The effects of spatial survey bias and habitat suitability on predicting the distribution of threatened species living in remote areas

Short title: Accessibility bias and habitat effects on species distributions

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Summary

Knowledge of a species' potential distribution and the suitability of available habitat are fundamental for effective conservation planning and management. However, the quality of information on the distribution of species and their required habitats is highly variable in terms of accuracy and availability across taxa and regions, particularly in tropical landscapes where accessibility is especially challenging. Species distribution models (SDMs) provide predictive tools for addressing gaps for poorly surveyed species, but they rarely consider biases in geographical distribution of records and their consequences. We applied SDMs and variation partitioning analyses to investigate the relative importance of habitat characteristics, human accessibility, and their joint effects in the global distribution of the Critically Endangered blue-throated macaw (*Ara glaucogularis*), a species endemic to the Amazonian flooded savannas of Bolivia. The probability of occurrence was skewed towards more accessible areas, mostly secondary roads. Variability in observed occurrence patterns was mostly accounted for by the pure effect of habitat characteristics (76.2%), indicating that bias in the geographical distribution of occurrences does not invalidate species-habitat relationships derived from niche models. However, observed spatial covariation between landuse at a landscape scale and accessibility (joint contribution: 22.3%) may confound the independent role of landuse in the species distribution. New surveys should prioritize collecting data in more remote (less accessible) areas better distributed with respect to landuse composition at a landscape scale. Our results encourage wider application of partitioning methods to quantify the extent of sampling bias in datasets used in habitat modelling for a better understanding of species-habitat relationships, and add insights into the potential distribution of our study species and opportunities for its conservation.

Keywords: *Ara glaucogularis;* Psittacidae; roadside bias; sampling; species distribution

models

Introduction

Knowledge of a species' potential distribution and the suitability of available habitat are fundamental for effective conservation planning and management, providing a basis for many assessment schemes (IUCN 2001). However, the quality of information on the distribution of species and their required habitats varies greatly across taxa and regions worldwide (Collen *et al.* 2008). For many species, geographical distributions mostly describe species limits based on expert knowledge, but often no information on species occurrence or density within those limits is available (Jetz *et al.* 2012). This is particularly challenging for species in tropical landscapes, where difficult accessibility to unpopulated areas has limited survey efforts and prevented obtaining high-quality census data (Collen *et al.* 2008, Raxworthy *et al.* 2003). When available, this data is often limited to small samples of observed localities obtained in limited recent surveys or from historical records in museum collections (Pearson *et al.* 2007).

These limitations hold for our knowledge of the distribution of many parrot species. Parrots (Psittaciformes) are among the most threatened bird taxa of the world, with nearly one third of total species threatened under IUCN criteria (IUCN 2016). The likelihood of parrot species being classified as threatened has been recently related to their life history traits, socio-economic factors (linked to anthropogenic threats such as logging, agriculture spread, hunting and trapping), and the historical distribution size of the species (Olah *et al.* 2016). Despite the fact that some parrot species have received conservation attention (Toft and Wright 2015), the distribution of many species in remote and difficult to access habitats has prevented obtaining basic biological and distributional information (e.g., Tella *et al.* 2013).

Species distribution models (SDMs) can provide valuable predictive tools for filling information gaps and can produce continuous predictions of potential distribution for poorly surveyed species. They may thereby better depict a species' actual distribution (Botero-Delgadillo *et al.* 2012b) and can be helpful for effective conservation management (Ferrer-Sánchez and Rodríguez-Estrella 2016, Peterson *et al.* 2011). Presence-only models, particularly, rely solely upon species presences and environmental data, and can provide accurate predictions of species' distributions with reduced numbers of known occurrences (Elith *et al.* 2006, Phillips *et al.* 2006). However, these models should account for potential spatial biases in geographical and environmental information to be useful (Phillips *et al.* 2006). One common bias in distributional data is the high concentration of observations along highly accessible areas such as roads and rivers (Kadmon *et al.* 2004, Reddy and Dávalos 2003). Although widely recognized, the potential effects of this bias on modelled distributions are often not considered, including the few cases when the distribution of tropical parrots has been modelled (Botero-Delgadillo *et al.* 2012a, Marini *et al.* 2010, Monterrubio-Rico *et al.* 2010, Pidgeon *et al.* 2015).

