fuller et al. 2007, Newton 2008), fewer have done so for the wintering grounds (e.g., Zwarts et al. 2009, Walther et al. 2010, 2011, Buij et al. 2012, Limiñana et al. 2012, Walther 2016).

Studies that focus on conservation measures for the wintering grounds are important because the population decline of migratory passerines is linked to environmental changes in their wintering grounds, whereby the Sahel zone is of special concern (summarized in Newton 2004, 2008, Walther et al. 2011, Walther 2016). The increasingly rapid conversion of natural and seminatural land cover into more intensive land uses, especially into intensive agriculture (Brink and Eva 2009, Walther et al. 2011, Walther 2016), necessitates the timely implementation of conservation measures. Therefore, the establishment of additional protected areas is of high importance, but better land use and management strategies compatible with long-term species survival in large parts of the African continent are even more important.

Many different decision criteria and tools for choosing the most important conservation sites have been developed in the last two decades (Moffett and Sarkar 2006, Sarkar et al. 2006, Margules and Sarkar 2007, Pressey et al. 2007, Moilanen et al. 2009). One criterion for selecting a priority site is that such a site should be an aggregation point for a high number of individuals or a significant part of one (or several) species' world population, including migratory or congregatory species. African examples include the Serengeti for mammals (Sinclair and Arcese 1995) and the Banc d'Arguin for birds (Isenmann 2006). BirdLife International includes this criterion in its criteria to distinguish Important Bird Areas (IBAs; Fishpool and Evans 2001, Buchanan et al. 2009).

Another criterion is that a site should be a hotspot of species richness, whereby one can use total, endemic, rare, or threatened species richness for selecting sites (e.g., Myers et al. 2000, Orme et al. 2005, Grenyer et al. 2006). Again, this criterion has been incorporated into the definition of IBAs as a "set of sites that together hold a suite of restricted-range species or biome-restricted species." For the passerine sub-Saharan migrants, which are the subject of this study, Walther et al. (2010) found that five African regions were especially species-rich: (1) Senegambia; (2) southern Mali; (3) northern Nigeria; (4) central Sudan; and (5) Uganda, southwestern Kenya, and northeastern Tanzania. For rare migrants, three regions stood out as species-rich: (1) southern Mauritania, Senegambia, southern Mali, and Burkina Faso; (2) central Sudan, northern Ethiopia, and the Red Sea Coast along Eritrea, Djibouti, and northwestern Somalia; and (3) Uganda, Kenya, and Tanzania.

Another way of selecting conservation priority sites is to use the principle of complementarity in which the goal is to preserve a full complement of species in the maximum number of sites at the least cost (e.g., Moilanen et al. 2009, Lourival et al. 2011). Although such complementarity analyses were performed for many African species (e.g., Lovett et al. 2000, Williams et al. 2000, Balmford et al. 2001, Brooks et al. 2001, Burgess et al. 2002, 2005, 2006, Moore et al. 2003, Küper et al. 2004, Dillon and Fjeldsø 2005, McClean et al. 2006, Rondinini et al. 2006), to our knowledge, only one study focused on migrant birds (Walther et al. 2010) and identified four priority areas based on

complementarity: (1) one centered on southern Mali; (2) one centered on Eritrea that includes large parts of central Sudan, northern Ethiopia, Djibouti, and northwestern Somalia; (3) one encompassing Uganda, southwestern Kenya, and northeastern Tanzania; and (4) one centered on northern Zimbabwe.

We here extend the study of Walther et al. (2010) by replacing the original area selection program **WORLDMAP** (Williams 2016) with the more advanced software **MARXAN** (Watts and Possingham 2013), which allowed us to add additional selection criteria. We added the following four criteria not considered in Walther et al. (2010): (1) inclusion of a boundary length modifier (BLM), which increases the clumping of selected sites by penalizing solutions with high fragmentation (Nhancale and Smith 2011); (2) exclusion of all sites with a high human footprint, i.e., cells that are affected greatly by humanity through a combination of high human population density, land transformation, human access such as roads and large rivers, and power infrastructure (Sanderson et al. 2002); (3) use of different weights (called species penalty factors) to adjust for the threat status of each bird species (Loos 2011); and (4) inclusion of all sites that include protected areas (IUCN-UNEP 2009).

These additional criteria are important extensions to the solutions presented in Walther et al. (2010), which was published at a time when the relevant software to test for these criteria had not yet been developed. For example, without a BLM, a selection procedure will only consider the conservation value of each grid cell by itself, but not the location of that grid cell in relation to all the other selected grid cells. Therefore, highly fragmented solutions are often selected, with selected grid cells separated by large distances. To counteract such fragmentation, **MARXAN** implemented the BLM, which penalizes solutions with high fragmentation and encourages solutions with several grid cells in direct contact with each other, thus creating solutions with larger, connected areas containing several grid cells (Smith et al. 2010, Nhancale and Smith 2011). Another possible critique of previously published solutions is that they may contain grid cells with high human impact, e.g., urban centers and other highly modified landscapes. Therefore, we also determined solutions that excluded any grid cells with a high human footprint, as defined by Sanderson et al. (2002).

