ABSTRACT

WILSON, JOHN WILLIAM. Conservation Planning in a Changing World: Mitigating the Deleterious Effects of Habitat Loss. (Under the direction of Nicholas M. Haddad).

Humans are driving species to extinction at rates faster than ever before. A major reason for this is habitat loss; with an ever-burgeoning human population and ever-increasing per-capita footprint, our natural heritage is losing the struggle to eke out suitable living spaces. We humans have left nothing untouched, from the deepest oceans to the highest mountains, the lithosphere and the atmosphere. Some urgent and serious initiative is required if we want our children and their children to have an enjoyable natural heritage, or even just their own livable habitat. In this dissertation, I focused my attention on developing practical guidelines to alleviate the deleterious effects of this yet unmitigated disaster, habitat loss. First, I offer guidelines on identifying potentially suitable, potentially unoccupied living spaces for rare species using satellite imagery. By allowing us to obtain continuous indices of our natural world in more detail than ever before, satellite images offer opportunities that classified landcover products can’t even approach. Being mindful that not all living spaces are equal, I then use the habitat maps derived from satellite imagery to suggest how potential reintroduction sites can be prioritized, by analyzing dispersal pathways between existing and envisaged populations of rare species. Such ‘connected’ reintroductions sites will enable those populations to better disperse to nearby unoccupied habitat as their sizes increase, and better equip them to adapt to changing environments in the long term. Lastly, while I disagree with the principle, I considered the unfortunate reality that we have limited resources at our disposal to ensure our children’s children will enjoy the same natural
wonders we enjoyed. With a lack of enough political and public will, we seem to be compelled to implement a triage system on our living wonders; to do more, with less. By projecting distribution ranges for birds endemic to the Guinean Forests of West Africa, I identify those species that will most likely be driven to extinction before the end of this century by the combined effects of climate change and habitat loss. For those reading this dissertation, I hope it motivates you to do more to ensure our children and their children will also enjoy the natural wonders we treasured.
Conservation Planning in a Changing World: Mitigating the Deleterious Effects of Habitat Loss

by

John William Wilson

A dissertation submitted to the Graduate Faculty of North Carolina State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Zoology

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DEDICATION

Vir my ouers, John and Magda. Ek volg my drome danksy jul onvoorwaardelike liefde
BIOGRAPHY

John William Wilson was born in Bloemfontein, South Africa on 9 June 1979. Throughout his childhood, Johnny’s parents and grandparents paid regular visits to nature reserves. Johnny enjoyed all these trips, but particularly enjoyed the Kruger National Park, so much so, he called it his first home. Here, as young as four years old, Johnny would grab the closest field guide lying around the car, and try to match what he saw outside with the pictures in the book. Kenneth Newman’s Birds of Kruger National Park hereby became the book in which Johnny learnt to read. From here on, Johnny’s life story has written itself.

Johnny, already a ‘game warden’ at 5 years old, introducing himself to the birds of Kruger National Park

Johnny plans to continue working on conservation issues, to do his bit to ensure his children and their children will find the same enjoyment from nature as he is.
I am grateful to my advisory committee, and in particular to Dr. Nick Haddad who showed
tremendous patience during my explorations of other scientific pursuits during my PhD.
These pursuits have led to the following peer-reviewed articles during my time at NCSU:

   Gallinula comeri: conservation implications for the moorhen and seabirds. Ardea 95:
   311-315

   importance of the environment, human activity and space in explaining species

   Green-winged Pytilia Pytilia melba. Ostrich 79: 87-90

   evaluation of morphological differences in the Karoo Thrush Turdus smithi – Olive
   Thrush Turdus olivaceus species complex. Ostrich 80: 171-175

   small mammals to natural and human-altered edges associated with Afromontane
   forests in South Africa. Forest Ecology & Management 259: 926-931

   success of Northern Rockhopper Penguins (Eudyptes moseleyi) at Gough Island, South
   Atlantic Ocean. Emu 110: 137-141

   Breeding biology of Brown Noddies at their southern-most breeding site, Gough
   Island, in comparison to other sites. Ardea 98: 242-246


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First and foremost, I would like to thank my lovely wife, Lesley. She has been a rock-solid foundation throughout, providing unwavering support whether in the heat of Ft Bragg or the humidity of Cameroon, and would simply drop whatever she was doing during the multiple times I asked her editing help. As the stress levels increased during this degree’s final stages, she married me when others would have run away. Without you, I would have never completed (or survived) this degree.

A doctoral degree is filled with fun, but also challenges. As I have also learned, it gets tougher the longer you stay. I would not have finished this journey without the support of my American family of friends. Many are now in other states and countries; others will stay in North Carolina while I move on. Wherever you are, I look forward to keeping in touch.

My journey to the Tar Heel State began during one of our annual South African power birding sessions when Stuart Pimm first floated the thought. After mentioning it to Dalia and Scott, two of Stuart’s students who traveled with him, the encouragement was ‘relentless’. I knew I just had to when a surprise package filled with GRE preparation books arrived at my Pretoria office! Once in North Carolina, Dalia and Scott made me feel at home, and introduced me to a group of wonderful people who became my American family of friends.

I also received a great deal of support from those in more formal capacity. Dean Urban, Stuart Pimm, and their respective students happily welcomed me in their labs during my spatial analysis training at Duke University. My lab group and graduate support crew at NCSU Biology were always helpful, supportive, and friendly. Nick was tremendous in his
advisory role, especially his patience and continued support with this sometimes perhaps too independent-minded student and his many ‘side projects’. To that end, a number of further-afield collaborators, especially Mike, ensured my wandering mind remained gainfully occupied at times when I became restless.

For any PhD, especially the ones taking an extra few years, funders become even more important. For that, I would like to acknowledge funding from NCSU’s Biological Sciences Department, and grants from the Endangered Species Branch at Ft. Bragg, NASA grant #NNX11AP61G to Nick Haddad, and NASA grant #NNX11AL49H to Gil Bohrer.

Laastens wil ek my familie in Suid Afrika bedank vir al hul steun en onwrikbare geloof in my. Dinge was soms maar woes gedurende hierdie graad, maar my ma, pa, Daline was altyd daar vir my, wanneer ek geweet het ek het hulle nodig, en wanneer ek dit nie geweet het was. Julle was enorm gewees; ek sal julle nooit genoeg kan bedank nie.
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The relative contribution of terrain, land cover, and vegetation structure indices to species distribution models

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ABSTRACT

Habitat assessments for biodiversity conservation are often complicated by the lack of detailed knowledge of a study species’ distribution. As an alternative to resource-intensive field-based methods to obtain such information, remotely sensed products can be utilized in species distribution models to infer a species’ distribution and ecological needs. Here we demonstrate how to arbitrate among a variety of remotely sensed predictor variables to estimate the distribution and ecological needs of an endangered butterfly species occurring mainly in inaccessible areas. We classified 19 continuous environmental predictor variables into three conceptually independent predictor classes, terrain, land cover, and vertical vegetation structure, and compared the accuracy of competing Maxent habitat models consisting of different combinations of each class. Each class contributed, though disproportionately, to our most reliable model that considered all 19 variables. We confirm that variables obtained from remote sensors can effectively estimate the distribution and ecological needs of a relatively unknown imperiled species occurring in inaccessible locations. Importantly, increasing the variety of predictor classes through multi-sensor fusion resulted in greater model accuracy than increasing the absolute number of predictor variables.

1. Introduction

Considering that habitat loss is a primary driver of species extinctions, detailed habitat assessments are among the most important first steps guiding conservation efforts for imperiled species (Mace and Lande, 1991). Through habitat assessments are, however, often complicated by the lack of detailed knowledge of a threatened species’ distribution, habitat status, and ecological needs (Anderson and Martinez-Meyer, 2004). Obtaining such information is not trivial. Threatened species are often sparsely distributed, hard to detect, and – due to biotic interactions, historical legacies, and dispersal barriers – not found in all suitable habitat patches (Pulliam, 2000). These qualities make it hard to separate unsuitable habitat from unoccupied suitable habitat (Gu and Swihart, 2004). In addition, time and monetary constraints typically prevent detailed bio-assessments that involve extensive surveys, experiments, and long-term demographic studies. Here we estimate the distribution and ecological needs of a relatively unknown imperiled species occurring in inaccessible locations, and, in doing so, develop methods to evaluate the contribution of a variety of readily accessible, continuous remotely sensed predictor variables that may be incorporated into species distribution models.

To overcome the challenges associated with imperiled species’ habitat assessments, ecologists employ species distribution models (SDMs) to estimate imperiled species’ distributions (Elith and Leathwick, 2009). Using spatial data describing distributions and environmental characteristics, SDMs estimate the relationship between the study species’ occurrences and the underlying environment. These approximations of the target species’ environmental niche are then used to model suitable ecological conditions over an entire study region (Elith and Leathwick, 2009). Because they enable researchers to overcome the challenges associated with resource-intensive bio-assessments, and because of improved model reliability, SDMs have become increasingly popular among ecologists and conservationists (Elith and Leathwick, 2009).

Progress in remote sensing technologies has strongly complemented advances in SDMs. As an alternative to resource-intensive field-based methods, air- and space-borne sensors enable researchers to acquire reliable environmental data at scales relevant to SDMs in a consistent and repeatable way (Gillespie et al., 2008), even from poorly known and inaccessible areas (Raxworthy et al., 2003). Despite their utility, remotely sensed predictor variables remain underutilized in SDMs, possibly because the literature offers little guidance on appropriate datasets (Buermann
et al., 2008) and interpretation of results obtained from remotely sensed data (Turner et al., 2003). Since the scale at which organisms perceive and interact with their environment is often much smaller than the scale at which many remotely sensed variables are obtained, concerns have also been raised as to whether remotely sensed data can be used to detect environmental variation at scales relevant to SDMs (Bristot et al., 2011; Laurent et al., 2005).

The accelerating availability of diverse, remotely sensed products has generated questions about which and how many parameters to incorporate into model building. These parameters can be categorized into four conceptually independent remotely sensed predictor classes – terrain, (horizontal) land cover, (vertical) vegetation structure, and climate. Building on a previous effort that only considered land cover variables to track temporal habitat changes (Bartel and Sexton, 2009), we develop SDMs using a range of continuous remotely sensed predictor variables within three of these four remotely sensed predictor classes for an endangered butterfly, the St. Francis’ satyr Neonympha mittelherrii francisci. From these, we developed seven SDMs based on each predictor class independently, and in combination with one another. Few of our SDMs thereby utilized data from more than one sensor simultaneously, termed “multi-sensor fusion” (Hall and Llinas, 1997). Using our SDM results, we compared the performance of each SDM, blocked by data source, in predicting St. Francis’ satyr presence. We also evaluated the relative contribution of each predictor variable to St. Francis’ satyr distribution. In conducting our investigation, we developed an approach that tests significance of different classes of remotely sensed variables that should be generally applicable to arbitrate among competing models that could include various data inputs.

2. Material and methods

2.1. Study species

St. Francis’ satyr, globally restricted to early-successional wetlands situated on United States Department of Defense lands at Ft. Bragg, NC (35°07’S, 79°08’W, 65,032 ha), is an ideal species for a case study on SDMs utilizing remotely sensed data for a number of reasons. First, the species is listed as Endangered under the United States’ Endangered Species Act because of its low population size and limited geographical range. Second, some previously healthy St. Francis’ satyr subpopulations are currently in decline as once-suitable habitat transitions toward late-successional stages (Kuefler et al., 2008; Bartel and Sexton, 2009), creating an urgent need to assess the status of suitable habitat to determine the likelihood of population recovery. Third, our study area offers what we believe to be several suitable early-successional wetlands that support St. Francis’ satyr’s one known host plant, Coreopsis dichotoma. Fourth, much of the distribution of St. Francis’ satyr falls within the restricted artillery impact zones at Ft. Bragg, where very limited and irregular access complicates efforts to confirm presences of this cryptic species with a short flight period (Kuefler et al., 2008). St. Francis’ satyr is thereby representative of many other species whose life history is poorly described, and/or that live in inaccessible areas.

