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RESEARCH ARTICLE

Comparative niche modeling of two bush-shrikes (*Laniarius*) and the conservation of mid-elevation Afromontane forests of the Albertine Rift

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ABSTRACT
Avian endemism in the Albertine Rift is among the highest of any region in Africa. Conservation of these forests is a high priority, but informed prioritization has been hampered by limited data for most endemic bird species. We employed ecological niche models, coupled with remote sensing and field data, to present a case study of 2 Albertine Rift bush-shrikes (*Laniarius*) that until recently had been considered conspecific. The ecological niche models are based on presence-only data from museum specimens and sight records from field surveys from the region. We generated a set of competing models with different subsets of environmental variables. We evaluated competing models with an intuitive and broadly applicable model-selection strategy appropriate for assessing suitable habitat for species of conservation concern. Based on its distribution, habitat requirements, and the boundaries of national parks in the Albertine Rift, our results demonstrate that the recently described and cryptic Willard's Sooty Boubou (*Laniarius willardi*) has lost most of its available habitat within its realized environmental niche and is highly endangered. The Mountain Sooty Boubou (*L. poensis*) occurs in areas above 2,000 m, where forests are more intact and better protected than mid-elevation forests where *L. willardi* occurs. These results highlight the plight not only of a recently described species, but also of additional biodiversity confined to mid-elevation forests in the Albertine Rift region.

Keywords: biogeography, *Laniarius poensis*, *L. willardi*, montane fauna, protected areas, species distribution

Modélisation comparative des niches de deux espèces de *Laniarius* et conservation des forêts afromontagnardes d'altitude moyenne du Rift Albertin

RÉSUMÉ
L'endémisme aviaire dans le Rift Albertin est l'un des plus élevés de toutes les régions d'Afrique. La conservation de ces forêts est hautement prioritaire, mais les données limitées pour la plupart des espèces d'oiseaux endémiques nuisent à une priorisation éclairée. Nous avons employé des modèles de niche écologique, en utilisant des données de télédétection et de terrain, pour présenter une étude de cas de deux espèces de *Laniarius* du Rift Albertin qui, jusqu'à tout récemment, étaient considérées comme des congénères. Les modèles de niche écologique sont basés sur des données de présence provenant de spécimens de musée et d'observations visuelles provenant de travaux de terrain dans la région. Nous avons généré un ensemble de modèles concurrents avec différents sous-ensembles de variables environnementales. Nous avons évalué les modèles avec une stratégie de sélection de modèle intuitive et largement applicable qui est appropriée pour évaluer l'habitat convenable pour des espèces préoccupantes avec des données limitées. Basé sur sa répartition, ses besoins en termes d'habitat et les frontières des parcs nationaux dans le Rift Albertin, nos résultats démontrent que *Laniarius willardi*, une espèce récemment décrite et cryptique, a perdu la plupart de son habitat disponible au sein de sa niche environnementale réalisée et qu'elle est en voie de disparition. *Laniarius poensis* fréquente les zones situées au-dessus de 2 000 m où les forêts sont plus intactes et mieux protégées que les forêts d'altitude moyenne où *Laniarius willardi* est présent. Ces résultats mettent en lumière la situation difficile non seulement pour une espèce récemment décrite, mais aussi pour la biodiversité confinée aux forêts d'altitude moyenne dans la région du Rift Albertin.

Mots-clés : biogéographie, *Laniarius poensis*, *L. willardi*, faune montagnarde, aires protégées, répartition des espèces

INTRODUCTION

Montane regions throughout the world are important for avian diversity (Chapman and Chapman 1996, Fjeldså et al. 2012, Quintero and Jetz 2018). These regions provide different habitats across elevational gradients, and the distinctive, often island-like, nature of these habitats has frequently resulted in significant local and regional avian endemism (Chapman and Chapman 1996, Quintero and Jetz 2018). In the Anthropocene, montane bird communities can be affected by climate change (Freeman and Freeman 2014), and as lowland forests are cleared, mid-elevation montane forests come under increasing risk of disturbance and deforestation (Hartter et al. 2011, Hansen et al. 2013). Here, we present data from ecological niche modeling to demonstrate that human-driven habitat loss is a particularly serious threat for mid-elevation forests of the Albertine Rift region of Central Africa.

The Albertine Rift is a collection of separated highlands that reaches ~5,000 m elevation, spans 6 nations, and is part of the Eastern Afromontane biodiversity hotspot (Mittermeier et al. 2004). Within the Albertine Rift, distinct highlands include the relatively well-known Rwenzori Mountains of Uganda and the Democratic Republic of Congo (DRC) and the Virunga Volcanoes of Rwanda, Uganda, and DRC, but also the Itombwe Plateau and Kahuzi-Biega National Park (DRC), Nyungwe National Park (Rwanda), and Kibira National Park (Burundi), among others. Evidence for elevational structuring of avian communities in the region is based on data for the Rwenzori Mountains (Willard et al. 1996, Dehn and Christiansen 2001) and the Itombwe Plateau (Prigogine 1980). The primary conservation focus in the Albertine Rift has been on montane forests, with less consideration of geography and species distributions (Kahindo et al. 2007, 2017), although recent models predict regional montane forest connectivity for some endemic birds in the face of climate change and intervening habitat (Bagchi et al. 2018). The region's flagship animals include endangered species such as the eastern gorilla (*Gorilla beringei*) and Grauer's Swamp Warbler (*Bradypterus graueri*; Kahindo et al. 2017), but the region is a hotspot for >40 endemic species of birds (Prigogine 1980, Bober et al. 2001, Plumptre et al. 2007). New vertebrate species are still being described from the area, including birds (Engel et al. 2014), small mammals (Kerbis Peterhans et al. 2013a, 2013b), lizards (Greenbaum et al. 2011, 2012), and amphibians (Evans et al. 2011, Greenbaum et al. 2013, Portillo and Greenbaum 2014a, 2014b).