Because the conservation value is not equal for all species, we also determined solutions that give a higher priority to threatened species (e.g., Drummond et al. 2009) to compare them to previous solutions, which did not distinguish between species of different conservation status. Finally, the solutions presented in Walther et al. (2010) did not consider whether a grid cell was within a protected area or not, which is another important criterion for whether to select a grid cell or not (e.g., Smith et al. 2010). Therefore, we determined if grid cells within protected areas mapped by IUCN-UNEP (2009) adequately protect the species in this study.

METHODS

Data acquisition and selection

Data about the distribution of the 65 modeled passerine migrants in Africa were acquired from four sources. First, > 200 individuals and several organizations (including SAFRING, now AFRING,

and all bird banding schemes within Europe through EURING) provided data, mostly in electronic form. Second, data from most important African ornithological atlases, field guides, and checklists were entered. Third, data from internet sites, e.g., Kenya Birdfinder and Ornis Net, were entered. Finally, we supplemented these three main data sources with a few additional data obtained via correspondence from the American Museum of Natural History (New York, USA), the Natural History Museum (Tring, UK), and the Royal Museum for Central Africa, Department of African Zoology (Tervuren, Belgium).

The first author entered and quality-checked all entered data, which are held in a Microsoft Access database. The database currently holds approximately 250,000 records, most of which are associated with geographic coordinates (see exact numbers in Walther et al. 2010). This database is now the most comprehensive database on Western Palearctic migrant passerines in Africa. Different portions of the data are publicly available from AFRING, EURING, the Global Biodiversity Information Facility, and the Internet sources (e.g., Kenya Birdfinder and Ornis Net) noted above.

These data were further verified by the following procedures. Any record deemed to be a misidentification (e.g., by a country's rarities committee) or assumed to be fraudulent was excluded. Any record for which the geographical coordinates lay outside the boundaries of continental Africa or the record's stated country was excluded. Any record that was either stated to be a vagrant in the original source or was far outside the normal ranges shown in the Birds of Africa series was excluded. Any record for which the EURING (1979) codes suggested that the spatial or temporal information was incorrect was excluded. Any record with a spatial inaccuracy of ± 30 min or worse was excluded. After these data exclusions, only records from November, December, January, and February were selected, as well as undated records well within the recorded wintering range of each species.

Niche modeling of species distributions

These tens of thousands of verified records of the 65 migratory bird species in combination with seven environmental data layers offered us the chance to model each species' ecological (or Hudsonian) niche using multivariate statistical techniques (Elith et al. 2006, Drew et al. 2011). To achieve this, we first acquired seven environmental data layers at a 10-min grid resolution ($10' \times 10'$). The Climate Research Unit CL 2.0 data set (New et al. 2002) was used to represent current climate, from which we produced six uncorrelated bioclimatic variables (selected after crosscorrelation evaluation from principal components analysis) representing the major climatic gradients in Africa, namely: mean annual potential evapotranspiration, annual growing degree-days, minimum temperature of the coldest month, maximum temperature of the warmest month, mean annual temperature, and annual sum of precipitation. Potential evapotranspiration estimates were calculated using the Food and Agriculture Organisation 56 Penman-Monteith combination equation (Allen et al. 1998). Data on land transformation were resampled from the 0.5' resolution "human footprint" data set (Sanderson et al. 2002) to the required $10' \times 10'$ resolution.

We then used the seven environmental layers to model each bird species' sub-Saharan distribution using BIOMOD (Thuiller

2003). BIOMOD aims to maximize the predictive accuracy of species distributions using different types of statistical modeling techniques, which were: artificial neural networks, classification tree analysis, generalized additive models, generalized boosting models, generalized linear models, multiple adaptive regression splines, mixture discriminant analysis, Breiman and Cutler's random forests for classification and regression, and surface range envelope (SRE). SRE identifies minimum and maximum values for each environmental variable from the localities where the species is present, and the predicted distribution includes any site with all variables falling between these minimum and maximum limits. While SRE only requires presence data, all the other models require presence-absence data. Once each predicted distribution had been generated, BIOMOD compared the performance of each model and chose the best performing one by using the area under the curve of the receiver-operating characteristic plot (Fielding and Bell 1997).