2.2. St. Francis’ satyr occurrence

During 2008 we extensively (i.e. daily, during both month-long flight periods, Kuefler et al., 2008) searched for St. Francis’ satyr butterflies in all known and accessible colonies (n = 17). For each butterfly observed, we obtained Universal Transverse Mercator (UTM) coordinates using a WAAS-enabled Trimble Nomad 9000GL Global Positioning System (GPS) unit (1–3 m accuracy). In total, 138 GPS points were obtained, all within 3 m of butterfly observations to maximize locational accuracy (Graham et al., 2008). Because of the temporary, successional nature of St. Francis’ satyr habitat, we based habitat suitability models on locations where we saw St. Francis’ satyr during one focal year, 2008 (the year for which we obtained Landsat data, see below).

2.3. Predictor variables

We tested the relative importance of three conceptually independent predictor classes of remotely sensed predictor variables – terrain, (horizontal) land cover, and (vertical) vegetation structure – in explaining St. Francis’ satyr distributions (Table 1). We omitted a fourth class consisting of climate measures because such data are usually coarsely scaled (Turner et al., 2003) and thus more appropriate for regional or continental SDMs (Gillespie et al., 2008; Elith and Leathwick, 2009). While some interpolated (e.g. Thornton et al., 1997) and combined (e.g. Herman et al., 1997) climate measures exist, remotely sensed climatic predictor variables are rare, especially for terrestrial surfaces.

Terrain variables, derived from Digital Elevation Models (DEMs) (Li et al., 2005), play an important, though indirect, role in SDMs through their influence on climate (Moore et al., 1990) and vegetation (Franklin, 1995). Five continuous terrain predictor variables were used in this study, which included proxies for moisture (flow accumulation and slope), solar radiation (aspect), and topography (relative slope position and terrain shape. Moore et al., 1990). All terrain variables in this study were derived from the USGS National Elevation Dataset (Ciesielski et al., 2002), which we obtained at 1/3 arc second resolution, resampled to 10 m resolution, and processed using tools contained in the ArcGIS Spatial Analyst and TauDEM v. 4.0 (Tarboton, 2008) packages.

Land cover predictor variables, obtained through passive optical multispectral sensors, are used to describe a study area’s physiographic and physiognomic characteristics. Most often, land cover

<table>
<thead>
<tr>
<th>Variable</th>
<th>Variable importance (%)</th>
<th>Permutation importance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Remoteley sensed class</td>
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<tr>
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<td>Flow Accumulation</td>
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<td>Land cover</td>
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<td>Brightness Seasonality</td>
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<tr>
<td>Winter greeness</td>
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<tr>
<td>Summer wetness</td>
<td>3.4</td>
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<tr>
<td>Winter brightness</td>
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<td>Winter wetness</td>
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<tr>
<td>Summer greeness</td>
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<tr>
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<td>1.4</td>
</tr>
<tr>
<td>Midstory density</td>
<td>1.8</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Variable importance is calculated heuristically and thus sensitive to collinearity and the order of variable importance. Permutation importance provides an alternative measure that is calculated from the AUIC of the final model, and thus robust to the path of input variables.
variables are converted to categorized thematic land-cover-landuse maps before use in SDMs (Laurent et al., 2005; Cord and Rödder, 2011). Recently however, continuous remotely sensed vegetation indices have gained some traction in SDMs (Sexton et al., 2006; Buermann et al., 2008; Cord and Rödder, 2011), though a range of other continuous land cover indices (e.g. for soil and wetness, Kauth and Thomas, 1976; Crist and Cicone, 1984) and land cover measures (e.g. thermal emissivity, Wang et al., 2008) remain largely neglected (although see Bartel and Sexton, 2009). Nine continuous land cover variables were used in this study. To obtain these variables, we georectified one cloud- and snow-free winter (January 2008) and one cloud-free summer (May 2008) Landsat-5 Thematic Mapper (TM) image of the study area (path/row: 16/36; resolution: 30 m). We then converted the six solar-reflective (non-thermal) TM bands (bands 1–5, 7) to radiance (Chander et al., 2007) and estimated surface reflectance using the DOS3 approach (Song et al., 2001). Surface reflectance values were then transformed to Tasseled-Cap “brightness,” “greenness” (Kauth and Thomas, 1976), and “wetness” indices (Crist and Cicone, 1984) in the ArcGIS 10 package. For each Tasseled-Cap Index, our SDMs incorporated summer and winter values, and the difference between summer and winter values to characterize seasonality, or “ deciduousness.”

Vegetation structure predictor variables are obtained primarily through active and passive optical remote sensing systems such as Interferometric Synthetic Aperture radar (INSAR) and Light Detection and Ranging (LiDAR) sensors (Lefsky et al., 2002). Though still under-utilized, continuous vegetation structure variables have recently been used more frequently in SDMs (Goetz et al., 2010; Welsey et al., 2012). Five continuous LiDAR-derived vegetation structure variables were used in this study. To obtain LiDAR data for our study area, we contracted an airborne Optech ALTM 2050 LiDAR System to fly over Ft Bragg in early July 2006 (while deciduous trees were in leaf-on condition) at a height of 4500 ft and a flight speed of approximately 120 knots. This instrument produced a spot spacing of 1 m, horizontal accuracy of 0.3 m, and vertical accuracy of 95% within ±1.2 m, from which we derived mean vertical density of vegetation in the understory (1–2 m above ground), shrub layer (2–5 m), midstory (5–10 m), subcanopy (10–20 m), and canopy (>20 m). We chose vegetation density as a predictor variable because it best characterizes the relative vertical structure of a habitat, an important aspect of habitat suitability for St. Francis’ satyr (Kufler et al., 2008). LiDAR data were processed at the 10 m resolution using a Maximum-Likelihood model (Moody et al., 2011).

2.4. Species distribution models

To model the distribution of St. Francis’ satyr, we used the Maxent software package (Phillips and Dudik, 2008; Elith et al., 2011), as has been previously used to map St. Francis’ satyr habitat (Bartel and Sexton, 2009). As a generative model, Maxent compares the environment underlying input presence points against a random sample of background points representing the availability and range of environmental conditions, and produces a raster map ranking each cell in the study area on an index representative of relative habitat suitability. Maxent accounts for interactions among predictor variables (Phillips and Dudik, 2008), and deals with model overfitting by employing the L1-regularization procedure (Hastie et al., 2009; Warren and Seifert, 2011), thus reducing the need to remove correlated predictor variables or preprocessing input before modeling (Phillips and Dudik, 2008; Elith et al., 2011). Originally designed for modeling rare and endangered species distributions, Maxent has gained popularity in part because it is less sensitive to the number of input presence locations (Wisz et al., 2008), and relies on presence-only data, thereby avoiding the possibility of indeterminacy of habitat vs. non-habitat when faced with issues of imperfect detection (Guisan et al., 2006).

We developed seven Maxent models to estimate habitat suitability of St. Francis’ satyr: one model combining all predictor variables from each of the three remotely sensed predictor classes (3 models), one model from each possible pair-wise combination of the three predictor classes (3 models), and one model combining all predictor variables from all three predictor classes (the full model). Developing these seven models allowed us to directly examine the ability of each remotely sensed predictor class, separately and in combination, to predict habitat suitability. Prior to Maxent modeling, all layers were clipped to Ft. Bragg’s boundary, to maintain a consistent extent across all SDMs. We also artificially downscaled all land cover predictors, obtained at the 30-m resolution, to 10-m resolution to align predictor variables and avoid losing the fine-scale detail present in LiDAR and DEM-derived variables (at the 10 m resolution). For each Maxent model, we used 10,000 background points and the default settings recommended by Phillips and Dudik (2008) for features and regularization for model training (but see Warren and Seifert, 2011). To estimate errors for model performance evaluation, we implemented Maxent’s built-in 10-fold cross-validation on each model to obtain 10 quasi-independent measures of a model’s predictive ability (Hastie et al., 2009).

2.5. Model evaluation

We calculated two model performance measures that have been formulated for use in situations where absences are unavailable. First, for each model we calculated the mean area under the receiver operating characteristic curve (AUC) (plotting model sensitivity [errors of commission] against 1-specificity [errors of omission]: a random prediction will result in an AUC value of 0.5 whereas a perfect prediction assumes the maximum possible AUC of 1.0 (Fielding and Bell, 1997), and AUC values >0.75 are suitable for conservation planning (Pearce and Ferrier, 2000, but see Lobo et al., 2008). Second, we calculated mean omission error as the percentage of the withheld 10% test sample of presence points not predicted to fall within suitable habitat. To distinguish suitable from unsuitable habitat along Maxent’s continuous habitat suitability index, we used the point on the AUC where model sensitivity is equal to specificity (sensitivity-specificity equality approach, Liu et al., 2005). However, because AUC is sensitive to the L1-regularization term, and omission error is highly sensitive to the amount of habitat predicted to be suitable, it cannot be used to compare model performance directly (Anderson et al., 2003). To allow for direct comparison of model performance, we calculated ‘standardized omission error’ based on binary habitat maps with the same amount of suitable area, which we set at the mean percentage of suitable area (0.08%) of the total study area) predicted across all SDMs.

To evaluate the ability of each remotely sensed predictor class, separately and in combinations, to predict St. Francis’ satyr presence, we compared our model performance measures (as dependent variables) against each of our seven groups of Maxent models (the factors) using two-way ANOVAs. For all significant ANOVA tests, post hoc pair-wise comparisons with Tukey’s HSD tests were used to further investigate differences in model performance among the seven Maxent models. We also examined each SDM’s heuristic estimates of how each predictor variable influenced the final model prediction (Phillips and Dudik, 2008). Lastly, we evaluated the importance of the number of predictor variables in SDM performance using ANCOVA analyses, with AUC values and standardized omission error as dependent variables, number of predictor variables as factors, and number of predictor classes as covariates.
Statistical analyses were conducted using R (R Development Core Team, 2011), and all means are reported ±1 Standard Deviation (SD).

3. Results

Overall, our SDMs performed well in predicting St. Francis' satyr habitat suitability. Mean AUC values across all models (0.95 ± 0.048; max possible is 1.0) fell within the range of excellent performance (AUC > 0.9; Pearce and Ferrier, 2000; Swets, 1988), while both mean omission rate (0.15 ± 0.06; 0.0 and 1.0 is best and worst respectively) and mean standardized omission rate (0.13 ± 0.12) were relatively low. All of our SDMs suggest that suitable St. Francis' satyr habitat is highly restricted, ranging from 0.03% to 0.22% of the total study area (Table 2). SDMs combining all three remotely sensed predictor classes performed best in predicting St. Francis' satyr presences; the full model (together with the terrain-land cover model) had the highest mean AUC, and the lowest mean standardized omission error. Conversely, each of the three one-class SDMs performed, on average, worse than those SDMs combining two and three classes, for both AUC and standardized omission error (Table 2). Despite predicting the greatest proportion of suitable habitat, the SDM based on only vegetation structure captured the least amount of the test sample of presence points, making it the worst performing model.