Voelker et al. (2010) showed that sooty bush-shrikes in the genus *Laniarius* that occur in mid-elevation forests in the Albertine Rift are morphologically and phylogenetically distinct from those that inhabit higher-elevations forests. They described the mid-elevation taxon as *Laniarius willardi* (Willard's Sooty Boubou), which is also vocally distinct (recordings deposited in xeno-canto: http://www.xeno-canto.org/). This new species had been overlooked as part of *L. poensis* (Mountain Sooty Boubou), another Albertine Rift species (e.g., Prigogine 1980, Fry et al. 2000, Harris 2000). Voelker et al. (2010) presented specimen locality data documenting that Willard's Sooty Boubou replaces Mountain Sooty Boubou at elevations below 2,000 m at several sites in the Albertine Rift; subsequent observational data have reinforced this pattern. The species is recognized by most taxonomic authorities (e.g., Clements et al. 2013, whose taxonomy we follow here; del Hoyo et al. 2013; Gill and Donsker 2014), with the notable exception of BirdLife International (2016), the Red List authority for birds. The latter authority chose not to recognize *L. willardi* as a species because Voelker et al. (2010) did not adequately deal with a sooty boubou population in the Cameroonian highlands (currently called *L. poensis camerunensis*). That highly disjunct population is of interest, but we chose not to include it in this study because our focus is on the Albertine Rift and, although Voelker et al. (2010) did not address its taxonomic status (because sampling was inadequate), it is genetically distinct from its sister (*L. willardi*). The taxonomic treatment by BirdLife International means that the conservation status of *L. willardi* is not considered a priority according to the Red List.

To investigate the distributions of *L. poensis* and *L. willardi*, we used ecological niche models (ENMs), along with remote sensing data and field data, to create binary maps of habitat suitability. We also developed a strategy to select among competing ENMs when other statistical measures do not allow selection of an outperforming model. We consider the implications of these results, not only for these 2 *Laniarius* species, but also for the conservation of mid-elevation species across this poorly known biodiversity hotspot.

METHODS

Ecological Niche Modeling
Ecological niche modeling is a consolidated tool for studying how abiotic conditions can be used to predict species' spatial distribution (Peterson 2001). For conservation, ENMs, combined with geographic data (e.g., tree cover and protected areas [PAs]) and land-use data, can help document and highlight issues that species face both now and in the future, especially in habitats that have become highly fragmented as a result of human activity (e.g., Peterson and Robins 2003). We used Maxent (Phillips et al. 2006), which has been used in similar conservation-related studies (Moreno et al. 2011, Reside et al. 2012, Bagchi et al. 2018) and to evaluate bird species distribution across elevational transects (e.g., Buermann et al. 2011).

Data Collection and Processing

We initially relied on museum-specimen records obtained from the Field Museum of Natural History (FMNH) and the American Museum of Natural History (AMNH), outlined in Voelker et al. (2010). We discarded records with vague localities and coordinates that could not be resolved within a few kilometers. Georeferenced museum records came from 13 localities, 3 for *L. willardi* and 10 for *L. poensis* (see Appendix Figure 3). To augment museum data for both species, we also analyzed modern survey records from the Wildlife Conservation Society (WCS; Bagchi et al. 2018). The WCS's Albertine Rift Program has surveyed birds, large mammals, and plants in most of the major montane forest blocks in this region. All the WCS data for these sooty shrikes were recorded as *L. poensis*, because *L. willardi* was unknown at the time of the surveys. The elevation of each occurrence was confirmed using digital elevation models. Elevational replacement between the 2 species at ~2,000 m is supported both by specimen data (from Kibira National Park, Burundi) and by more recent observational data from Bwindi Impenetrable National Park (Uganda; D. Ochanda personal communication, J. M. Bates et al. personal observation) and Nyungwe National Park (B. Finch personal communication). This lower elevational limit for *L. poensis* also conforms to other parts of the Albertine Rift where *L. willardi* is apparently absent. On the basis of these data, we reclassified WCS records of sooty shrikes from below 2,000 m as *L. willardi* in our analyses. We also include recent sight records that were also identified as *L. willardi* by call (archived in xeno-canto). We added a buffer of ±50 m to extend the 2,000 m threshold, avoiding a single arbitrary threshold. We also discarded 26 records between 1,950 and 2,050 m with questionable elevation data (see Appendix). These 26 records comprised only 2% of all the records. If we would extend this buffer between 1,900 and 2,100 m, we would find only 26 more records, so the choice of 2,000 m or any elevation within ±100 m has a small influence on the classification of the presence points. The combined specimen–observation dataset included 1,155 records above 2,050 m (*L. poensis*) and 59 below 1,950 m (*L. willardi*). By default, Maxent uses only one sample per grid cell (our cell size is 1 km^2); as a result, we had 309 unique locations for *L. poensis* and 27 for *L. willardi*.

Study Area

We designated geographic boundaries covering all primary regions of the Albertine Rift (Figure 1). These included all suitable inhabited sites and the areas around those sites that the species could inhabit (Barve et al. 2011), including the largest PAs and adjacent upland regions that might have offered, in prehuman settlement times, suitable habitat for mid-elevation and lowland birds.