Our niche modeling procedure consisted of seven steps. (1) We ran the SRE model with the presence-only data. (2) Because it is widely acknowledged that presence-only modeling techniques often overpredict species distributions (Brottons et al. 2004, Elith et al. 2006), we then restricted the SRE prediction to the ecoregions, regions, and countries where the respective species had actually been recorded, using available country and ecoregion shape files; this procedure was previously employed in Walther et al. (2004, 2007, 2010), Wisz et al. (2007), and Bairlein et al. (2009). (3) Pseudoabsences were randomly placed inside the African mainland but outside the restricted SRE prediction generated in step 2. Because the performance of AUC scores is best at intermediate sampling prevalence, i.e., the proportion of data points that are presences (McPherson et al. 2004), a balanced design of an equal number of presences and pseudoabsences for each species was chosen. (4) We ran all models provided by BIOMOD on both the presence and the pseudoabsence data. (5) We chose the best set of the generated model predictions according to the highest AUC score calculated from 30% of the original data set left aside as an evaluation data set (Thuiller 2004). (6) The best prediction was used within the restricted SRE prediction generated in step 2, thus combining the results from the presence-only model with the results from the best model chosen by using the presence and pseudoabsence data. (7) Those grid pixels whose values were below or above a certain threshold were converted to zeros (absences) and ones (presences), respectively. We a priori chose the MaxKappa criterion, which is one of the top two criteria for yielding unbiased estimates of species prevalence and also has the highest mean kappa (Freeman and Moisen 2008). Step 7 was not included in Walther et al. (2010).

The 65 distribution maps resulting after the first six modeling steps and further details about the methods are presented in Walther et al. (2010). Each of these 65 maps of $10' \times 10'$ grid resolution was then converted to $1^\circ \times 1^\circ$ grid resolution using an ArcGIS script. Three species distributions were manually entered into the $1^\circ \times 1^\circ$ grid resolution because these three species could not be modeled due to low sample size: Meadow Pipit *Anthus pratensis*, Black Redstart *Phoenicurus ochruros*, and Pale Rockfinch *Carpospiza brachydactyla*. For these three species, maps presented in the *Birds of Africa* series (Keith et al. 1992, Fry and Keith 2004) were transferred to generate their distributions.

Therefore, 68 Western Palearctic passerine migrant species (Appendix 1) that migrate in substantial numbers to the sub-Saharan region were included in our analysis (Walther 2005).

Selection of conservation priority areas

We used the MARXAN version 1.8.20 software (Ball and Possingham 2000, Watts and Possingham 2013) to select grid cells that have certain conservation-relevant features, e.g., presence or absence of species, economic cost of purchase or management, etc. The selected set of grid cells is called a solution. MARXAN maximizes the number of species in a solution to match preset conservation targets by performing a number of runs. During each run, MARXAN applies a simulated annealing optimization algorithm to select one near-optimal solution per simulation (the optimal solution is usually unknown). This near-optimal solution must simultaneously satisfy the preselected targets (e.g., species to be protected) and minimize the total solution cost. Costs are defined by the user and can be both ecological and economic in nature. For example, the species penalty factor is an ecological cost because not including a species will increase the overall cost of the solution. Economic costs can be the costs of purchasing or managing the grid cells for conservation purposes. Whereas we varied ecological costs, we did not vary economic costs in our analysis.

MARXAN yields two outputs: the near “best” or “optimal” solution that achieves the conservation targets for the lowest overall cost (i.e., by minimizing costs), and a selection frequency output that counts the number of times each grid cell appeared as part of the different solutions (grid cells that were selected more often are shown with a more saturated color in Fig. 1). For further details, one should consult the MARXAN user guide and the publications on its website (Watts and Possingham 2013). In each selection procedure, we conducted 500 runs with 1 million annealing iterations. All other MARXAN parameters were set to default: “Run Options” was set to “Simulated Annealing” with “Two Step Iterative Improvement.” The cost of each grid cell was kept constant at 10 in all simulations because we considered the economic cost of acquiring a grid cell equal across the African continent. Although some studies (e.g., Moore et al. 2004) have considered the possibly differential economic costs of acquiring grid cells, this was not an object of our analysis.

Next, we present details of each of the selection procedures adopted in our analysis.

Null selection procedure: The first simulation added no constraints to the selection procedure in terms of including or excluding grid cells or weighing species. In this case, MARXAN minimized the cost of the overall solution whereby we used a relatively high species penalty factor (SPF) of 100 (Table 1) because we wanted all species to be included in the final solution. Therefore, the cost of ignoring a species (cost = 100) was set much higher than the cost of selecting an area (cost = 10). Consequently, MARXAN was forced to include grid cells even if they contained just one (or a few) rare bird species. The selection target was thus the minimum number of occurrences of each species. This selection procedure is most similar to the one used previously by Walther et al. (2010).

Table 1. Numerical settings used in six selection procedures (for further details, see Methods). The target is a number such that if fewer occurrences than the target number are in the solution, then every missing species applies its species penalty factor (SPF) to the score of the solution. The SPF and the boundary length modifier (BLM) are the two parameters that MARXAN uses to determine the best solution to reach the target during each simulation. Grid cells with the highest human footprint were either excluded from the final solution (yes) or not excluded (no). The last column shows the identifier of the corresponding figure.