Comparisons of both AUC values ($F_{5,69} = 131.94, P < 0.001, r^2 = 0.926$) and standardized omission errors ($F_{5,69} = 63.20, P < 0.001, r^2 = 0.858$) indicated statistically significant differences in model performance among our seven Maxent models (Table 3). Notably, the SDM based on only terrain predictors performed significantly better than any other single-class model, while SDMs combining terrain variables with other classes performed significantly better than models without terrain variables. Lastly, the number of variables included in an SDM strongly influenced model performance. After accounting for the number of classes included in each model, models with many variables had significantly higher AUC values than those with few variables (ANCOVA, $F_{5,66} = 7.66, P < 0.007$). However, we found no significant differences in standardized omission error values among models with different numbers of variables. Further investigation suggested that predictor class might be more important than absolute number of variables. Although not always statistically significant, the terrain-only SDM (5 predictor variables) was more reliable in predicting St. Francis' satyr presences than the land cover-only SDM (9 predictor variables) and land cover-vegetation structure SDM (14 predictor variables) (Table 2).

The permutation importance values (which are less sensitive to variable order than variable importance values) of our best-performing SDM (the full model) suggest that at least some predictor variables from all three remotely sensed predictor classes contributed to model reliability (Table 1). The most important predictor variables were: a land cover predictor, summer-winter greenness differences (41.3%), followed by two terrain predictors, slope (25.3%) and relative slope position (10%). Canopy density was the fourth-largest contributor (8.5%) to the final model prediction, and the only vegetation structure predictor contributing more than 5% of the overall prediction. The influence of these predictor variables on occurrence reflects St. Francis' satyr's presence in streams and floodplains (from terrain predictors) with semi-deciduous vegetation (from land cover) and an open canopy (from vegetation structure) (Fig. A1).

Competing SDMs resulted in considerable overlap in the extent of predicted suitable St. Francis' satyr habitat (Fig 1). Importantly, areas of suitable habitat predicted from SDMs combining two different predictor classes resembled the intersection of those two predictor classes when considered in isolation (Fig 1). This habitat prediction pattern was also observed when all three predictor classes were modeled together. Despite predicting the least amount of

Table 2

<table>
<thead>
<tr>
<th>Predictor classes</th>
<th>Number of predictor variables</th>
<th>Logistic threshold</th>
<th>AUC value</th>
<th>Omission error (proportion)</th>
<th>Standardized omission error (proportion)</th>
<th>Suitable habitat (% of total area)</th>
</tr>
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<tbody>
<tr>
<td>Terrain</td>
<td>5</td>
<td>0.22 ± 0.02</td>
<td>0.97 ± 0.01</td>
<td>0.07 ± 0.08</td>
<td>0.07 ± 0.05</td>
<td>0.07 ± 0.01</td>
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<tr>
<td>Land cover</td>
<td>9</td>
<td>0.21 ± 0.02</td>
<td>0.96 ± 0.01</td>
<td>0.12 ± 0.07</td>
<td>0.17 ± 0.06</td>
<td>0.08 ± 0.01</td>
</tr>
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<td>Vegetation structure</td>
<td>5</td>
<td>0.21 ± 0.03</td>
<td>0.83 ± 0.04</td>
<td>0.27 ± 0.00</td>
<td>0.41 ± 0.08</td>
<td>0.22 ± 0.02</td>
</tr>
<tr>
<td>One-class model means</td>
<td>14</td>
<td>0.14 ± 0.02</td>
<td>0.98 ± 0.01</td>
<td>0.13 ± 0.08</td>
<td>0.04 ± 0.02</td>
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<tr>
<td>Two-class model means</td>
<td>10</td>
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<td>0.12 ± 0.07</td>
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<td>0.06 ± 0.01</td>
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<tr>
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<td>0.16 ± 0.03</td>
<td>0.98 ± 0.01</td>
<td>0.10 ± 0.06</td>
<td>0.03 ± 0.03</td>
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Table 3

<table>
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<th>Land cover</th>
<th>Veg. structure</th>
<th>Terrain – Land cover</th>
<th>Terrain – Veg. structure</th>
<th>Land cover – Veg. structure</th>
<th>Full model (all variables)</th>
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</thead>
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<td>-0.01 ± 0.02</td>
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<tr>
<td>Land cover</td>
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<td>0.24 ± 0.07**</td>
<td>0.14 ± 0.02**</td>
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<td>-0.01 ± 0.02</td>
<td>-0.01 ± 0.02</td>
<td>-0.01 ± 0.02</td>
</tr>
<tr>
<td>Veg. structure</td>
<td>0.24 ± 0.07**</td>
<td>0.14 ± 0.02**</td>
<td>0.07 ± 0.07**</td>
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<td>-0.16 ± 0.02</td>
<td>-0.16 ± 0.02</td>
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<tr>
<td>Land cover – Veg. structure</td>
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<td>-0.01 ± 0.07</td>
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<tr>
<td>Full model (all variables)</td>
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<td>-0.13 ± 0.07</td>
<td>-0.37 ± 0.07**</td>
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<td>-0.05 ± 0.07</td>
<td>-0.05 ± 0.07</td>
<td>-0.05 ± 0.07</td>
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</tbody>
</table>

* -- 0.05 Significance.  
** -- 0.01 Significance.
suitable habitat (Table 2), the SDM combining all predictor classes predicted suitable habitat towards the northeast; these areas were not predicted by the terrain-based SDM, and therefore a reflection of the land cover class' strong influence on the final prediction (Fig 1).

We found little correlation between our predictor variables (Table 81). Terrain variables provided the greatest amount of unique information, with only one (Pearson's correlation value of 0.54 for relative slope position vs. terrain shape) of 99 pair-wise comparisons providing a correlation >0.3. Among the 85 pair-wise combinations of each vegetation structure and other variables, four combinations provided correlations >0.3 but <0.5, while one comparison yielded a correlation greater than 0.5 (density of understorey vs. shrub layer: 0.59). Among the 90 pair-wise combinations of each land cover and other variables, eight correlations fell between 0.3 and 0.5, twelve correlations between 0.5 and 0.7, and six correlations between 0.7 and 1. However, apart from the six correlations between 0.3 and 0.5 (comprising comparisons between subcanopy density and each summer and winter land cover index), all values higher than 0.3 were from comparisons among different land cover indices.

4. Discussion

Our estimates of SDM reliability indicate that we were successful in exclusively using continuous remotely sensed predictor variables to model a rare species' habitat suitability. By comparing model reliability of SDMs consisting of conceptually independent predictor classes, we also found that all remotely sensed classes contributed, though disproportionately, to final model predictions. Moreover, the variety of variables included in each SDM contributed more to model reliability than the number of variables. Our results, admittedly based on a single study case at a local scale, suggest that increasing the variety of continuous remotely sensed variables leads to significant improvements in SDM reliability. Further research is required to confirm whether our approach, which is highly flexible, is applicable to other species, spatial scales, modeling algorithms, and predictor variables.

Our study confirms that current remote sensors are able to provide environmental predictor variables relevant to SDMs (Laurent et al., 2005; Bradley and Fleishman, 2008; Bistat et al., 2011). Despite challenges in interpreting remote sensing-based SDM output (Bradley and Fleishman, 2008; Cord and Rödder, 2011), remotely sensed datasets provide unbiased, high-resolution environmental data over larger areas through logistically and economically more efficient means than traditional field-based methods (Gillespie et al., 2008). Continuous remotely sensed products retain information along environmental gradients (Bradley and Fleishman, 2008; McGarigal et al., 2009; Cord and Rödder, 2011) and thus reduce classification and interpretation errors common in categorized predictor variables (Laurent et al., 2005; McGarigal et al., 2009). This is particularly beneficial when modeling species distributions at ecological transitional zones or in heterogeneous environments that are difficult to characterize using categorical or interpolated predictor variables (Alvarez-Martinez et al., 2010).
The availability of an up-to-date time-series of synoptic products (Turner et al., 2003) allows researchers to track temporal changes in habitat availability (Bartel and Sexton, 2008; Tuannu et al., 2011), assess catastrophic and human-driven environmental changes (Tuannu et al., 2011), as well as account for inter-annual and seasonal changes in the environment (this study, Cord and Rödder, 2011; Tuannu et al., 2011). Furthermore, the consistency and near global coverage of many remotely sensed products may allow for greater model transferability over space, a major challenge of SDMs (Rand et al., 2006).

The choice of predictor variables significantly influences SDM predictions (Peterson and Nakazawa, 2008). We found that utilizing a greater variety of remotely sensed predictor variables produced more accurate models than solely increasing the number of variables, perhaps because more predictor classes capture a greater amount of environmental variation, including complementary attributes not detected in single-sensor models (Swatantran et al., 2012). Our results support this, particularly our maps showing where areas of suitable habitat predicted from multi-sensor fusion resembled the intersection of those predicted for each class when considered in isolation. The availability of multiple remotely sensed sensors allows models to simultaneously use climate, terrain, land cover, and vegetation structure classes with great ease over larger spatial scales (Gillespie et al., 2008), which in turn allows researchers to detect more subtle variations in a species’ habitat than obtained from single-class models (Swatantran et al., 2012). It would be interesting to know how downscaled models would respond to the inclusion of remotely sensed climate predictors at broader scales, assuming that climatic predictors correlate with terrain predictors at local scales (Moore et al., 1990; Tarboton, 2009), and land cover predictors at coarse scales (Zimmermann et al., 2007).

To overcome potential confusion when comparing between the variety of remotely sensed predictor variables and the absolute amount of variables, we categorized remotely sensed variables into four conceptually independent classes, of which we used three. Even so, much variability exists within different classes, complicating the highly subjective task of increasing predictor variable variety. Such decisions are important, because naively maximizing the amount of SDM variables may compromise SDM building through misleading results, while there is also a danger of over-fitting (Elith and Leathwick, 2009; Tuannu et al., 2011). Two main schools of thought address the issue of model predictors (Elith and Leathwick, 2009; Warren and Seifert, 2011). The first school argues that the choice of variables should be made a priori, based on existing knowledge of ecophysiological and biophysical processes driving a species’ distribution. The second school argues for maximizing the number of variables, and allowing the model to identify those that are important. Our results support aspects from both schools: maximizing the number of variables did not necessarily improve model predictions. However, the inclusion of environmental variables aimed at maximizing the types of environmental variation also improved our understanding of a relatively unknown species’ relationship with its environment; such information may otherwise have been lost if those variables were omitted a priori. The difference between these two schools reflects subtle differences in intention (Elith and Leathwick, 2009). While the first school focuses on examining a species’ response to a specific set of variables, the second school focuses more on prediction, especially for species for which little knowledge exist. So, in essence, the first approach avoids overfitting by placing greater emphasis on fundamental, invariant niche relationships, whereas the latter approach merely seeks empirical patterns.

While terrain and land cover variables are expected to strongly influence SDMs at local scales (Pearson and Dawson, 2003), we were surprised by the weak contribution of vegetation structure to our model predictions. In fact, our full model hardly improved upon models that did not include (expensive) vegetation structure variables. Vegetation structure is generally important in SDMs (Rattwinkel et al., 2009). We also expected that vegetation structure would contribute to habitat suitability for St. Francis’ satyr, as suitable habitat – early successional wetlands – is distinct from the surrounding landscape (Kuefer et al., 2008). We propose three explanations. First, and most likely, correlations among vegetation structure and other variables may reduce the predictive power of variables relating to vegetation structure (Swatantran et al., 2012). Though we detected little to no correlation among vegetation structure and other variables, it is possible that terrain and land cover variables together already captured similar aspects of the environment (see Bolstad et al., 1998; Hill and Thompson, 2005), leading to undetected correlations among variables. If correlations between vegetation structure and the combination of other sources of remotely sensed variables exist, then habitat suitability can be detected with high accuracy using freely available remotely sensed data (i.e. terrain and land cover variables) without the need to obtain expensive and sparsely distributed vegetation structure variables (Swatantran et al., 2012). Second, suitable St. Francis’ satyr habitat changes rapidly (Kuefer et al., 2008); consequently there may be a mismatch between our vegetation structure variables, collected 2 years before our St. Francis’ satyr presences, and St. Francis’ satyr habitat we attempted to model. Third, vegetation structure alone may not play a prominent role in habitat suitability. Wilsey et al. (2012) found that vegetation structure improved SDMs of black-capped vireos, Vireo atricapilla, only when used in combination with other variables and in the absence of other vegetation variables.