Environmental Variables

In addition to species presence data, Maxent relies on abiotic and biotic data whose choice should be based on the ecology of the study taxa (Guisan et al. 2006, Austin 2007). However, because the ecology of Albertine Rift boubous in genus *Laniarius* is poorly known, we selected different subsets of environmental variables based on Maxent "percent contribution" and "permutation importance" scores, and on Pearson's correlation coefficient. These subsets contained different combinations of World-Clim data (temperature, precipitation, and 19 bioclimatic variables; http://worldclim.org/, Hijmans et al. 2005), in addition to slope and aspect (see Appendix). Each subset was used in conjunction with different Maxent settings to generate a set of niche models for the 2 species. Specifically, in addition to Maxent default settings, we used a range of regularization multiplier and feature class settings (Shcheglovitova and Anderson 2013) to account for the small sample size of *L. willardi*. Furthermore, the regularization multiplier setting reduces model overfitting when a small sample size is used in a model with a high number of environmental variables.

Model Selection

Model selection with the use of area under the curve (AUC) has been discouraged because AUC can be misleading (Pearson et al. 2007, Lobo et al. 2008). In a preliminary phase, we also considered Akaike's information criterion (AIC), but models with the lowest AIC were overpredicting distribution and had a high number of parameters. Instead of AUC and AIC, we used an intuitive statistical test to compare the performance of the competing models we generated. This test is based on the relationship between 2 statistics provided by Maxent: test omission rate (TOR) and minimum training presence area (MTPA). In a Maxent simulation when the presence data are split in "training" and "test" subsets, TOR is a measure of how many test points (the points not used to train the model) fall outside the predicted suitable habitat generated with the training data. MTPA is simply the total predicted area of suitable habitat based on the minimum presence threshold. A model predicting a large suitable area, MTPA, has a high probability that more test points fall within the MTPA, leading to a lower TOR. Conversely, models predicting a small MTPA are more likely to have a high TOR. Thus, the trade-off between MTPA and TOR can be used to compare models according to the following guidelines. If models had similar TOR, we preferred the model predicting a smaller MTPA. If models predicted a similar MTPA, we preferred the one with lower TOR. We also preferred the model with smaller MTPA and lower TOR. Lastly, when none of these cases occurred, we selected the model predicting a smaller MTPA. Thus, our approach links a measurement of model performance
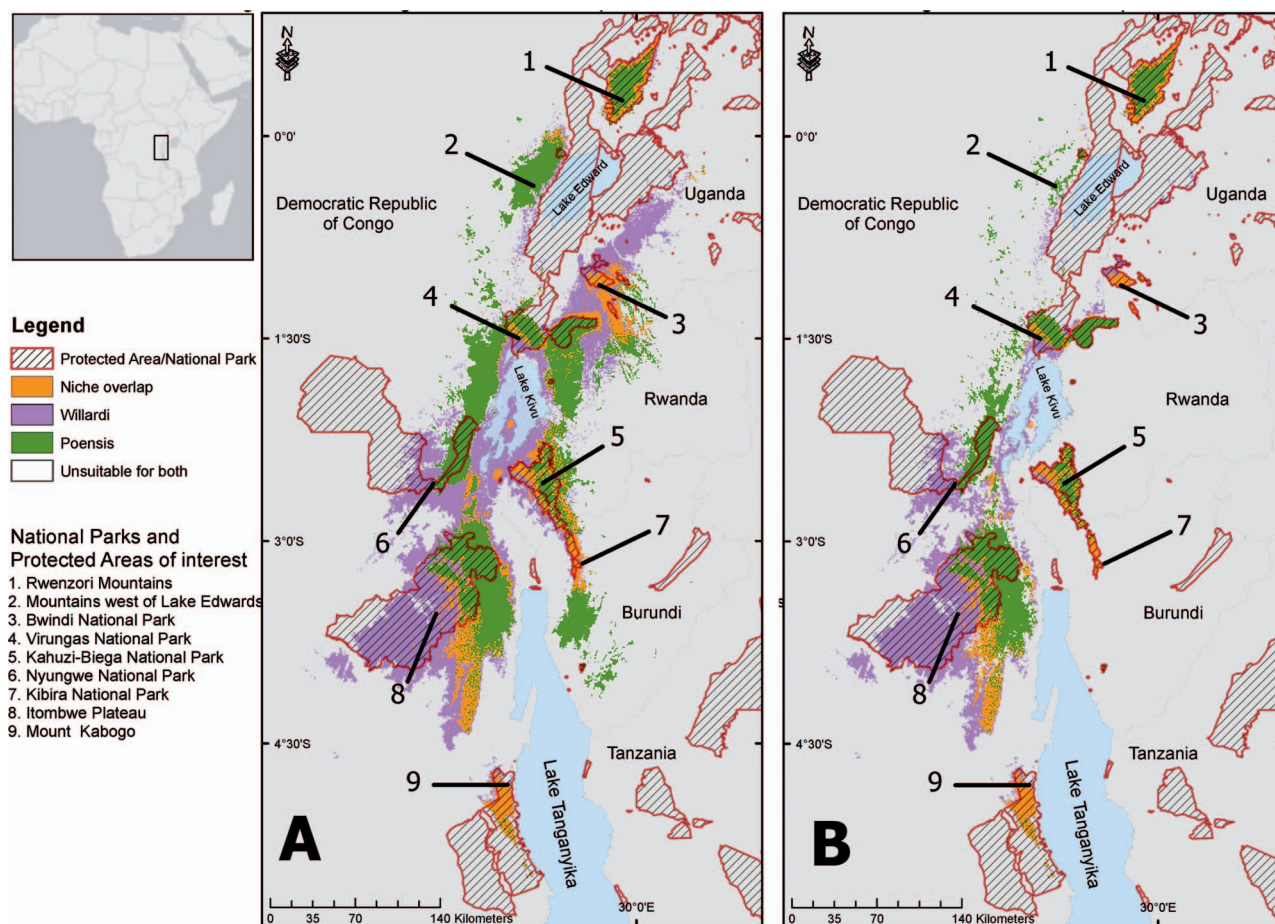
FIGURE 1. Predicted suitable habitat for *Laniarius willardi* and *L. poensis*: (**A**) potential distribution and (**B**) remaining suitable habitat according to WCS land cover data.