Selection procedure	Target	SPF	BLM	Human footprint	Figure
Null	1	100	0	no	1A
Null	5	100	0	no	S1A
Null	10	100	0	no	S1B
Null	25	100	0	no	S1C
Null	50	100	0	no	S1D
BLM	50	100	0	no	1B
BLM	50	100	0.01	no	1C
BLM	50	100	0.1 [†]	no	1D
Human footprint	1	100	0.1	yes	S2A
Human footprint	5	100	0.1	yes	S2B
Human footprint	10	100	0.1	yes	S2C
Human footprint	25	100	0.1	yes	S2D
Human footprint	50	100	0.1	yes	1E
SPF	50	0.05	0.1	yes	S3A
SPF	50	0.1	0.1	yes	1F
SPF	50	0.25	0.1	yes	S3B
SPF	50	0.5	0.1	yes	S3C
SPF	50	0.75	0.1	yes	S3D
SPF	50	1.0	0.1	yes	S3E
SPF	50	10	0.1	yes	S3F
Maximum target	max [*]	0.04	0	yes	1G
Maximum target	max [*]	0.05	0	yes	S4A
Maximum target	max [*]	0.06	0	yes	S4B
Maximum target	max [*]	0.07	0	yes	S4C
Maximum target	max [*]	0.08	0	yes	S4D
Maximum target	max [*]	0.09	0	yes	S4E
Maximum target	max [*]	0.10	0	yes	S4F
Maximum target	max [*]	0.11	0	yes	S4G
Maximum target	max [*]	0.12	0	yes	S4H
Threatened status	50	0.05, 0.2 [§]	0.1	yes	1H
Threatened status	50	0.05, 0.2 [§]	0	yes	1I

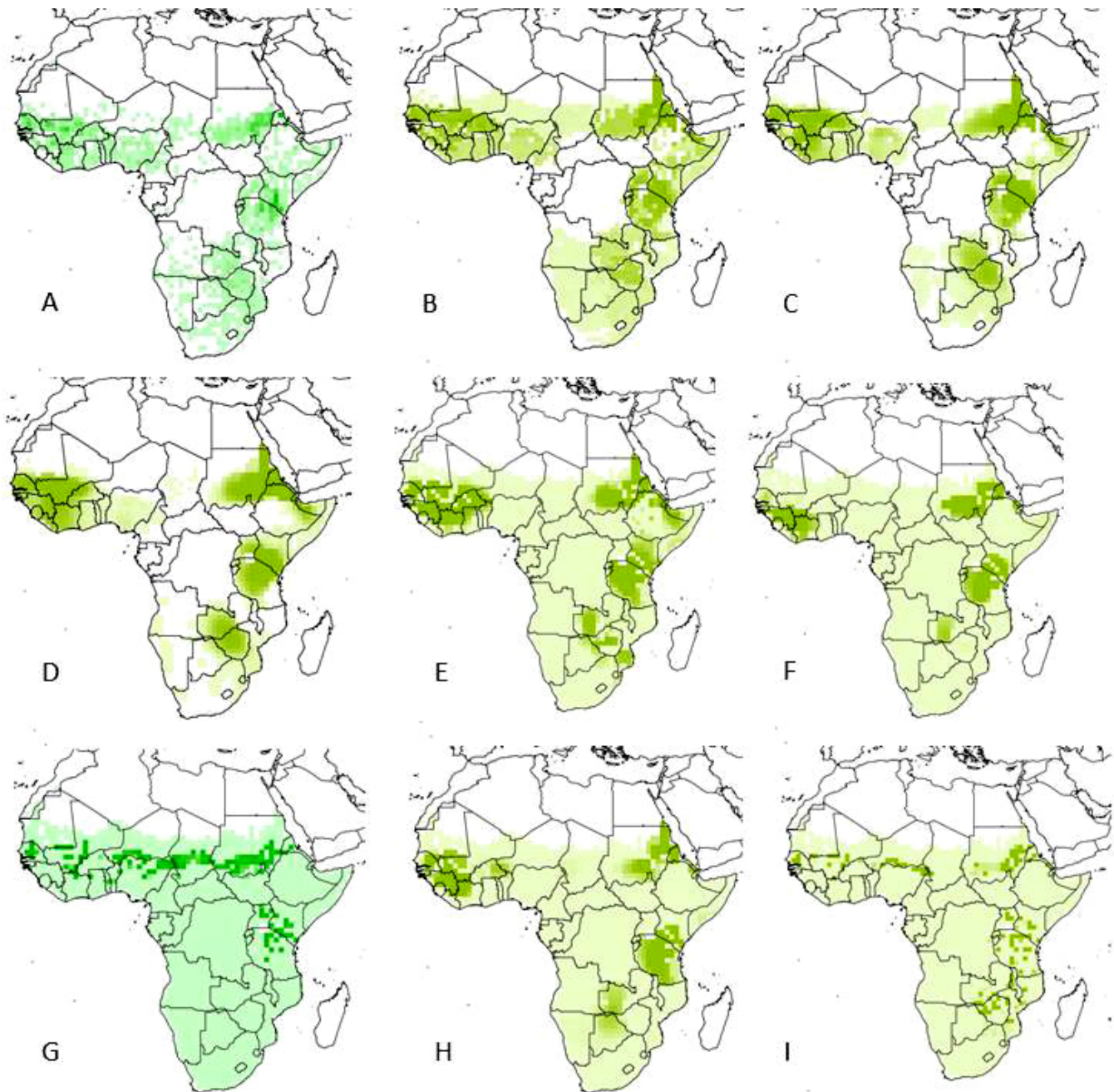
[†]We used a visual comparison of Fig. 1B–D to choose the BLM that resulted in a reasonable amount of clumping of the grid cells, namely 0.1 (Fig. 1D), which was then kept constant in the human footprint and SPF selection procedures.