In light of this, we show that continuous remotely sensed predictor variables, which offer many notable advantages over categorical variables, can be used exclusively and effectively in SDMs to estimate a species’ distribution, habitat status, and ecological needs. While we have used only a small subset of potentially useful remotely sensed variables, a great number exist. Incorporating a wider range of remote sensing predictor classes into models can significantly improve model reliability, and detect highly subtle variations in a species’ habitat needs. The application of continuous remotely sensed variables shows high promise to obtain direct, accurate, relatively inexpensive, and logically feasible habitat assessments, even for little known species in remote and inaccessible terrain.

Acknowledgements

We thank the Ft. Bragg Endangered Species Branch and the Strategic Environmental Research and Development Program (SERDP) for financial support, Brian Ball and Erich Hoffman for facilitating our work, and Lesley Starke for comments on earlier drafts of this manuscript. JWW was supported on a NASA Earth and Space Science Fellowship.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bioccon.2013.04.021.

References

APPENDICES
Supplementary Figure 1. Heuristic estimates of single-variable responses of St. Francis satyr at Ft Bragg, NC to terrain, land cover and vegetation structure variables, as obtained using the Maxent software package (Phillips & Dudík 2008). Each model was implemented with ten-fold cross-validations, with red lines and blue regions respectively indicate mean ± 1SD. Note that x-axis values in these responses curves are unbounded (but held constant outside the study area’s environmental range) to avoid extrapolation problems associated with exponential models.
Supplementary Table 1. Pearson correlation matrix for 10,000 randomly sampled points of 19 predictor variables used to predict habitat suitability of the St. Francis’ satyr butterfly at Ft. Bragg NC

<table>
<thead>
<tr>
<th>Terrain Variables</th>
<th>Slope</th>
<th>Relative Slope Position</th>
<th>Terrain Shape</th>
<th>Aspect</th>
<th>Flow Accumulation</th>
<th>Topographic Position Index</th>
<th>Deciduousness</th>
<th>Summer brightness</th>
<th>Wetness seasonality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relative Slope Position</td>
<td>0.093</td>
<td>0.537</td>
<td>0.212</td>
<td>0.117</td>
<td>0.200</td>
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<td>-0.003</td>
<td>0.145</td>
<td>0.041</td>
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<tr>
<td>Aspect</td>
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<td>0.145</td>
<td>0.014</td>
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<td>0.003</td>
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<td>-0.086</td>
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<table>
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<tr>
<th>Land cover variables</th>
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<th>Winter greenness</th>
<th>Summer wetness</th>
<th>Winter brightness</th>
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<th>Understory density</th>
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<td>-0.384</td>
<td>0.030</td>
<td>-0.026</td>
<td>-0.046</td>
<td>-0.272</td>
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<td>0.299</td>
<td>-0.384</td>
<td>0.030</td>
<td>0.001</td>
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<td>-0.046</td>
<td>-0.272</td>
<td>-0.082</td>
</tr>
<tr>
<td>Canopy density</td>
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<td>0.242</td>
<td>0.299</td>
<td>-0.384</td>
<td>0.030</td>
<td>0.001</td>
<td>-0.064</td>
<td>-0.046</td>
<td>-0.272</td>
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<td>Understory density</td>
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<td>-0.064</td>
<td>-0.384</td>
<td>0.030</td>
<td>-0.026</td>
<td>-0.046</td>
<td>-0.272</td>
<td>-0.082</td>
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<td>Shrub density</td>
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<td>Subcanopy density</td>
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20
CONSIDERING CONNECTIVITY WHEN IDENTIFYING REINTRODUCTION SITES FOR RARE SPECIES

ABSTRACT

Despite being critical for ecosystem functioning and conservation management, landscape connectivity continues to be neglected in reintroduction biology. Here we present a case study demonstrating how a graph-theoretical framework can be used to incorporate connectivity in selecting reintroduction sites for rare species. We do this by modeling dispersal dynamics for the St. Francis’ satyr *Neonympha mitchelli francisci*, an imperiled butterfly species restricted to a localized network of wetlands in the southeastern United States. Through graph theory, we rank potential reintroduction sites first by identifying those sites connected to the greatest number of occupied habitat patches, and thereafter by identifying the reintroduction site that leads to the greatest increase in network-wide connectivity. After deriving our network graph using a habitat suitability map and implementing known dispersal limitations, we found that St. Francis’ satyrs persist as four disjunct metapopulations, with the most connected reintroduction site directly connected to sixteen occupied habitat patches. Only one reintroduction site we considered was able to (re)connect disjunct metapopulations. Reintroductions at highly connected sites enable better dispersal to nearby unoccupied habitat as population sizes increase, and should better equip reintroduced populations to adapt to changing environments in the long term.
INTRODUCTION

In conservation biology, reintroduction is the deliberate attempt to establish an imperiled species into suitable but unoccupied habitat within that species’ former range (IUCN 1998; Armstrong & Seddon 2007; Schultz et al. 2008a). Using stock originating from either captive populations or healthy populations elsewhere, reintroduced populations can be released in previously occupied sites that continue to be suitable, and in intact or restored habitat that has never been occupied. Despite numerous recent advances in reintroduction biology (Armstrong & Seddon 2007), reintroduction sites continue to be selected subjectively, with experts making ad hoc judgments based on the reintroduced species’ ecological requirements, environmental characteristics of potential reintroduction sites, and relevant cultural, logistical, and political considerations (Armstrong & Seddon 2007; McIntire et al. 2007; Schultz et al. 2008a). Rarely considered are dispersal opportunities for a reintroduced population, which could impact, or even jeopardize long-term reintroduction objectives. Here, we develop a framework that incorporates dispersal opportunities in conservation management, by evaluating landscape connectivity in the selection of reintroduction sites.

Landscape connectivity describes a landscape’s ability to facilitate dispersal of individuals among suitable but disjunct habitat patches (Crooks & Sanjayan 2006). Dispersal opportunities are critical to population viability as dispersal facilitates the rescue of declining populations, re-establishment of extirpated populations, and maintenance of genetic diversity.
(Hanski & Gilpin 1997; Calabrese & Fagan 2004; Crooks & Sanjayan 2006; McRae & Beier 2007; Rayfield et al. 2011). Such benefits will certainly also apply to reintroduced populations, in addition to allowing individuals from successfully reintroduced populations to disperse into new suitable areas.

In this paper, we present a case study to demonstrate how a graph-theoretical framework (Calabrese & Fagan 2004; Fall et al. 2007; Urban et al. 2009) can be used to account for landscape connectivity in conservation management, specifically in selecting reintroduction sites for endangered species. We do this by analyzing regional patch dynamics for an imperiled butterfly species, the St. Francis’ satyr Neonympha mitchellii francisci. Being highly flexible in its characterization of network features, graph theory can effectively consider spatial configurations and interactions within large and complex networks, and has, as a consequence, gained popularity among landscape ecologists in recent years (Calabrese & Fagan 2004; Fall et al. 2007; Urban et al. 2009; Rayfield et al. 2011). Most studies however have used graph theory to infer connectivity and dispersal pathways across the landscape, with very few applying it to practical conservation management (Creech et al. 2014), as we have done here. Drawing from extensive empirical work on the St. Francis’ satyr’s distribution (Bartel & Sexton 2008; Bartel et al. 2010; Wilson et al. 2013), population dynamics (Kuefler et al. 2008), and dispersal (Kuefler et al. 2010; Hudgens et al. 2012; Milko et al. 2012), we prioritize potential reintroduction sites, which can be intact habitat or potential restoration sites, by ranking each reintroduction site’s potential to increase connectivity among the few remaining St. Francis satyr subpopulations.
METHODS

Study species

St. Francis’ satyr is a US federally endangered butterfly species globally restricted to less than 50 ha of distributed wetland in an area encompassing 65,000 ha on United States Department of Defense lands at Ft. Bragg, NC (35°07’S, 79°08’W). Previous work has established that the St. Francis’ satyr is highly dependent on disturbance, particularly beaver activity and fire that maintain this early-successional wetland specialist’s habitat (Kuefler et al. 2008; Bartel et al. 2010). Both beaver activity and fire were heavily suppressed during the past century, leading to drastic population declines of St. Francis’ satyr. Although these disturbance factors are being actively restored on Ft. Bragg, distribution modeling using a range of continuous remotely sensed variables derived from optical and active sensors suggest that St. Francis’ satyr habitat remains highly limited (Bartel & Sexton 2008; Wilson et al. 2013). Moreover, the species has poor dispersal abilities (Kuefler et al. 2008; Hudgens et al. 2012) coupled with a highly fragmented stream network along which it disperses (Milko et al. 2012) preventing St. Francis’ satyr from colonizing unoccupied habitat as previously suitable habitat transforms to late-successional stages (Kuefler et al. 2008), contributing to the continued decline of this species. The continued persistence of St. Francis’ satyr may thus require human intervention, particularly through reintroduction of captive-bred individuals to highly connected habitat patches that will facilitate future dispersal opportunities. This butterfly thereby presents an ideal case study to demonstrate the accounting for connectivity in selecting reintroduction sites.
**Graph theory**

The graph-theoretic approach represents landscape connectivity as a set of habitat patches (“nodes”) inter-connected by dispersal paths (“edges”, Fig. 1). Both nodes (suitable/unsuitable) and edges (connected or not) may be binary and/or weighted (e.g. habitat quality for nodes, dispersal resistance for edges) to represent a multivariate ecological framework. Any two nodes not directly connected may be connected through intermediate nodes that represent stepping-stone habitats. Conversely, a graph in which not all nodes are connected consists of two or more “subgraphs,” in which all the connected nodes represent disjunct metapopulations. Network “hubs” are those nodes connected to more nodes (relative to other nodes in the network), while “cut-nodes” provide a critical link between what would otherwise be disjunct subgraphs.

A number of graph-based network measures suitable for landscape connectivity analyses (Calabrese & Fagan 2004; Rayfield et al. 2011) are useful for conservation management in the broad sense and in particular the selection of reintroduction sites. At the local (patch) scale, important dispersal pathways or stepping-stones can be assessed with a “node degree” measure, which is the number of other nodes directly connected to the node of interest. At the landscape scale, the overall level of connectivity is represented by “graph size”, the total number of connections within the graph, while network traversability can be represented by “characteristic path length”, which is the mean value of all edges in the graph.
**Graph development**

We defined the location of our graphs’ core or fixed nodes as the centroids of 56 putative colonies, which are wetlands where St. Francis’ Satyr has been recorded after 2000. We considered 32 total reintroduction sites, two previously identified as suitable but unoccupied habitat patches (Wilson et al. 2013), seven historical wetlands colonized prior to 2000 (Kuefler et al. 2008) that may require some preparation work before reintroduction, and 26 potential habitat restoration sites. Potential restoration sites were identified as those sites situated at five to seven Horton-Strahler stream order crossings (Horton 1945; Strahler 1952), calculated from a USGS National Elevation Dataset (Gesch et al. 2002), which corresponds with those areas where beaver activity may create or maintain suitable butterfly habitat.