(TOR) with a spatial measure (MTPA), both easily interpretable. Our model selection reduces the chances of selecting an overpredicting model because it couples conservative TOR/MTPA guidelines with different subsets of environmental variables and Maxent settings. The *L. poensis* models were very similar, with a low TOR (.05–1%) and a difference in MTPA of ≤10%, indicating low variability among models. With fewer data points, *L. willardi* models had a higher variation with TOR (10–14%) and a bigger range of MTPA (≤20% difference among models).

On the basis of the TOR/MTPA model selection criteria, we selected one model for each species, and without splitting the data in training vs. test, we averaged 100 Maxent runs to account for stochasticity (Edrén et al. 2010, Anadón et al. 2012). The environmental variables used in the selected models were, for *L. poensis*, maximum temperature (March, August, and November), temperature seasonality, temperature annual range, and precipitation (February, July, and November); and, for *L. willardi*, November maximum and mean temperature, precipitation

(October and June), temperature seasonality, maximum temperature of the warmest month, precipitation of coldest quarter, and temperature annual range. We used the minimum training presence logistic threshold to create binary maps of suitability (Thomé et al. 2010) and combined them to create a niche overlap map. This threshold represents the minimum suitable conditions for each species in sites where it is present. We added to the map a layer containing the PA boundaries provided by WCS.

RESULTS

Voelker et al. (2010) reported that *L. willardi* and *L. poensis* overlap minimally across their distributions in the Albertine Rift, and our models (Figure 1) document marginal overlap, indicating that the climate envelopes derived from these data are largely distinctive. Models based only on the limited museum-specimen data reflect general patterns seen in the models incorporating the observational data, particularly for *L. poensis* (Appendix

TABLE 1. Area (km^2) of predicted suitable habitat for *Laniarius willardi* and *L. poensis* (PAs = protected areas, WCS = Wildlife Conservation Society).

GlobCover 2009

Species	Total	Inside PAs	WCS reclassified	Above 2,000 m	Below 2,000 m
L. poensis	29,471	5,547	11,090	24,133	5,316
L. willardi	19,915	5,555	10,969	118	19,794
Overlap	8,889	3,583	6,207	6,281	2,583

TABLE 2. Niche statistics (m) for *Laniarius willardi* and *L. poensis*: average elevation, elevation frequency distribution quantiles, and elevation range.

Species	Average	SD	2.5%	97.5%	Range
L. poensis	2,442	516	1,821	3,829	2,008
L. willardi	1,529	197	1,202	1,936	734
Overlap	2,120	187	1,832	2,573	741

Figure 2). The specimen-only model for *L. willardi* relied on 3 samples and, thus, has to be interpreted with caution, but it also predicts a similar (though broader) distribution compared to the model with observational data. We relied on the models that include both observational data and museum specimens to evaluate the niches of both species.

Human habitat alteration in this region is substantial. Only a fraction of the total area with suitable conditions based on the model is truly available to either species (Table 1). We have extensive on-the-ground experience throughout the region, and we consider the layer with boundaries of PAs to be an accurate indicator of remaining suitable habitat (i.e. little or no upland forest remains outside of PAs). Our data suggest that remaining suitable habitat in PAs is nearly equivalent and includes substantial overlap for the 2 species (Table 1). The GlobCover 2009 land cover map (reclassified by WCS experts; Bagchi et al. 2018) indicates that remaining habitat (classified as "natural vegetation") extends beyond PAs (Table 1) in some areas.

Elevation and the elevation frequency distribution (EFD) across suitable habitat (Table 2) show that 97.5% and 2.5% quantiles of the EFD are in areas where the 2 species do not overlap. The elevational range of *L. poensis* is broader (1,821–3,829 m) than that of *L. willardi* (1,202–1,936 m). Our analysis suggests that the range of *L. poensis* could extend more below 2,000 m than the range of *L. willardi* extends above 2,000 m. Given that presence points between 1,950 and 2,050 m were not included, the model output does not show a bias toward the 2,000 m limit. In other words, the model seems to be free from the threshold we chose, implying a potential difference between realized and fundamental niches. The mean elevation of overlap is 2,120 m. *Laniarius willardi* is unrecorded above 2,000 m, however, perhaps because physiological limitations or competition restrict its upper elevational limit. Additionally, 70% of the overlap area is above 2,000 m and is spread over a large elevational gradient, while 95% of the overlap habitat under 2,000 m is between 1,800 and 2,000 m. Even with the smaller sample size for *L. willardi*, which increases the uncertainty in predicting its potential distribution, the model still shows high statistical accuracy (10% TOR) and highlights

areas that we suspected, a priori, to be suitable habitat for *L. willardi*. Anecdotally, after we had generated a preliminary distribution map, several new records we received for both species were within the range predicted by the model.