^{*}Max refers to the maximized target solutions whereby a given species’ target is set to the total number of occurrences of that species throughout the grid cells.

[§]We used an a priori SPF of 0.05 for stable species and 0.2 for “worrying” species to give worrying species higher importance.

BLM selection procedure: The second selection procedure applied an increasing value for the BLM. Highly fragmented solutions have a higher boundary edge length because fewer of their boundaries are shared with other selected grid cells. Consequently, such solutions may not be ecologically or economically viable because of the highly fragmented location of

Fig. 1. Selected grid cells in Africa for 68 Palearctic passerine migrant birds using nine different MARXAN settings. See Table 1 for the respective MARXAN settings used to generate each panel. For all panels, the results are summarized over 500 runs, with a more saturated color indicating the more numerous selection of a grid cell (see details in Methods).



the selected grid cells (Smith et al. 2010, Nhancale and Smith 2011). To counteract the possible effects of selecting grid cells without consideration of the resulting fragmentation, MARXAN allows the calculation of the total cost for solutions that meet all the targets as the combined grid cell costs plus the boundary length cost. In other words, the BLM adds another cost to the ecological and economic costs, and MARXAN then attempts to

minimize these three different costs. This boundary length cost is the product of multiplying total edge length by a user-defined BLM value. The edge length is the length of all the edges of selected cells that are adjacent to unselected cells. If the BLM value is increased, MARXAN will identify less fragmented but more extensive solutions. Such solutions usually select more grid cells, but these selected grid cells are more connected to each other

than in solutions without a BLM cost. We varied the BLM value from zero (as in the null selection procedure) to 0.1 (Table 1). We also used values of 1 to 10, but the results became nonsensical because all of Africa was selected.

Human footprint selection procedure: The third selection procedure excluded (i.e., locked out) all grid cells with high anthropogenic impact. We assumed a priori that grid cells with high anthropogenic impact (e.g., urban centers) are unlikely to be useful for the conservation of the species in this analysis. For this purpose, we used the aforementioned human footprint data set (Sanderson et al. 2002), which was resampled to the required resolution of $1^\circ \times 1^\circ$ using linear interpolation as implemented by ArcGIS 10.1. We then excluded the 10% of grid cells within the study area with the highest human footprint values. Otherwise, we used the same settings as for the second selection procedure while increasing the selection target (Table 1).

SPF selection procedure: The fourth selection procedure varied the SPF from 0.01 to 10 (Table 1). The rationale was to find a more efficient solution. When the SPF is too high, MARXAN will select every grid cell it needs to meet the preset targets without consideration for how species-rich a grid cell is (and thus select even species-poor areas if they contain a species not yet represented in the solution). The lower the SPF, the more species-rich a grid cell must be to be included in the solution. The reason for this procedure is thus to eliminate species-poor grid cells from the analysis.

Maximum target selection procedure: The fifth selection procedure maximized the target of every species to the total number of occurrences of that species. We set the BLM to zero and then tested a variety of SPFs (Table 1). We performed these simulations to determine how to set appropriate SPFs for threatened species in the sixth selection procedure.

Threatened status selection procedure: The sixth selection procedure aimed to give higher importance to threatened species than to nonthreatened species. To separate threatened from nonthreatened species, Walther et al. (2011) used several relevant conservation-related criteria to categorize the passerine species into threatened and nonthreatened species (called “worrying” and “stable” species). The criteria to define a threatened species were: the species is globally threatened (BirdLife International 2016), the species is given “unfavourable” status by BirdLife International (2004), or the species declined severely during the period 1970–2000 (for details, see Walther et al. 2011; also note that the Isabelline Shrike *Lanius isabellinus* listed in Walther et al. 2011 could not be categorized because of a lack of comparable conservation-related data). Consequently, we applied a higher SPF to threatened species than to nonthreatened species (Table 1) for MARXAN to prioritize the selection of threatened species over nonthreatened species.