At the most basic level, graph edges can be represented by a matrix \( N \) whose elements \( n_{ij} \) represent the shortest (Euclidian) distances between nodes \( i \) and \( j \) (Urban & Keitt 2001). For \( n \) nodes, \( N \) is an \( n \) by \( n \) matrix, but because \( n_{ij} = n_{ji} \) and \( n_{ii} = n_{jj} = 0 \), it is sufficient to compute only the lower-left triangle of the matrix. Graph edges are often derived from Euclidian distances; however, this metric will make little sense in an ecologically realistic framework, since a dispersing individual will encounter various forms of resistance to movement, such as grassland for a dispersing forest specialist, or a dam wall for a fish dispersing along a stream. It would thus make sense to produce a graph where each edge is representative of the actual resistance a dispersing individual may encounter (Fagan & Calabrese 2006; Bodin & Norbert 2007; Treml et al. 2008). Following this logic, we derived the edges of our graph by calculating the path of least resistance (Pinto & Keitt 2008; Urban
et al. 2009; Rayfield et al. 2010) available to a dispersing St. Francis’ satyr. Deriving graph edge values $n_{ij}$ through least-cost path modeling combines distance $(x, y)$ and the cost of traversing a pixel $(z)$ to obtain a spatially explicit dispersal surface. To derive $z$, we used the St. Francis’ satyr habitat suitability map we previously created (Wilson et al. 2013). But because the habitat suitability map’s values ranged from 0 (least suitable) to 1 (most suitable), we inverted the habitat suitability values such that zero now represents no resistance and one represents the highest resistance, to be more comparable to dispersal distance. Lastly, we only considered edges for which Euclidian distance $n_{ij}$ was shorter than 2600 m, the maximum known dispersal distance for St. Francis’ satyr (Kuefler et al. 2008, Hudgens et al. 2012).

**Evaluating reintroduction sites**

We ranked reintroduction sites using two analyses to quantify each node’s role in network-wide connectivity. First, we performed a hub analysis by iteratively adding each of the 32 reintroduction sites to our core graph consisting of 56 putative colony nodes, we reconstituted the graph’s matrix, and then determined the number of putative colonies directly connected to the reintroduction site (the node’s degree value) and the resulting graph’s characteristic path length. Using this analysis, our top-ranked reintroduction site had the highest degree value. If a graph consisted of multiple subgraphs (disjunct metapopulations), we identified a top-ranked reintroduction site in each subgraph. Second, we performed a cut-node analysis by determining which reintroduction site had the greatest
positive impact on network-wide connectivity; that is, the reintroduction site whose inclusion established a dispersal pathway between two or more subgraphs. If no subgraphs were connected, no cut-node was identified; conversely, if multiple cut-nodes were identified, the cut-node with the highest degree value was considered our top reintroduction priority. Data were prepared and displayed in ArcGIS 10.1 (ESRI, Redlands, CA), while graphs were created and analyzed using the NetworkX package (Hagberg et al. 2008) in the Python 2.6 scripting environment. All raster surfaces were processed at the 10 m resolution, and all graphs were assumed directional (DiGraphs) to simulate dispersal away from reintroduction locations. Means are presented with ±1SD.

**RESULTS**

The graph comprising only putative St. Francis’ satyr colonies consisted of 56 nodes and 136 edges, with a characteristic path length of 1100 ± 681 m (Fig. 2). This core graph consisted of four subgraphs, the largest consisting of 44 nodes and 120 edges (characteristic path length: 1123 ± 679 m), followed by a subgraph with six nodes and ten edges (characteristic path length: 1092 ± 655 m). The smallest subgraph in this study consisted of only two nodes separated by 1351 m, while the fourth subgraph consisted of four nodes and three edges (characteristic path length: 494 ± 209 m). Putative colonies were on average connected to 5 ± 2.5 other colonies, while the most connected colony, situated in the graph with 44 nodes, was connected to 13 other colonies. No colonies were completely isolated; however continued monitoring at the three smallest subgraphs suggests that the colonies comprising these
networks are on the brink of extinction.

Reintroduction sites in this study were, on average, connected to 2.7 ± 3.5 putative colonies, with no difference in the level of connectivity between potential habitat restoration sites (connection to 2.9 ± 3.9 colonies) and potentially suitable but unoccupied sites (connected to 2.1 ± 2.1 colonies; t = 0.540; p = 0.296). Twelve potential reintroduction sites were connected to more than two colonies, 11 sites were connected to either one or two colonies, and 12 reintroduction sites were completely isolated; that is, not connected to any putative colonies (Table 1).

Using a graph-theoretic approach to analyze connectivity of restoration sites to putative St. Francis’ satyr colonies (nodes), we were able to identify reintroduction sites that served as hubs connecting many other nodes (Table 1). The most connected site was a restoration site connected to sixteen putative St. Francis’ satyr colonies, a large improvement on the second-most connected reintroduction sites, also a restoration site, that was connected to ten putative colonies (Fig. 2). Not a single reintroduction site reduced its subgraph or the entire network’s characteristic path length. For example, the most connected reintroduction site increased the characteristic path length of the entire network and its 44-node subgraph to 1119m and 1140m, respectively, while the second-ranked reintroduction site increased the characteristic path length of the entire network and its 44-node subgraph to 1130 m and 1152 m, respectively. The most connected reintroduction site in the six-node subgraph was connected to each of that subgraph’s colonies. Similarly, both reintroduction sites associated with the two-node subgraph were connected to all of that subgraph’s colonies.
Through our graph-theoretic approach, we were able to identify only one reintroduction site that can be considered a cut-node, which is the site that connected disjunct subgraphs in our landscape. This cut-node connected two subgraphs with each other, the 44-node subgraphs and six-node subgraphs (Fig. 2), was connected to six putative colonies, and increased the characteristic path length of the entire network to 1138 m.

DISCUSSION

We have demonstrated a graph-theoretical approach to incorporate connectivity in the selection of reintroduction locations. We did this by prioritizing potential reintroduction sites based on their level of connectivity to existing occupied habitat, and their ability to (re)connect disjunct metapopulations. While our methods and results are based on a single case study at a local scale, the method we have used is broadly applicable and highly flexible, as evident from the wide variety of studies that have utilized graph theory for other purposes, considering, amongst others, birds (Bunn et al. 2000; Minor & Urban 2007; Urban & Keitt 2001), salmon (Schick & Lindley 2007), mammals (Bunn et al. 2000; Creech et al. 2014) and corals (Treml et al. 2008). Our study expands the graph-theoretic framework, already used in this wide variety of landscapes, to a new and pressing arena of conservation management namely reintroduction.

Incorporating connectivity in reintroduction initiatives holds short-term, medium, and long-term benefits for both reintroduction initiatives and the reintroduced populations. Many reintroduction initiatives continue to fail due to inadequate knowledge of reintroduced
species’ ecological needs (Armstrong et al. 2007; Armstrong & Seddon 2007; Schultz et al. 2008a). Obtaining the ecological data required for successful reintroduction is seldom a trivial matter since rare species are often hard to detect, sparsely distributed, and not always present in suitable habitat patches (Pulliam 2000). In the short term, reintroduction at highly connected sites can act as an insurance policy against the selection of potentially inferior reintroduction sites, by offering reintroduced populations opportunities to disperse to more suitable habitat patches, if required. Over the medium term, successful reintroduction at highly connected sites may also facilitate unassisted dispersal of surplus individuals to nearby suitable habitat as reintroduced population sizes increase. This becomes essential in the context of reintroduced populations that live in ephemeral habitats, such as St. Francis’ satyr, that would otherwise require valuable resources for more pro-active conservation management strategies such as assisted colonization (Seddon 2010). The long-term benefits of reintroduction at highly connected sites pertain to the ability of reintroduced populations to adapt their ranges to a dynamic or changing environment. This is particularly true if successfully reintroduced populations’ continued persistence depend on dispersing within a network of ever-changing transient habitat patches, such as St. Francis’ satyr (Kuefler et al. 2008) or needing to undergo range shifts to keep track of their climatic envelopes under climate change (Parmesan 2006; Minor & Urban 2008).

Ecologists generally employ two methods to quantify landscape connectivity, namely graph theory (Urban et al. 2009; Rayfield et al. 2011) and circuit theory (McRae et al. 2008), with the specific branch of graph theory that concerns functional or topological relationships
among nodes often referred to as network theory (Urban et al. 2009). In this paper, we used graph theory because of its ability to prioritize network efficiency by analyzing the strength of connectivity among discrete objects (Rayfield et al. 2011), and its ability to implement directional graphs to simulate dispersal away from reintroduction sites (McRae et al. 2008). Alternatively, circuit theory can also be used to model alternative pathways between nodes to analyze e.g. path redundancy (McRae et al. 2008; see Pinto & Keitt (2009) for an example using graph theory), though circuit theory cannot implement directional dispersal (McRae et al. 2008). Regardless of the method implemented, both graph theory and circuit theory lend themselves to incorporating connectivity into reintroduction biology, particularly through their flexibility in deriving edge values (Minor & Urban 2007; Urban et al. 2009) to simulate dispersal across the landscape.

We relied on a habitat suitability product obtained from presence data and land-cover data freely available at a global scale (Wilson et al. 2013) to derive the cost values for our edges. While such an option should in theory be available for any reintroduction program, multiple other methods exist to obtain spatially explicit cost-surface products (Urban et al. 2009; Rayfield et al. 2010). More challenging is obtaining information on dispersal limitations, specifically the potential for long-distance dispersal, and the degree of resistance imposed by different habitats. In our case we obtained dispersal limits of the St. Francis’ satyr from a resource-intensive mark-recapture study (Keufler et al. 2008), which greatly affected the level of connectivity within our graphs. However, most studies do not have the luxury to obtain such information, in which case sensitivity-analysis, expert opinion, or
dispersal characteristics of a related (surrogate) species may suffice. It is important however to consider that dispersal data will have a major influence on site prioritization as it determines the presence of connections between graph nodes.

In this study we utilized two different analyses to identify priority reintroduction sites, including a hub analysis that aims to increase connectivity within connected populations and a cut-node analysis that aims to increase connectivity among disjunct populations. The decision as to which analysis will be followed will depend on each reintroduction initiative’s goals, data limitations, logistical constraints, and case-specific biological considerations, factors not necessarily mutually exclusive. Considering a study’s spatial scale is however also of crucial importance. Land managers may prioritize reintroduction sites at the local (subgraph or metapopulations level) or regional scale. When reintroduction aims to connect disjunct metapopulations, as we have illustrated through our cut-node analysis, it is important to consider that historically isolated metapopulations may have unique local adaptations and genetic compositions (Allendorf & Leary 1986) that land managers may wish to maintain. In such cases, it may be prudent to avoid outbreeding depression (Templeton 1986) by focusing on maximizing connectivity within metapopulations or ecologically separate management units (but see Frankham et al. 2011) through a hub analysis.

When incorporating connectivity in reintroduction biology, it may be important to consider when reintroduction at isolated patches may be preferable. Two possibilities come to mind. First, improving landscape connectivity may have several drawbacks that include
promoting the spread of diseases, parasites, and other antagonistic species (Simberloff et al. 1992; McCallum & Dobson 2002), and synchronizing population dynamics which could drive simultaneous collapse of previously unsynchronized metapopulations (Hudgens & Haddad 2003). While reintroduction managers should certainly consider these drawbacks at the reintroduction site, it is also worthy to note that several studies found that such events are rare, and that connectivity’s benefits generally outweigh possible negative consequences (Haddad et al. 2011; Haddad et al. 2014). Second, in cases where the reintroduced population is small or its reproductive biology is limited by dispersal capabilities, dispersing individuals may exclude themselves from the reproductive population if they leave the reintroduction site, especially when such opportunities are rare elsewhere. Reintroduction at isolated habitat patches may thus offer some benefits that may be harnessed depending on each reintroduction project’s specific goals and the biology of the reintroduced species. While our study focused mostly on selecting highly connected sites, our analysis also clearly identified all the isolated patches, which can be utilized when appropriate for the program.