Looking at the predicted suitable habitat for these species (Figure 1), Willard's Sooty Boubou appears to have just as much habitat as the Mountain Sooty Boubou. However, in Burundi, Rwanda, and Uganda, 70% of habitat suitable for *L. willardi* is outside of PAs where all mid-elevation forest outside of PAs has been converted to agriculture. Values for DRC are only slightly better. These mid-elevations of the Albertine Rift (1,300–2,000 m) are either rural landscapes or PAs with borders sharply defined by adjacent agriculture (Fjeldså and Burgess 2008). The vast majority of these PAs are above 2,000 m (and therefore unsuitable habitat for *L. willardi*). To add another quantitative measure, we used forest-cover-change data from Hansen et al. (2013) to compare remaining forest cover inside and outside PAs. We found that in 2012, the percentage of land covered by forests was 81.4% (SD = 22.68) inside PAs and 43.13% (SD = 29.44) outside PAs. However, these data are overly optimistic because Hansen et al. (2013) classify vegetation >5 m tall as forest cover, thereby including cultivated plants (e.g., eucalyptus and bananas).

DISCUSSION

Species segregation across elevational gradients is a striking feature of montane ecosystems, and documenting these patterns requires accurate data (e.g., McCain 2009). *Laniarius willardi* is a recently discovered, cryptic species of the mid-elevation Albertine Rift forests (1,300–2,000 m). It was overlooked until detailed genetic and morphologic analyses of museum specimens were conducted (Voelker et al. 2010).

Although caution is warranted in interpreting species delimitations that rely on ecological niche modeling (Tocchio et al. 2015), the ENMs presented here indicate that *L. willardi* differs in its realized environmental niche from *L. poensis* of the Albertine Rift. Thus, *L. willardi* joins other poorly known mid-elevation bird species endemic to this region (e.g., Chapin's Mountain-Babbler [*Turdoides chapini*] and Yellow-crested Helmetshrike [*Prionops al-*

berti]) that are listed as Near Threatened or Vulnerable by the IUCN. Our results suggest that *L. willardi*, and therefore other mid-elevation Albertine Rift taxa, face a tenuous future due to high human population density (Linard et al. 2012) that encroaches extensively upon the elevations where these species occur. The models suggest that *L. willardi*, now known from very few sites across the Albertine Rift, has likely undergone significant population declines from regional habitat loss that has been going on for centuries.

Mid-elevation Forests Are Both Distinctive and Endangered in the Albertine Rift

A recent niche-modeling study of 12 endemic Albertine Rift birds highlights climate change as a primary determinant of connectivity in models of future movements in the region (Bagchi et al. 2018). The focus of that analysis was on assessing future connectivity, which will be critical, but it does not go into geographic detail with respect to present-day issues facing mid-elevation taxa like *L. willardi*. These mid-elevation taxa are possibly being pushed to the higher end of their ranges because of habitat destruction at lower elevations, which may represent a more immediate threat than climate change. Our results suggest that *L. willardi*'s current distribution is within a much narrower elevational band than that of the higher-elevation *L. poensis*, and these elevations are not well represented in PAs.

The combined museum-specimen and observational data on Albertine Rift sooty boubous had been assumed to represent a single species that was considered common across these highlands. The discovery of *L. willardi* does not change the "least concern" conservation status of the higher-elevation *L. poensis* (BirdLife International 2016), which inhabits brushy forest undergrowth, clearings, and forest edge and therefore persists in areas with only remnant forest. Although such areas are few outside of PAs in most parts of the Albertine Rift, we have found *L. poensis* to be fairly common in undergrowth in actively logged forest at 2,300 m on the eastern slope of the Itombwe Plateau (see below). Natural history data for *L. willardi* are still limited. Its ability to adapt to forest edge situations is unknown, although it was recently recorded in tall secondary forest in Nyungwe National Park (B. Finch personal communication).

Importance of Protected Areas for *L. willardi*

Our ecological niche modeling highlights PA-specific management issues for major Albertine Rift highland units, with particular focus on mid-elevation forest (in geographical order from north to south; Figure 1).

(1) *Laniarius willardi* is currently unknown from the northern Albertine Rift. Our ENMs predict little habitat for the *L. willardi* species, including in the Rwenzori Mountains National Park, where, despite forest being present below 2,000 m on the western (DRC) side, the species is not predicted to occur. WCS records of sooty boubous from the Rwenzoris are all above 2,300 m. Specimen records of *L. poensis* exist down to 2,075 m (Mubuku Valley, FMNH data; Willard et al. 1996, Voelker et al. 2010) on the eastern (Ugandan) slopes; however, no sooty boubous were recorded at 1960 m on the park's eastern border (Willard et al. 1996), below which there is no forest today.

(2) Our ENMs suggest suitable habitat for *L. willardi* in the mountains immediately west of Lake Edward (DRC), and this is possibly supported by historical specimens that have not been identified to species (AMNH specimens from the early 1900s with vague locality data from 1,600 m in this region; Voelker et al. 2010). Today, PAs to the west of the main rift (Tayna and Kisimba Ikobo Reserves in the DRC) include mid-elevation forests, but our models do not predict the species there. No forest remains at mid-elevations near the lake (one small forested area on Mt. Tshiabirimu remains, but this forest is above 2,000 m). The models suggest that the largest suitable area would have been at the southern end of these highlands.