Protected areas selection procedure: The seventh selection procedure included (i.e., locked in) all protected areas that fulfilled the IUCN criteria Ia, Ib, II, III, IV, V, and VI (Dudley 2008) to test if grid cells within protected areas adequately protect the species analyzed here. For this purpose, we downloaded the global file for protected areas from the World Database on Protected Areas (IUCN-UNEP 2009). Using the select tools of ArcGIS 10.1, we excluded all those protected areas within the study area

that were not tagged with the aforementioned IUCN criteria. Using the Union tool of ArcGIS 10.1, we then determined all $1^\circ \times 1^\circ$ grid cells whose area was covered > 50% by protected areas. The 298 grid cells fulfilling this criterion were automatically locked into the solution. We then applied this additional criterion (i.e., 298 grid cells locked into the solution) to all the selection procedures mentioned above. However, we found that no more than 12 additional grid cells were needed to satisfy the target solution. In other words, the solutions using the protected areas selection procedure hardly differed from the solutions of the selection procedures listed above. Consequently, this procedure did not give us much additional information; therefore, we do not present these results, but only the results from the other six procedures.

Here, we present only those solutions that gave high priority to approximately 10–20% of the sub-Saharan region (Fig. 1). Other solutions, which prioritized much larger portions of the sub-Saharan region, are also informative but not very practical in that they prioritize too much of the region. We provide these remaining solutions in Appendix 1.

RESULTS

The null selection procedure closely mirrored the methods and therefore also the results of Walther et al. (2010); the same four regions were selected (Fig. 1A) when the selection target was set at 1 (Table 1). These regions were (1) one centered on southern Mali; (2) one including Eritrea, central Sudan, and northern Ethiopia; (3) one encompassing southwestern Kenya, much of Tanzania, and Uganda; and (4) one including much of Zimbabwe and southwestern Zambia. When we increased the selection target all the way to 50 (Table 1), the solutions became increasingly similar to the total species richness map of all the species (Appendix 1, Fig. S1A–D; see also Fig. 4 in Walther et al. 2010).

The BLM selection procedure began with BLM set to zero (Table 1, Fig. 1B), which was equivalent to the final setting of the null selection procedure (Appendix 1, Fig. S1D). The effect of subsequently increasing the BLM to 0.01 (Fig. 1C) and 0.1 (Fig. 1D) concentrated the selection of grid cells within the four previously mentioned regions, whereas the grid cells outside of these four regions were eliminated.

The human footprint selection procedure was the same as the null selection procedure, but we changed BLM to 0.1 and excluded the grid cells with a high human footprint (Table 1). As the selection target was increased from 1 to 50 (Table 1), more of the grid cells were selected within the previously mentioned four regions (Fig. 1E; Appendix 1, Fig. S2). A low selection target pinpointed the most valuable grid cells (Appendix 1, Fig. S2A), whereas a high selection target pinpointed the most valuable regions (Fig. 1E). The results from the final setting of the BLM selection procedure (Fig. 1D) and the results from the final setting of the human footprint selection procedure (Fig. 1E) are identical except for the exclusion of grid cells with the highest human footprint (Table 1); some high-footprint grid cells were excluded along the coastline of West African countries and in central Burkina Faso, eastern Sudan, northern Ethiopia, western Kenya, most of Uganda, northern Tanzania, central Zambia, and northern and southern Zimbabwe. The excluded grid cells were replaced with grid cells in central Nigeria, northern Kenya, and southern Mozambique.

The SPF selection procedure was the same as the final setting for the human footprint selection procedure (Fig. 1E) except that we varied the SPF from 0.05 (Appendix 1, Fig. S3A) to 10 (Appendix 1, Fig. S3F; Table 1). The lowest SPF selected four regions, whereby the one usually selected in West Africa was moved further south (Appendix 1, Fig. S3A). However, this region expanded to the east, north, and west at higher SPF values (Fig. 1F; Appendix 1, Fig. S3B–F). Central Chad was a region that was only included at an SPF of 0.05; at all higher SPF values, it disappeared. The two regions in East Africa consistently selected were (1) central and eastern Sudan, Eritrea, northern Ethiopia, and western Somalia (or Somaliland), and (2) Kenya and Tanzania. The final regions that appeared only at SPF values ≥ 0.25 were western Zambia, central Zimbabwe, and southern Mozambique.

The maximum target selection procedure maximized the target solutions whereby each given species' target was set to the total number of occurrences of that species throughout the grid cells and then the SPF was increased from 0.04 to 0.012 (Table 1). At the lowest SPF, only a strip of grid cells across the Sahel region was selected plus scattered grid cells across Uganda, Kenya, and Tanzania (Fig. 1G). At increasing SPF, the selected grid cells covered an increasing share of the African continent until they basically covered all regions where migrant species overwinter (Appendix 1, Fig. S4A–H).

The threatened status selection procedure was the same as the final setting for the human footprint selection procedure (Fig. 1E) except that we gave higher importance to species of conservation concern (Table 1). The main change was that the four selected regions became more restricted (Fig. 1H). When we repeated this procedure but without a BLM (BLM = 0), a much more scattered string of grid cells was selected along the Sahel zone and down East Africa from Uganda and Kenya to Zimbabwe and Mozambique (Fig. 1I).