Over the last decade, conservation biologists have invested significant resources in advancing the field of connectivity biology, both in terms of its theory, tools and, practical application (Crooks & Sanjayan 2006; Beier et al. 2008). In this study we demonstrated a flexible method that leverages existing tools to incorporate connectivity in reintroduction initiatives. While we are not proposing that connectivity as a panacea for reintroduction initiatives, we believe its incorporation may certainly enhance the potential for reintroduction success, by translating into larger distributions, and higher chance of persistence in other
sites connected to the restored sites. We thus strongly suggest that guidelines for reintroduction (e.g. IUCN 1998) be revised to include connectivity as a key consideration, and that reintroduction reviews (e.g. Schultz et al. 2008b) not merely mention but strongly advise towards the use of connectivity theory in reintroduction initiatives.

ACKNOWLEDGEMENTS

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Table 1. Patch characteristics of priority reintroduction sites identified for the St. Francis’ satyr butterfly using a graph-theoretic approach: the two network hubs (site 114, 119, the sites with the highest betweenness values), the cut-node (site 116, connecting subgraphs 6 and 44), and the most connected unoccupied reintroduction site (site 5). Site 106, 112 and 121 represent a random selection of isolated reintroduction sites (connected to no other sites), all which have the same characteristics. Graph ID reflects the number of nodes in that particular subgraph.

<table>
<thead>
<tr>
<th>Site ID</th>
<th>Site type</th>
<th>Graph ID</th>
<th>Node degree</th>
<th>Graph path length pre-inclusion (m)</th>
<th>Graph path length post-inclusion (m)</th>
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<td>16</td>
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<tr>
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<tr>
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<td>Unoccupied</td>
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<td>5</td>
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Figure 1. A hypothetical graph consists of nodes (patches) and edges (dispersal paths).

Reintroduction priorities would consist of network hubs (highly connected nodes) or cut-notes (nodes keeping subgraphs connected).
Figure 2. The dispersal network among putative St. Francis’ satyr colonies (black nodes and edges) on Ft. Bragg, NC consists of four subgraphs assuming a maximum dispersal distance of 2600 m (Kuefler et al. 2008). Identified reintroduction priorities include cut-nodes (the reintroduction site connecting two subgraphs) and hubs (the most connected (left) and second-most connected (right) reintroduction site).
THE INDEPENDENT AND SYNERGISTIC EFFECTS OF HABITAT LOSS AND CLIMATE CHANGE

ABSTRACT

Habitat loss and climate change pose a great challenge to biodiversity conservation over the next century. While most studies consider these threats independently, we also tested whether these threats act synergistically or summative, by examining predicted distributions of 24 forest bird species endemic to the Guinean Forests of West Africa. Combining satellite imagery with landuse information dating back to 1936, we found that western Cameroon has already lost 40.7% of its original forests, and we project it to lose >71.3% before the end of this century. Modeling future distributions subjected to habitat loss and climate change suggest that western Cameroon’s forest birds would lose 84.56 ±17.11% of their habitat by 2080, with eleven species losing more than 95%. Importantly, we found that climate change and habitat loss act synergistically to hasten extinctions, causing species to lose an additional 12.87 ±51.78% habitat that would have been the case if these threats were summative. Our results guide science-based policy and management by delineating spatially explicit conservation priorities within the region.

Keywords: Birds, Cameroon, Distribution modeling, Niche, Roads, Summative effects,
INTRODUCTION

Habitat loss and climate change are two of the greatest threats to the continued persistence of biodiversity. Even more concerning, these two threats may increase each other’s impact by acting synergistically on one another to accelerate species extinctions (Brook et al. 2008; Jetz et al. 2007; Mantyka-Pringle et al. 2012). As Earth’s climate changes, many species will need to adapt their ranges to track their shifting climatic niches. Habitat loss may impede range adaption, as the lack of contiguous habitat (‘range-shift gaps’, Colwell et al. 2008) may make it impossible for habitat specialists to disperse to keep up with suitable climatic conditions (Williams et al. 2007; Brook et al. 2008; Colwell et al. 2008). The combined effects of habitat loss and climate change may thereby accelerate species extinction rates (Pimm et al. 2014).

Ecologists frequently forecast how changes in landscapes subject to habitat loss (Laurance et al. 2001; Linkie et al. 2004) and climate change (Sekercioglu et al. 2008; Williams et al. 2007; Colwell et al. 2008) will influence future species distributions. However, these impacts are mostly considered in isolation, with few studies examining the combined effects of these stressors on biodiversity (Brook et al. 2008; Jetz et al. 2007; Mantyka-Pringle et al. 2012). Furthermore, multiple studies assume climate change and habitat loss act synergistically (Brook et al. 2008; Jetz et al. 2007; Mantyka-Pringle et al. 2012), yet no study has tested whether these threats’ effects are synergistic or summative; that is, whether the effect of these two threats acting together exceeds the sum of their effects when acting separately.
We examined the independent and combined effects of climate change and habitat loss by predicting the future distributions of 24 bird species that are forest specialists and either endemic or have isolated subpopulations in the Lower Guinean Forests of West Africa (Fig. 1). The region is a Biodiversity Hotspot because of its exceptional levels of endemism and the extent of habitat loss: approximately 85% of its original forest cover has been lost as landuse has shifted to support some of the densest human populations in Africa (Mittermeier et al. 2005). The region’s topographic complexity and tropical climate (Mittermeier et al. 2005) may also render its biodiversity vulnerable to climate change (Colwell et al. 2008).

METHODS

Study area

We focused our research on the Northwest and Southwest provinces of western Cameroon due to the region’s exceptional levels of endemic biodiversity (Oates et al. 2004), as well as unprecedented historical datasets that were available to us, including a 74-year archive of landuse data and a 37-year archive of NASA Landsat imagery (Roy et al. 2014). In addition, vast expanses of intact or connected forests still remain in Cameroon (Oates et al. 2004), making future conservation planning based on our results more pragmatic here than elsewhere in the Lower Guinean Forests.

How did forest cover of the study region change from the pre-industrial era to 2010?

We collected Landsat images covering our study area for the periods 1973-1978 (period
1975), 1984-1986 (period 1985), 1997-2000 (period 2000), and 2009-2011 (period 2010). After we identified each period’s Landsat image with the least amount of cloud cover, and replaced any remaining cloudy or otherwise missing pixels with data from Landsat images within the same period, we geometrically, atmospherically, and radiometrically corrected (Lillesand et al. 2008) the selected images and extracted their false color composites (bands 7/4/2 for TM and ETM images; bands 6/5/4 for MSS images). Thereafter, we used ArgGIS 10.1’s ISO Unsupervised Classification tool (ESRI, Redlands CA) on the false-color composites to generate a three-class landcover map of the region’s water features, and obtain forest cover maps for periods 1975, 1985, 2000 and 2010.

Because they have similar spectral signatures, separating forest cover from plantation agriculture is challenging but nevertheless important, otherwise the true status of a species dependent on forests may be masked by an apparent abundance of intact habitat that is in fact lost (Tropek et al. 2014). To overcome this challenge, we assumed cleared tropical forests did not regenerate during the 40-year timespan for which we created forest maps (1975-2010), which is reasonable considering that Cameroon’s tropical forests regenerate over more than 70 years (Lawton et al. 1998). By doing this we thus assume that any area that appeared to have been cleared earlier but reforested later during the study period indicates an area presumably covered by fast-growing plantation agriculture (Fig. 2).

We validated our 2000 forest cover map by comparing, across 5000 reference points, our forest cover with two global forest cover datasets for those same years (Hanson et al. 2013; Sexton et al. 2013), and our 2010 forest cover map using Hanson et al.’s (2013) 2010
forest map updated to account for their mapped forest loss, as well as a collection of 500 independent reference points opportunistically obtained during a fieldtrip to the study area in January 2013. Validation using two recent global forest cover datasets (forests being >50% tree cover, Hanson et al. 2013) suggested our mapping accuracy was 66.1% (Sexton et al. 2013) and 86.0% for 2000, and 83.3% for 2010, while validation using our field-collected reference points suggested our 2010 map’s accuracy was 94%. Our improvement on the two global forest cover datasets suggests that our method of finding areas apparently reforested within relatively short time periods can be used effectively to reduce misclassification between forest cover and plantation agriculture. We then used a pre-industrial forest cover map of the region (Mittermeier et al. 2005) to calculate the total area of remaining forested land at each of our four time periods, which we used to track the extent of deforestation from the pre-industrial era to 2010.

**How may human activity alter the remaining forest cover in the future?**

We generated a time series of six continuous explanatory variables representing environmental and human activity variables that may influence deforestation rates. Although the distribution of human settlements is potentially the strongest driver of deforestation (Laurance et al. 2009; Sodhi et al. 2010), finding a time series of reliable human population data in remote areas remains challenging. Because roads provide access to unexploited forests (coined “Pandora’s Box Effect”, Laurance et al. 2009), including southern Cameroon where an estimated 80% of deforestation occurs within 2 km of roads (Mertens & Lambin
road maps present a highly suitable metric of human impact that has been used successfully to predict deforestation in e.g. Sumatra (Linkie et al. 2004) and Amazonia (Laurance et al. 2001). Thus, to obtain the first set of explanatory variables, we digitized an unprecedented archive of historical road maps for the region from 1936, 1959, and 1966, updated for 1975, 1985, 2000 and 2010 using the archive of Landsat images we used to generate our forest maps. With the goal of using landscape features in relation to road presence to predict future deforestation, we calculated, for each year we have road data, the Euclidian distance of each study area pixel to the nearest major road (explanatory variable 1). Also considered, for each forest mapping period, were three variables derived directly from our landcover maps: (2) distance to nearest deforestation, (3) distance to nearest forest edge, and (4) distance to nearest major water feature. Because no comprehensive land cover data existed before NASA’s Landsat missions, we used the land cover variables obtained from the 1975 mapping to complete our deforestation, forest edge, and water feature datasets for 1936, 1959, and 1966. Lastly, we created two predictor variable maps that remained static throughout the study period: (5) elevation and (6) terrain slope derived from a NASA SRTM Digital Elevation Model (Rabus et al. 2003).

We used the time series of forest cover and explanatory variable maps to generate probabilistic forest cover maps for each decade from 2020 to 2080. To do this, we predicted future deforestation probability as a binomial process (Linkie et al. 2004) (forested = 1; deforested = 0) using a logistic regression,

\[
\ln \left( \frac{p}{1-p} \right) = \beta x + \epsilon
\]
where \( p \) is deforestation probability, \( x \) a matrix of explanatory variables, \( \beta \) the parameter estimate linking \( x \) and \( p \), and \( \varepsilon \) the error term. To populate dependent variable set \( p \), we recorded, for 1000 randomly sampled points across the study area, whether the underlying cells from each of the 1975-2010 forest maps were forested or not. We also populated seven matrices \( x \), one for each year for which we had explanatory data (1936, 1959, 1966, 1975, 1985, 2000 and 2010), with each matrix consisting of six columns, one for each explanatory variable. To populate each matrix, we recorded, for the same 1000 randomly sampled points used to populate \( p \), the values from each of the six explanatory variable maps. To estimate \( \beta \) and \( \varepsilon \), we regressed each matrix \( x \) against only those \( p \)’s derived from dates future of that matrix \( x \) to obtain parameter estimates of deforestation probability over a time span ranging between 10 and 75 years (18 parameter sets in total). Prior to analysis, correlations among variables were calculated using Pearson’s correlation coefficient to test for collinearity, with no correlations found among any variables (\( r < 0.5, P > 0.05 \)). We subsequently applied the parameters of the most parsimonious model (determined with an Akaike’s Information Criteria, AIC, Burnham & Anderson 2002) to the 2010 map to obtain a series of probabilistic forest cover maps for 2020 to 2080.