(3) A stronghold for *L. willardi* is Bwindi National Park, Uganda, which protects the most extensive mid-elevation forests in the eastern Albertine Rift. Kalinzu-Maramagambo Forest Reserve also contains forest up to 1,845 m, and Kasyoha-Kitomi Forest Reserve has forest between 975 and 2,136 m, but sooty boubous are unrecorded there (Baltzer 1996a, 1996b, Engel and Kerbis 2016, Ugandan Wildlife Authority personal communication). Other PAs in the region do not include appropriate elevations. Sooty boubous of any species are unrecorded from lower-elevation forests such as Kibale Forest National Park (Matthews 1996, WCS data). All records of sooty boubous from other PAs in the region, such as Mgahinga Gorilla National Park and Echuya Forest Reserve, are from 2,300 m or higher (WCS and FMNH data), and known specimens are *L. poensis* (Voelker et al. 2010). The models predict extensive areas to be suitable outside of PAs, but all these lands have long been converted to agriculture.

(4) The Virunga National Park stretches several hundred kilometers on the Albertine Rift's west side, straddling the borders of Uganda, Rwanda, and the DRC. Little forest exists below 2,000 m in the park, but there is forest around the active volcanoes near Goma at the north end of Lake Kivu. WCS surveys include 2 records of sooty boubous at 1,651 m and 1,837 m on a forest border on the western (DRC) side of the park. Outside of PAs in this region, other patches in the DRC, including the Masisi highlands, west of the park, may still have some remnant forest (Figure 1). Models that did not take into account current land use and forest cover predict suitable habitat in northern Rwanda. There are sooty boubou museum specimens from the early

1900s from this region (Voelker et al. 2010), but no mid-elevation forests exist in this part of Rwanda today.

(5) Kahuzi-Biega National Park in the DRC is a UNESCO World Heritage site, but 25 yr of civil war have rendered portions largely inaccessible. No historical surveys of the park's birds exist (Demey and Louette 2001). The park's eastern highland sector has borders beginning at 2,100 m, and no forest exists outside this part of the park at elevations below that limit. All records of sooty boubous are from above 2,000 m, and all specimens are *L. poensis* (WCS data, FMNH data, Voelker et al. 2010). Our model identifies some forests in the western sector of the park as suitable for *L. willardi*. Much of the potentially suitable forest, in a corridor connecting eastern and western sectors, was invaded and deforested during the civil war. These areas have been too dangerous to survey; once the regional political situation improves, searching here for *L. willardi* is a priority. Models that do not take into account current land use predict suitable habitat for *L. willardi* between Kahuzi-Biega and Nyungwe national parks and the Itombwe Plateau. This region includes human-populated lands in Rwanda and the eastern DRC bordering Lake Kivu and the western highlands between Lake Kivu and Lake Tanganyika.

(6) The lowest elevations of Nyungwe National Park in Rwanda have not been surveyed thoroughly for *L. willardi*, but there are recent observations and recordings (B. Finch personal communication; xeno-canto), and intact forest extends down to 1,700 m on the west side of the park. The park's borders are well defined, but suitable habitat for *L. willardi* is limited because most of the park is well above 2,000 m. Cyamudongo forest, which was formerly connected to Nyungwe National Park, is 300 ha of habitat between 1,700 and 2,000 m that could harbor a population (Behrens et al. 2015).

(7) Contiguous to Nyungwe National Park, the montane forest of Burundi's Kibira National Park is one of the localities where *L. willardi* was first collected (Voelker et al. 2010). The amount of suitable mid-elevation forest is limited, possibly to several hundred hectares, although, as with Nyungwe National Park, the borders of the park are stable despite ongoing political instability in the country.

(8) The Itombwe Plateau, west of Lake Tanganyika, is the most extensive upland region in Central Africa, but it remains incompletely known despite extensive surveys by Alexander Prigogine in the 1940s. His analysis of the elevational distribution of birds across the plateau did not include discussion of *Laniarius* species (Prigogine 1980). The most substantial areas of remaining habitat for *L. willardi* are likely to be on the western side of the plateau; however, insecurity throughout this region has made access difficult. Thus, the identity of sooty boubous at mid-elevations of the plateau requires confirmation (in addition, another species, the Lowland Sooty Boubou [*L. leucorhynchus*], occurs in the Congo basin to the west; see Voelker et al. 2010). Recently, the governmental agency Institut Congolais pour la Conservation de la Nature has started ranger patrols in the Itombwe region and the official borders of a national park have been established, but laws cannot be enforced, and there is substantial human habitation throughout the PA. The formerly extensive forest on the plateau's steep eastern slopes, above Lake Tanganyika, is largely gone. During 2012 fieldwork on the northern part of the eastern escarpment, we saw a few narrow bands of disturbed forest that reached down to 1,800 m, but forest in this area, extending to well above 2,000 m, was being extensively cut. The plateau is considered a high conservation priority. Several poorly known birds (e.g., Congo Bay-Owl [*Phodilus prigoginei*] and Rockefeller's Sunbird [*Nectarinia rockefelleri*]) are restricted to high elevations of this region. Recent herpetological surveys have described new species of frogs that replace each other by elevation on the plateau (Portillo and Greenbaum 2014a, 2014b). Much remains to be learned about the fauna of the Itombwe Plateau, but surveying and conservation efforts will be difficult for years to come.

(9) Models predict that Mt. Kabogo (also referred to as Kobobo) in the DRC, where forest extends to Lake Tanganyika at 760 m, is suitable for either species, but WCS surveys encountered black shrikes mostly above 2,000 m. Three records come from 1,892 m. Currently, no genetic or vocal data exist for these birds, so their specific identity remains in question. Additional survey work would be a priority here.