DISCUSSION

Our results differ from the previous findings of Walther et al. (2010) in two important aspects. Most importantly, the maximum target and threatened status selection procedures placed much greater emphasis on a belt of grid cells across what is commonly defined as the Sahel region, demonstrating the importance of this region to migratory songbirds (Fig. 1G and I). This region was already found to be important when simple species richness maps were used to distinguish regions where especially threatened migratory bird species overwinter (Walther et al. 2011). A review of recent ecological changes in the Sahel (Walther 2016) further demonstrated that this threat is likely connected to the rapid land-use and biodiversity changes that have taken place in the Sahel over the last few decades, which appear to be faster and more widespread than in any other region of Africa, including legal and illegal land grabs (Osinubi et al. 2016).

Our study is also the first to exclude grid cells (human footprint, SPF, maximum target, and threatened status selection procedures; see Table 1) with a high human footprint, which resulted in the exclusion of grid cells across much of northern Ethiopia and most of Uganda and Zimbabwe. Therefore, these regions are not useful for conservation efforts that could help most of the 68 species considered here.

However, when we used similar settings to those used by Walther et al. (2010), their previous findings were supported. Again, the

four main regions identified as most important for conservation efforts were: (1) one centered on southern Mali and containing large parts of the surrounding countries except toward the north; (2) one centered on Eritrea that includes large parts of central Sudan and northern Ethiopia; (3) one encompassing southwestern Kenya and much of Tanzania and Uganda (although most of Uganda becomes excluded if the human footprint is taken into account); and (4) one including much of Zimbabwe and southwestern Zambia. These regions appeared especially distinctly when the BLM was increased because this forced increased clumping of grid cells (Fig. 1B–D). Many previous studies (summarized by Walther et al. 2010) also emphasized the importance of these four priority regions, especially the Sahel and the broadleaf savannas just south of the Sahel, for both passerine and nonpasserine migrants, although the Great Rift Valley, Uganda, Kenya, or Zambia are also important regions for migrant conservation. However, none of these previous studies used such a fine spatial scale as we did ($1^\circ \times 1^\circ$) or performed complementarity analyses.

In our opinion, the principal inference from these results is that these four regularly selected regions should be priority regions for both research and conservation efforts for the bird species considered here. In addition, our work further emphasizes the special importance of the Sahel region, especially the most western and eastern parts of the Sahel. Given that this region is in dire need of better biodiversity protection (Walther 2016), efforts to protect these migratory species could have many additional benefits, including better protection for many other threatened species, increased resilience of the ecosystem to climate change and other human-induced drivers of landscape change such as overgrazing and soil erosion, and better education and income for local people through ecotourism (e.g., Jarjou 2016). However, for those migrant bird species that overwinter exclusively in East Africa (e.g., the Endangered Basra Reed Warbler *Acrocephalus griseldis*; Walther et al. 2004, 2011, Walther 2006), the two East African regions pinpointed by our results should also become foci for increased research and conservation. Uganda could be an interesting test case because most of its grid cells were excluded because of high human impact. However, some migrant species apparently fare better or at least as well in degraded habitats as in undisturbed habitats (Walther et al. 2011, Adams et al. 2014, Atkinson et al. 2014, Walther 2016). Therefore, conservation of a few of the study species could be fostered in regions with high human population densities and ecological impacts.

The complementarity analyses implemented in MARXAN are not based on species richness, so some species-rich areas such as southern Niger, northern Nigeria, and central Chad (Walther et al. 2010) were not selected because they contain species that are also found in other regions (e.g., Senegambia, Eritrea). However, these species-rich regions were selected in the maximum target selection procedure (Fig. 1G), further emphasizing the importance of the entire Sahel region for many migrant bird species.

It must also be emphasized that priority regions pinpointed here are based on the best available estimate of each species' wintering distribution. Therefore, by definition, they do not include important migration stopover sites because those sites are not included in the definition of wintering areas (Walther et al. 2010).

For example, the northeastern tip of Somalia may be a very important refueling site for migrants returning to their breeding grounds (G. Nikolaus, *unpublished data and personal communication* 2015), but our results do not capture such areas.

Finally, it should be noted that there are inherent methodological uncertainties in both the distribution modeling of the species as well as the MARXAN analyses. Uncertainty in distribution modeling has recently been explored in the context of ensemble models of species distributions (e.g., Gould et al. 2014, Tassarolo et al. 2014). However, our models were built using the best model approach (Thuiller 2003), which does not allow for such calculations. Furthermore, it is obvious that the threshold chosen for turning the probabilistic species distribution model into a binary distribution model (Nenzén and Araújo 2011) also influences which grid cells are considered as occupied by a species or not, which introduces further uncertainty. Uncertainty in the MARXAN analyses is depicted by the different frequencies by which grid cells are chosen. Given these uncertainties, the results may have been different for some individual grid cells, but we doubt that our overall conclusions about which regions are important to conservation efforts of the study species would have been any different.