To obtain a cut-off threshold separating forested and non-forested areas on our probabilistic future forest cover maps, we used the same process explained above to obtain probabilistic forest maps for 1985, 2000, and 2010 using predictor variables from 1975. By comparing these probabilistic forest cover maps with observed deforestation, we found that areas with probability values higher than 0.55 were most likely to be deforested within 10-30
years; we subsequently used this value as a threshold to generate binary maps separating forested and deforested areas, which when applied to the 2000 forest map, corresponded with an annual deforestation rate of 0.7%. Applying this threshold to our probabilistic forest maps for 1985, 2000, and 2010 also allowed us to obtain reliability estimates for our forest mapping predictions. Comparisons of observed and predicted deforestation events at 1000 randomly sampled points showed that our predictions were better than random; however, predictions over 10 years (kappa statistic = 0.676-0.722, n = 3, Congalton 1991) were more accurate than those over 20 years (kappa = 0.662-0.565, n = 2) and 35 years (kappa = 0.532, n = 1). We subsequently applied the parameters of our 10-year model to the explanatory variables for 2010 to generate a forest cover map for 2020, and iterated this process over subsequent decades to generate a decadal time series of forest cover maps to 2080 at the 30m resolution.

**Mapping species distributions**

Because species often respond independently from one another to climate change (Walther et al. 2002; Bush et al. 2004; Williams et al. 2007), we modeled each species’ response individually rather than the response of the entire forest community. This allowed us to set explicit conservation priorities by identifying areas where the individual species most threatened by the combined effects of habitat loss and climate change occurs, which we hope will guide science-driven policy and management decisions in the region.
Mapping species’ distributions to evaluate the independent and combined influences of climate change and habitat loss involved a four-step process. First, we obtained updated distribution maps (Birdlife International & NatureServ 2011) for the 24 bird species that are forest specialists with either endemic or isolated subpopulations in the Guinean Forests of western Cameroon. Coarsely scaled species distribution maps generally over-estimate species’ ranges through interpolation, which may lead to underestimates of proportional habitat loss and extinction risk (Sekercioglu et al. 2008; Jetz et al. 2007). Thus, we refined the historical and current estimates of each study species’ distribution by clipping each species’ digitized distribution map to correspond to the time series of forest cover maps we generated, and to their estimated maximum and minimum elevation distributional limits (del Hoyo et al. 2013) using a NASA SRTM Digital Elevation Model (Rabus et al. 2003). As a second step, we estimated our study species’ future distributions by constraining each species’ current distribution map to correspond to the predicted (2020-2080) forest cover maps we generated, which represented distributions accounting for future habitat loss, independent of climate change.

The distribution maps generated above that account solely for habitat loss assume that a species’ range either contracts or remains static, depending on whether a population is subjected to habitat loss or not. This assumption may not hold under climate change, as many species may need to disperse to keep pace with their respective shifting climatic envelopes. As a third step, we modeled each species’ distribution to account for climate change independent of habitat loss, assuming species are able to disperse freely to a more suitable
environment, using the Maxent software package (Phillips & Dudík 2008). Maxent uses machine-learning algorithms to find model parameters for a stable collection of predictor variables from a larger set of alternatives. While a number of species distribution modeling algorithms exist, Maxent is particularly suitable for questions involving rare species with small ranges and limited occurrence data due to the regularization procedure that counteracts model over-fitting when using few input occurrences (Elith et al. 2011; Hernandez et al. 2006) and the ability to handle complex relationships between variables (Elith et al. 2011). In addition, Maxent only requires presence data, without the need for pseudo-absence points that may affect model reliability in discriminatory models, when those pseudo-absence points overlay suitable but unoccupied habitat (Phillips & Dudík 2008).

Using Maxent’s future distribution modeling algorithm (Phillips & Dudík 2008), we modeled the climate-adapted distributions of our 24 study species for 2020, 2050 and 2080. Models were trained on 24 bioclimatic variables derived from monthly temperature and rainfall data collected between 1950 and 2000 (Hijmans et al. 2005), and projected using corresponding bioclimatic variables derived from spatially downscaled and gridded temperature and precipitation data for emission scenarios A1B, A2A, and B2A, drawing from seven IPCC AR4 GCMs models (CCCMA, CSIRO, IPSL, ECHAM5, NCAR-CCSM3, HadCM3, HadGEM), obtained from the CCAFS-climate data portal (http://www.ccafs-climate.org/).

While some species could extend their distribution bounds beyond their current limits under climate change (Thomas et al. 2001), we constrained each species’ future range to their
refined 2010 distributions limits to account for factors other than climate, such as physiological limitations and biogeographic associations, that may also play a role in determining distributions. We also found obtaining sufficient presence data challenging, because we did not obtain sufficient spatial coverage (Phillips et al. 2009) or data (Hernandez et al. 2006) on all species during a field trip to the study area, and were unable to fill data coverage gaps with data from publically accessible natural history collection databases such as the Global Biodiversity Information Facility (http://www.gbif.org). To overcome this lack of data, we obtained ‘pseudo-presence’ data for each species by randomly selecting 25 points (deemed sufficient for Maxent, Hernandez et al. 2006) from our refined 2010 distribution maps from step one. Lastly, as a fourth step, we created future ranges for each species that account for the combined effects of habitat loss and climate change by constraining each species’ future distribution based on climate change to the limits of the future forest cover maps of the same period we generated.

**Data analysis**

We evaluated differences between each species’ previous, current, and future distributions using one-way ANOVAs, with species and climate scenario as random factors. First, we tested whether the region’s avifauna lost more habitat between 2010 and 2080 (our dependent variable) through synergistic effects (i.e. the intersection) between habitat loss and climate change than through their summative effects (i.e. the union between habitat lost through forest loss and climate change). Second, we tested how the region’s bird
distributions may change using threat (climate change and forest loss, each independently and combined) as predictor variables, and current and future area of occupancy (percentage habitat lost [in ha], latitude at southern range boundary, and minimum elevation) as dependent variables. Lastly, using the percentage habitat loss as a weighted measure of threat facing each species, we created spatially explicit maps of conservation priorities based on the independent and combined effects of climate change, by first assigning the expected habitat loss (%) that each species faces to each pixel in that species’ current range, and then summing those values for all species over the entire study area. All analyses were performed at a 30m resolution, landcover mapping was done in ArcGIS 10.1 (ESRI, Redlands CA), geoprocessing was performed in Python 2.7 (Python Software Foundation 2008), and statistical analyses were conducted in R 3.1 (R Core Team 2013), using data collected from 1000 randomly placed points unless otherwise noted. Summary statistics for climate change, habitat loss, and their combined effects are presented as means (for all species, and all climate scenarios where relevant) ±1SD.

RESULTS AND DISCUSSION
Western Cameroon had lost approximately 40.74% of its original Guinean Forest cover by 2010 (Fig. 3, Table 1). While most forest cover was lost before 1975 (27.5%, plus an additional 13.52% after 1975), deforestation rates have accelerated since 1975, with annual losses nearly three times greater after 1985 than before (Table 1). There was an apparent decline in the annual deforestation rate after 2000, which may be a consequence of increased
conservation awareness since 2000, which included the proclamation of seven new national parks in 2000 that cover 1,534,512 ha (Tchindjang et al. 2005). Despite these protective measures, due to large-scale forest losses prior to 2000, deforestation rates as a function of remaining forests continued to increase after 2000 (Table 1). The increased deforestation rates we observed in western Cameroon broadly correspond with observations in the Congo Basin (Céline et al. 2013) that extend into southern Cameroon; however annual deforestation rates in western Cameroon were 411% higher.

The location of deforestation was more likely closer to roads (logistic regression: \( z = -8.35, p < 0.001 \)), particularly within 1024 m (Fig. 4), agreeing with work done previously in southern Cameroon (Mertens & Lambin 1997). Nevertheless, distance to the nearest road played no role in our most parsimonious model predicting deforestation probability, which was determined by the relationship:

\[
\text{Deforestation probability} = -0.012 \times \text{distance to forest edge (m)} - 0.015 \times \text{slope (rad)} - 0.003 \times \text{distance to previous decade’s deforestation (m)} - 0.350 \quad (i)
\]

(Model AIC: 3607; Mean AIC of all models: 3858). While the variables in our most parsimonious model have seldom been used to predict deforestation, their influence on deforestation makes intuitive sense: steep slopes are difficult to access, while deforestation will more likely occur near actively logged areas or forest clearings (presumably deforested in earlier decades), which are presumably more likely near roads. Assuming that deforestation will continue at the current annual rate of 0.7%, we predict that by 2080, >60% of western Cameroon’s primary forest cover will have been lost (Fig. 3, Table 1). Current
deforestation rates may, however, increase over the next several decades as the palm oil industry increases its footprint in western Cameroon (Hoyle & Levang 2012; Linder et al. 2013). More realistically, if the percentage of the remaining forest lost increases at an annual rate of 0.01% (mean annual increase from 1975 to 2010), we project that by 2080 annual deforestation rates would be 1.4%, resulting in western Cameroon losing >71.8% of its original forest cover before the end of the current century.

Considering only forest losses, endemic bird species of western Cameroon’s Guinean Forests had lost, on average, 53.5 ±30.4% of their original suitable habitat by 2010. Montane forest specialists generally lost a larger proportion of their range through habitat loss than lowland forest species \( t = 9.53, n = 21, p = 0.0001 \) because habitat was available on higher elevations (logistic regression, forest cover predicted by elevation: \( z = 13.47, p < 0.0001 \)), causing these species to have smaller ranges \( t = 26.13, n = 21; p < 0.0001 \), which in turn is the single best predictor of extinction risk for terrestrial birds (Harris & Pimm 2007). The two species most threatened by habitat loss were Banded Wattle-eye \( Platysteira laticincta \) (classified as endangered, IUCN 2014) and Black-collared Apalis \( Oreolais pulchra \) (classified least concern); both of these montane forest specialists had lost more than 90% of their original habitat by 2010 (Table 2). Conversely, despite having the most restricted distribution of all species considered (679 km\(^2\), Birdlife International & Natureserv 2011), the Mount Kupe Bush-shrike \( Telephorus kupeensis \) has largely escaped habitat reductions (Table 2) because of its distribution on mountaintops that continue to pose access difficulties. If current deforestation trends were to continue, our 24 study species are predicted to lose on
average 69.46 ±24.3% of their original ranges by 2080, with the Banded Wattle-eye and Black-collared Apalis facing habitat reductions >99% (Table 2).

While previous studies generally found that the negative effects of habitat loss are greater than those of climate change (Mantyka-Pringle et al. 2012), our results suggest that they have a similar contractive effect ($t = 0.235, n =24, p = 0.408$), with species expected to lose 70.98 ±21.4% of their original habitat by 2080 through climate change (Table 2). One possibility could be that the impact of climate change has finally caught up with landuse modifications (Lemoine et al. 2007), or else that previous studies have used earlier, more modest, climate change predictions (IPCC 2007), thereby under-estimating the impact of climate change. While the mechanisms governing range adaptations under climate change are complex (Thomas et al. 2001; Walther et al. 2002), our results agree with general expectations (Walther et al. 2002; Williams et al. 2007; Colwell et al. 2008) that montane specialists will shift their ranges to higher elevations ($F_{42,658} = 111.4, r^2 = 0.877, p < 0.0001$), and lowland species move their southern distribution limits to higher latitudes ($F_{38,437} = 11.31, r^2 = 0.496, p < 0.0001$). Because less habitat is available at higher altitudes, thus restricting options for range shifts, high-elevation species, already at an elevated risk of extinction from habitat loss, are also more vulnerable to climate change ($F_{1,23} = 15.87, r^2 = 0.408, p < 0.001$). Importantly though, species thought to be escaping the effects of habitat loss, particularly those living on mountaintops, appear more vulnerable to climate change given that these species are at the physical limits of their distributions, leaving them no space to adapt their ranges to higher elevations under climate change (Williams et al. 2007;
A prime example is the Mount Kupe Bush-shrike, expected to lose 81.11 ±2.1% of its habitat through climate change by 2080, compared to 8.27% through habitat loss (Table 2).