Conservation Implications for *L. willardi*

Areas that are predicted to be suitable for both *L. poensis* and *L. willardi* are narrow, and current data suggest possible competitive exclusion between the 2 species. In areas of potential overlap, only *L. poensis* has been recorded (specimen data and recent surveys that used the now-known vocal differences between the 2 species). These regions include higher elevations of Bwindi National Park (D. Ochanda personal communication) and parts of Nyungwe National Park (J. M. Bates, xeno-canto recordings); more detailed study of interspecific interactions is warranted, but these observations indicate that Kabogo birds may be mostly or only *L. poensis*.

Niche modeling combined with data layers on current land use and forest cover confirm that few areas outside of designated PAs have suitable habitat for *L. willardi*. Before humans dominated this landscape, extensive forest would have existed between 1,300 and 2,000 m. Today, outside of PAs at these elevations, forest has been replaced by some of the highest densities of rural human settlements on the African continent (Linard et al. 2012). Potentially suitable areas in the presumed western range of *L. willardi* (e.g., the

Itombwe Plateau) have been largely inaccessible for survey work because of regional insecurity.

We still have more to learn about the distributions of species in the Albertine Rift, and more animals and plants likely will have distributions limited to mid-elevation forests inhabited by *L. willardi*. One such taxon is the recently described Kabembe treefrog (*Leptopelis mtoewaate*; Portillo and Greenbaum 2014a). These mid-elevation forests have generally been ignored as a specific conservation priority, yet they are largely devastated across the region. It is critical to develop strategies to both study and conserve their unique biodiversity. Our results suggest that when addressing climate change and other issues (Bagchi et al. 2018), the plight of such mid-elevation species and their greatly reduced habitats is as serious as that of higher-elevation species, and potentially more so.

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APPENDIX

Details on Data Collection, Verification, and Processing

We discarded 26 records between 1,950 and 2,050 m to account for errors in elevation measurements. These records were in or near highly sampled areas, and their exclusion had negligible effects on the models' output according to preliminary simulations that included them. Additionally, only 12 of 26 records had unique latitude–longitude locations.

To confirm the elevation of each record, we compared the georeferenced presence points with the elevation given by 2 digital elevation models (DEMs): ASTER Global Digital Elevation Map (GDEM, 30 m resolution) from the Earth Remote Sensing Data Analysis Center (http://gdem.ersdac.jspacesystems.or.jp/) and Shuttle Radar Topographic Mission 3 (SRTM3, 90 m resolution extracted with GPS Visualizer, http://www.gpsvisualizer.com/about.html). This operation was critical to verifying georeferencing errors and to eliminate records that were within 50 m from the 2,000 m threshold. We manually used Google Earth to evaluate records with high discrepancy between the field survey-reported elevation and the DEMs.

Climate layers used for modeling were downloaded from the WorldClim website (http://worldclim.org/; Hijmans et al. 2005) at the highest available resolution of 30 arc-seconds ($\sim$1 km^2). The layers comprise current condition (ca. 1950–2000) split into monthly averages for maximum temperature, minimum temperature, mean temperature, and precipitation, in addition to 19 bioclimatic variables. We calculated aspect and slope from WorldClim elevation data.

Preliminary Model Design

Ideally, the choice of environmental variables should be driven by ecological factors (Guisan et al. 2006, Austin 2007). However, because the ecology of *Laniarius* species in the Albertine Rift is poorly known, we do not know what abiotic and biotic factors are most relevant ecologically. When such basic information is absent, some studies have ranked variables based on Pearson's correlation coefficient and avoided highly correlated variables (Liang and Stohlgren 2011). Another option involves a recursive variable selection process based on a combination of variable contribution to the model and correlation (D. Warren personal communication). Thus, we created different subsets of environmental variables according to the different methodologies described above.