The four regions recommended above have very little overlap with regions recommended in previous continent-wide complementarity studies (Lovett et al. 2000, Williams et al. 2000, Balmford et al. 2001, Brooks et al. 2001, Burgess et al. 2002, 2005, 2006, Moore et al. 2003, Küper et al. 2004, Dillon and Fjeldså 2005, McClean et al. 2006, Rondinini et al. 2006), mostly because those studies focused on different taxa (e.g., African plants and African megafauna), but also because of methodological differences (e.g., all of the studies published up to 2005 used WORLDMAP). The only region regularly highlighted by both the previous studies and our study was the Uganda-Kenya-Tanzania region; a few times, the Ethiopian region and the Zambia-Zimbabwe region were also selected. However, it is now well established that different taxa often yield different priority sites or regions (e.g., Brooks et al. 2001, Moore et al. 2003) because they occupy different niches, habitats, and ecoregions, and that different selection criteria also result in different recommendations for priority sites (e.g., Reyers et al. 2002, Bonn and Gaston 2005, Wu et al. 2013, 2014).

Unfortunately, a major knowledge gap that remains to be filled is the sub-Saharan distributions of all the nonpasserine bird species that migrate between the Western Palearctic and sub-Saharan Africa. These species could not be included in our analysis but there is urgency for them to be included. So far, and despite repeated attempts by the first author, it was not possible to mobilize the resources to enter the required data into this or any other database to perform a similar analysis for nonpasserine species. Given that massive amounts of data have already been collected (e.g., Scott and Rose 1996, Delany et al. 2009, Zwarts et al. 2009, and all the national African atlases), a renewed push for such a comprehensive data analysis is highly encouraged.

Other possible critiques of continent-wide analyses such as this one are that they mean little for local, on-the-ground conservation, and that the protection of large regions is unrealistic. We disagree for the following reasons. Continent-wide analyses have been used previously to focus conservation efforts, including financial support of local and regional conservation projects, by

conservation nongovernmental organizations such as BirdLife International and Conservation International. Further, continent-wide analyses may encourage national leaders to increase conservation efforts if they notice that their country is actually an important one for a particular species or suite of species. Such analyses will hopefully also encourage local and national conservation initiatives to work together on a more regional basis because they emphasize that long-term conservation can often only succeed when conducted in collaboration across countries or even continents (the Peace Parks Foundation is a good example).

Moreover, continent-wide analyses emphasize the magnitude of the conservation challenge. While it may be realistic in the short term to hope for a few more relatively small and isolated reserves in the regions prioritized by our study, it is also clear that such reserves would very likely do little for the long-term survival of many of the migratory bird species studied here (just as they have done little for most of the large birds and mammals of the Sahel; see Walther 2016). Given that the wintering grounds are spread across large regions of Africa, we will not be able to protect them adequately unless we can achieve land-use and management strategies compatible with species survival in large parts of the African continent. Unless systemic change in land use and land management across large regions of the African continent is achieved, the migratory bird populations will continue to decline. A recent review of the Sahel's state of biodiversity (Walther 2016) came to the same conclusion for the Sahel's native plants and resident large birds and mammals, and Rondinini et al. (2005) called for 30–100% expansion of Africa's reserve system just to achieve minimal conservation targets.

Finally, the objective of science should be to tell what is necessary, not what is realistic. Therefore, if species require large areas for their survival, we should say so, not dampen down our conclusions to fit "realistic" requirements, whatever they may be. Therefore, the conclusions that we derived from our analyses are located on the "necessary" side of the conservation biology argument, along the lines of Wilson's (2016) assertion that half of the planet must be conserved for wild nature for the biosphere to have a decent chance for survival.

It should also be clear that national governments, international organizations, and nongovernmental organizations will not likely make sufficient funds available to protect or purchase the vast areas of land that would be needed to halt or even reverse biodiversity loss. Rather, to achieve positive continent-wide conservation outcomes, continent-wide conservation analyses strongly advance the notion that a wholesale change in policy priorities is needed, including regulation and enforcement of conservation-based laws on a continent-wide scale to change an environmentally destructive socioeconomic system into a fundamentally sustainable one (e.g., Trauger et al. 2003, Daly and Farley 2011, Czech 2013, Walsh 2013, UNEP 2016) in which the link between biodiversity and human health and well-being is firmly acknowledged and nurtured (Clark et al. 2014, Sandifer et al. 2015, Walther et al. 2016). Thus, positive conservation outcomes would not just be restricted to protected areas, but would be implemented across entire landscapes and regions. Without the support of African governments and civil society, analyses such as this one are essentially meaningless exercises in

number crunching. With their support, however, such analyses could be the launching pads for a sustainable future for the African continent.

Responses to this article can be read online at:
<http://www.ace-eco.org/issues/responses.php/934>

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Appendix 1. Supplement

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