The combined impact of climate change and habitat loss is expected to reduce the habitat available to western Cameroon’s endemic forest birds by approximately 84.56 ±17.11% by 2080 (Table 2). Moreover, these combined effects contribute to greater habitat losses than the independent effects of habitat loss or climate change ($F_{2,2011} = 307.3$, $r^2 = 0.234$, $p < 0.001$). With montane forest species threatened by both the independent effects of climate change and habitat loss, it comes as no surprise that these threats’ combined effect have a particularly pronounced impact on these species ($t = 3.431$, $df = 24$, $p = 0.0001$; Table 2). A total of eleven species (46%) are expected to lose >95% of their ranges under the combined effect of climate change and habitat loss by 2080. The two high-altitude species most threatened by habitat loss and climate change independently, namely Black-collared Apalis and Banded Wattle-eye, are expected to lose >95% of their original habitat by 2020, while an additional two high-altitude species, the endemic Cameroon Olive-Pigeon *Columba sjorstedti* and endemic subspecies of the African Hill-babbler *Pseudoalcippe abyssinica monachus* (both considered non-threatened, IUCN 2014) are expected to lose >90% of their ranges by 2020. Critically, without considering other extinction drivers in Cameroon, notably bushmeat collection (Fa et al. 2006), only a single species, the Yellow-casqued hornbill *Ceratogymna elata* (ironically threatened by hunting pressure, IUCN 2014) falls below an extinction threshold of 50% habitat loss identified for habitat specialists (Travis
2003), which is alarming considering that many of our study species do not currently appear
on global extinction watch-lists (Table 2).

A major aim of this study was to test whether habitat loss and climate change act
synergistically or summative; that is, whether these two threats acting together exceeds the
sum of their effects when acting independently. Comparing the amount of habitat expected to
be lost through the combined (i.e. the union) and summed (i.e. intersection) effects of habitat
loss and climate change show that by 2080 western Cameroon’s forest birds will lose an
additional 12.87 ±51.78% of their ranges through the combined effects of these two threats,
which is significantly more than if these threats’ effects were summative
(Wilcoxon signed rank test: z = 7.84, p < 0.0001, n = 86; Fig. 5). A spatially explicit map of
conservation priorities identifying those areas where conservation action is most urgently
needed (Fig. 6), suggest the most of the species threatened by climate change and habitat loss
occur in mountainous areas; this is because the proportional impact of range contractions are
much larger on these species, which have area available to expand their ranges.

We have shown how habitat loss and climate change act synergistically on one
another in compromising the future viability of an entire community of endemic bird species.
Both habitat loss and climate change is expected to continue unabated at least in the
foreseeable future, and in some cases even accelerate, for example in Cameroon due to
impending large-scale oil palm production (Hoyle & Levang 2012; Linder et al. 2013).
Importantly, considering that we neglected the role of other stressors such as invasive species
and over-harvesting we are likely under-estimating the true threat these species face from
multiple extinction drivers. Our results strongly encourage the development of more holistic tools for assessments of species’ threat status when faced with multiple stressors. While climate change requires complex cross-border action to mitigate, individual countries have the ability to directly influence their biodiversity’s viability through slowing habitat loss. Our holistic approach on climate change and habitat loss allow conservation managers to delineate spatially explicit conservation priorities; those areas where conservation action is most urgently needed, which will hopefully better facilitate conservation planning towards slowing current extinction rates.

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Table 1. Loss of Guinean Forests of West Africa in western Cameroon from pre-industrial forest cover estimates (Mittermeier et al. 2005) to 2010, with projections for 2020 to 2080 assuming deforestation rates of 0.7% \( \cdot y^{-1} \).

<table>
<thead>
<tr>
<th>Year</th>
<th>Forest cover remaining (ha)</th>
<th>Deforestation rate (ha\cdot y^{-1})</th>
<th>Remaining forest lost (%\cdot y^{-1})</th>
<th>Forest lost (% of original)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-industrial</td>
<td>213,389</td>
<td>No data</td>
<td>No data</td>
<td>No data</td>
</tr>
<tr>
<td>1975</td>
<td>226,379</td>
<td>No data</td>
<td>No data</td>
<td>27.53</td>
</tr>
<tr>
<td>1985</td>
<td>220,229</td>
<td>615.1</td>
<td>0.27</td>
<td>29.50</td>
</tr>
<tr>
<td>2000</td>
<td>199,000</td>
<td>1415.2</td>
<td>0.64</td>
<td>36.30</td>
</tr>
<tr>
<td>2010</td>
<td>185,135</td>
<td>1386.6</td>
<td>0.70</td>
<td>40.74</td>
</tr>
<tr>
<td>2020</td>
<td>172,132</td>
<td>1300.1</td>
<td>0.70</td>
<td>44.90</td>
</tr>
<tr>
<td>2050</td>
<td>142,877</td>
<td>975.2</td>
<td>0.70</td>
<td>54.26</td>
</tr>
<tr>
<td>2080</td>
<td>122,646</td>
<td>674.3</td>
<td>0.70</td>
<td>60.74</td>
</tr>
</tbody>
</table>
Table 2. Expected range reductions for the 24 bird species and subpopulations endemic to the Guinean Forests of West Africa in western Cameroon. Range losses are calculated as percentages from each species’ original range (Birdlife International & NatureServ 2011) to 2080, as a function of projected habitat loss independently, projected climate loss independently, and climate change and habitat loss combined. The current IUCN (2014) threat status of each species is indicated in parenthesis. All values are presented as means ±1SD.

* indicates lowland forest specialists; ** indicates montane forest specialists (del Hoyo et al. 2013).
Table 2. Continued

<table>
<thead>
<tr>
<th>Species</th>
<th>Original range (ha)</th>
<th>Range lost by 2010, habitat loss (%)</th>
<th>Range lost by 2080, habitat loss (%)</th>
<th>Range lost by 2080, climate change (%)</th>
<th>Range lost by 2080, habitat loss &amp; climate change (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apaloderma vittatum (LC)**</td>
<td>104894</td>
<td>81.23</td>
<td>89.93</td>
<td>89.51±3.61</td>
<td>96.75±1.52</td>
</tr>
<tr>
<td>Campethera tullbergi(LC)*</td>
<td>104081</td>
<td>81.10</td>
<td>89.85</td>
<td>92.65±2.54</td>
<td>98.51±0.91</td>
</tr>
<tr>
<td>Ceratogymna elata (VU)*</td>
<td>191345</td>
<td>18.27</td>
<td>44.38</td>
<td>21.33±7.11</td>
<td>48.6±5.56</td>
</tr>
<tr>
<td>Columba albinucha (NT)**</td>
<td>50453</td>
<td>21.19</td>
<td>52.47</td>
<td>52.76±32.85</td>
<td>66.98±15.48</td>
</tr>
<tr>
<td>Columba sjostedti (LC)**</td>
<td>93227</td>
<td>83.85</td>
<td>91.68</td>
<td>90.59±2.26</td>
<td>96.95±1.94</td>
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<tr>
<td>Cosyphicula roberti (LC)</td>
<td>79193</td>
<td>60.45</td>
<td>76</td>
<td>79.88±5.14</td>
<td>93.07±2.84</td>
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<tr>
<td>Dendropicos pyrrhogaster (LC) *</td>
<td>214905</td>
<td>19.92</td>
<td>45.22</td>
<td>30.29±14.31</td>
<td>51.39±5.13</td>
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<tr>
<td>Francolinus cameronensis (EN)**</td>
<td>1234</td>
<td>53.31</td>
<td>81.82</td>
<td>64.17±19.13</td>
<td>85.34±5.4</td>
</tr>
<tr>
<td>Kakamega poliothorax (LC)**</td>
<td>106624</td>
<td>77.77</td>
<td>87.11</td>
<td>84.93±11.47</td>
<td>96.83±1.82</td>
</tr>
<tr>
<td>Kupeornis gilberti (EN)**</td>
<td>7342</td>
<td>34.50</td>
<td>63.71</td>
<td>65.93±20.03</td>
<td>90.91±6.42</td>
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<tr>
<td>Malimbus erythrogaster (LC)*</td>
<td>81222</td>
<td>14.13</td>
<td>41.03</td>
<td>45.21±15.61</td>
<td>56.28±15.66</td>
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<tr>
<td>Melignomon eisentrauti (DD)*</td>
<td>36155</td>
<td>34.97</td>
<td>64.84</td>
<td>69.22±12.24</td>
<td>88.87±10.48</td>
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<tr>
<td>Onychognathus walleri (LC)*</td>
<td>93414</td>
<td>83.18</td>
<td>91.37</td>
<td>91.27±2.14</td>
<td>97.34±1.43</td>
</tr>
<tr>
<td>Oreolais pulchra (LC)**</td>
<td>32564</td>
<td>92.65</td>
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<td>95.21±1.84</td>
<td>99.75±0.16</td>
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<td>40.40</td>
<td>60.51</td>
<td>50.2±6.78</td>
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<td>173909</td>
<td>12.52</td>
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<td>57.73±17.31</td>
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<td>53.19</td>
<td>69</td>
<td>91.45±3.98</td>
<td>98.46±2.19</td>
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<td>88.23</td>
<td>95.36</td>
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<td>97.01±0.92</td>
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<td>98.83</td>
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<td>3.09</td>
<td>8.27</td>
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<td>10.01</td>
<td>37.46</td>
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</table>
Figure 1. The location of the Guinean Forests of West Africa (Mittermeier et al. 2005), with the historical extent of the Lower Guinean Forests highlighted.
Figure 2. Landsat images of the same area in western Cameroon, showing (in the black box) a forested area (1975) that was deforested in 2000 but appeared forested again in 2010. Because tropical forests regenerate over >70 years (Lawton et al. 1998), we can safely assume that the area that appear reforested within ten years consist of fast-growing plantation agriculture. (The white lines on the 2010 image indicate missing data due to a scan-line corrector failure that affects all ETM+ images after 31 May 2003, Irish 2000).
Figure 3. Forest cover maps of the southern section of the Lower Guinean Forests of Cameroon in 1975, 1985, 2000 and 2010, with predicted forest cover for 2020 to 2080, overlaid onto a historical forest map of the study region (Mittermeier et al. 2005).
Figure 4. The frequency of deforestation events in the Guinean Forests in western Cameroon was much higher closer to roads, with most deforestation occurring within 1024 m from the nearest road (Jenks Natural Breaks; Goodness of Fit = 0.989; Tabular accuracy = 0.889).
Figure 5. Projected mean range losses attributed to the combined, summed, and independent effects of climate change and habitat loss, for 24 bird species that are forest specialists, and either endemic or have isolated subpopulations in the Guinean Forest of West Africa in western Cameroon.
Figure 6. Spatially-explicit conservation prioritization based on the cumulative percentages of range contractions facing the endemic forest birds of the Lower Guinean Forest of West Africa in western Cameroon, due to the combined and independent influences of climate change and habitat loss, overlaid on a shaded elevation map of the area.