First, we calculated the correlation among all variables with ENMTools (http://www.danwarren.net/enmtools/builds/ENMTools_1.4.4.zip) and discarded those with a correlation >0.70. Then we created 2 subsets: (1) the least correlated variables across all categories and (2) the least correlated variables by category (minimum temperature, maximum temperature, mean temperature, precipitation, bioclim). We then ran the model with all WorldClim variables and selected variables on the basis of their combined contribution and permutation scores (an important indicator for including or excluding variables [see http://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc]; most of the layers had to be discarded because they had a low combined score) to create 2 additional subsets: (3) variables that had a combined contribution and permutation score >4.0, because we wanted to have a small number of environmental variables; and (4) the same criterion as subset 3, but if 2 variables from the same category (i.e. minimum temperature, maximum temperature) had a correlation
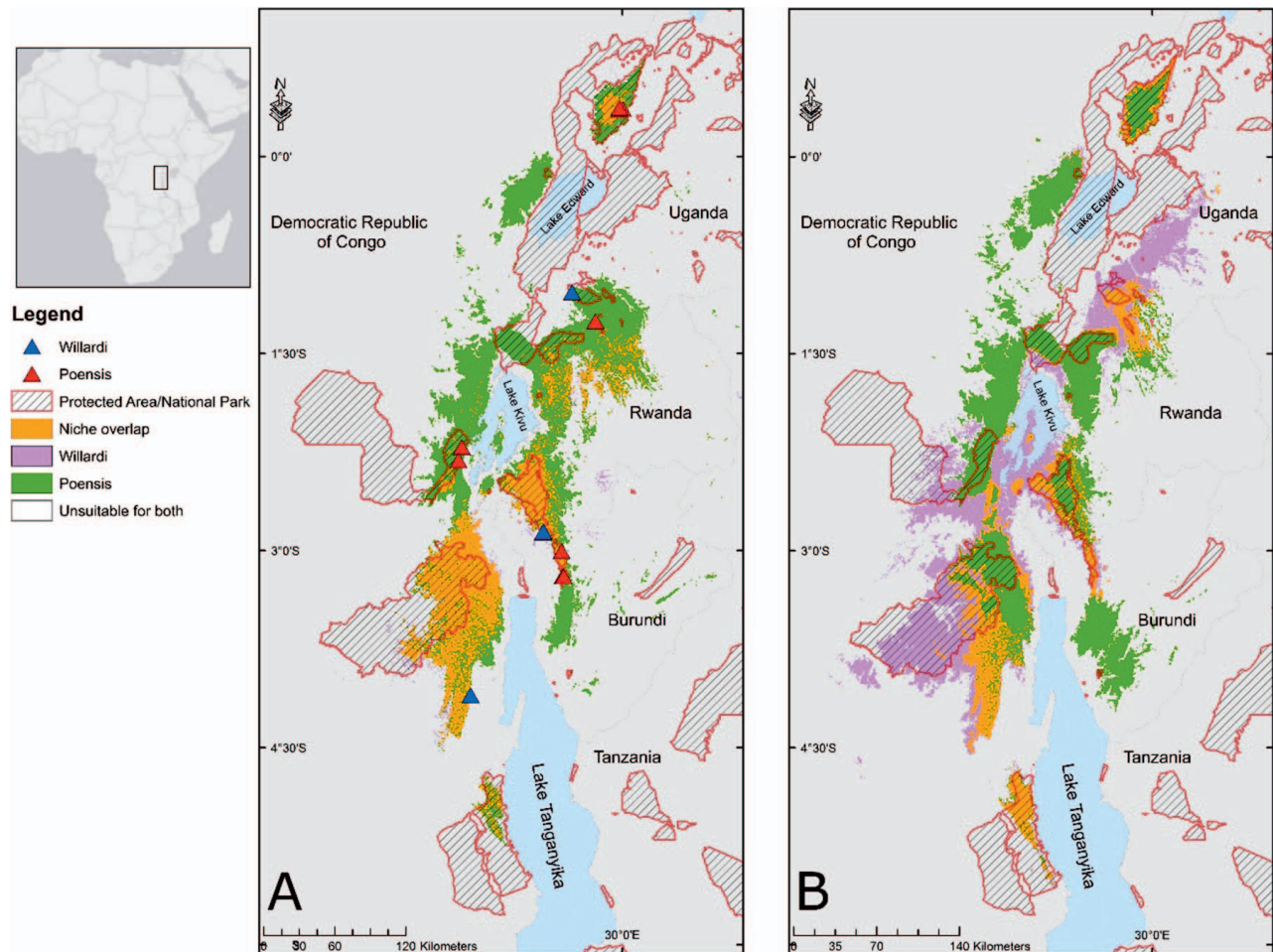
APPENDIX FIGURE 2. Predicted suitable habitat for *Laniarius willardi* and *L. poensis,* according to model based only on museum specimens.

>0.75, then only the one with the higher contribution and permutation score was retained.

Only for *L. willardi*'s models, each subset of environmental variables was paired with a different combination of feature classes and regularization multiplier settings following Shcheglovitova and Anderson (2013). Models were generated according to the average of 100 runs with subsampling run type and 30% of the samples set aside to test the model and 70% to train the model.

Following the methodology explained in the text, we then assessed model quality and selected, for both species, the model generated with environmental subset 3. The regularization multiplier helped improve performance for *L. willardi*'s models, and the effect of feature class was negligible. Competing models for the same species were similar in their output, although a few areas showed slight changes in the predicted value. Slope and aspect always had low permutation and contribution scores.
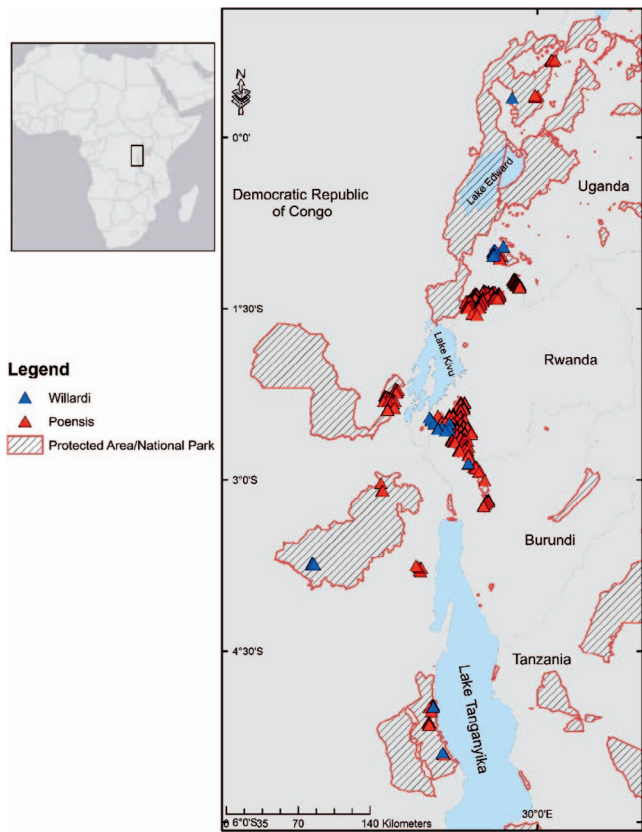
APPENDIX FIGURE 3. Sample distribution of *Laniarius willardi* and *L. poensis* across the study area.