In this study we use species distribution models to disentangle the relative importance of habitat characteristics, accessibility and the combination of these factors in the distribution of the Critically Endangered blue-throated macaw (*Ara glaucogularis*) throughout its known range in the wild. Historically, this was a poorly-known species endemic to Bolivia, not discovered in the wild until 1992, and considered among the most threatened species in the world with a population size estimated between 250 and 300 individuals (BirdLife International 2015). Individuals are concentrated in three subpopulations with a maximum of 16 known breeding pairs occurring over a vast region (Berkunsky *et al.* 2014). As it has been found in other

Endangered macaw species (Pacífico *et al.* 2014, Tella *et al.* 2013), breeding individuals might constitute a small fraction of the overall population. However, due to logistic difficulties and limited accessibility to a large part of its distributional range, population size and the breeding and global distribution of the species could have been underestimated. This species exclusively inhabits an expansive region of Amazonian flooded savannahs in the Llanos de Moxos, Beni Department, Bolivia, where it occupies forest islands dominated by palms and, secondarily, gallery forests (BirdLife International 2015, Yamashita and De Barros 1997). The few geographic records available for this species impeded accurate estimates of its area of occupancy, which was previously estimated between 9,236 and 61,500 km^2 (Herzog *et al.* 2012, BirdLife International 2015). Surveys of remote, potential areas where unknown populations of the species could persist have been highlighted as important conservation actions (BirdLife International 2015). Our modelling approach aims to identify potential spatial bias of previous surveys to more accessible areas, and to offer a better prediction of its potential (or even actual) distribution, to guide further surveys, research and management actions.

Methods

Study area and data compilation

The study area is located in the Beni department, north-eastern Bolivia and comprises approximately 200,000 km^2 (Fig. 1). The region is made up of seasonally flooded savannahs interspersed with a complex mosaic of forest islands, gallery forest, grasslands and cerrado (Mayle *et al.* 2007, Yamashita and De Barros 1997). Forest

patches are restricted to areas that are elevated just enough to avoid flooding. Most of these are eroded relics of natural or man-made levees or terraces of abandoned river channels (Hanagarth and Beck 1996). Annual precipitation ranges from 1,300 to 2,000 mm and is mostly concentrated from November to May (Hanagarth and Beck 1996). Human settlements currently inhabit the region at low densities, but there is an extensive human use of nearly the entire region, with cattle-ranching being the primary economic activity (Mayle *et al.* 2007).

The breeding population of blue-throated macaw in the study area has been monitored intensively since 2002 (Berkunsky *et al.* 2014, J.A. Díaz unpubl. data). Each year, known breeding sites and other potentially suitable areas were searched intensively for Blue-throated macaws from early August to January. Potentially suitable areas were considered to be fragments of gallery forest and forest islands located close (1-3km) to areas where the species was already known to occur. Additionally, other areas with similar vegetation structure and areas where local people reported the presence of blue-throated macaws were also explored. The access to the surveyed areas was done either by car, airplane, horseback, or on foot. Most records consisted of visual observations of individuals, but occasionally presence was confirmed by acoustical contacts or identification of recently moulted feathers. In total, 79 occurrences were recorded throughout the study period (33 with evidence of reproduction, i.e., active nests of breeding pairs detected).

Occurrence locations were entered into a Geographic Information System at 10 arcseconds (~30m) resolution. We compiled data on 6 variables to represent habitat variability and accessibility in the study area (Table 1). Climatic variability was low in the study area, and thus we preferred to focus only on the fine-grain habitat suitability and accessibility which are likely to be more important at fine spatial scales (Herzog et

al. 2012). These variables were derived at 10 arcseconds to match the species

occurrence data. Additionally, we used spatial statistics to derive a landuse variable

related to the dominant landscape composition at 1km radius around each ~30m pixel.

For this we used "focal statistics" in ArcMap 9.3 with the "majority" statistic.

Modelling

We built a SDM (Peterson and Soberón 2012) to estimate the probability of distribution

of blue-throated macaw using the occurrence data and environmental variables. Models

were conducted using all occurrence data to maximize sample size, although similar

results were obtained when only considering occurrences with evidence of reproduction

(Supplementary Information, Appendix 1). SDMs were implemented in Maxent 3.3.3k

software (Elith *et al.* 2011). We selected 500 iterations for model convergence and

employed the default regularization procedure to prevent overfitting (Phillips and Dudík

2008). To construct the models, random samples of background pixels (10,000) within

the study area were used as pseudoabsences (Phillips and Dudík 2008). To address our

questions, we followed a hierarchical approach and ran Maxent with three models based

on different combinations of the variable sets, namely an environmental model that

included single habitat variables (habitat); an accessibility model that included single

variables of human accessibility (access); and a habitat and accessibility model that

included both habitat variables and variables of human accessibility (habitat+access).

Model accuracy was assessed by dividing the species occurrence data into random

training (70%) and test (30%) datasets. To reduce uncertainty caused by sampling

artefacts of training and test data, we conducted 10 replicates for each model. Models

were evaluated on the test data using the Area Under the receiver operating

characteristics Curve (AUC) and test gain as threshold-independent assessment measures (Phillips *et al.* 2006). Note that AUC values in MAXENT are used for the problem of classifying presences vs. background points (which may or may not be true absences; Phillips *et al.* 2006). AUC values range from 0 to 1, where 1 indicates perfect model performance and 0.5 indicates predictive discrimination no better than random. We also calculated the true skill statistic (TSS). TSS ranges from -1 to $+1$, where $+1$ indicates perfect agreement and values of zero or less indicate a performance no better than random (Allouche *et al.* 2006). Additionally, model significance was tested using threshold-dependent binomial probability tests. For this, we used the 10 percentile training presence and the maximum sensitivity plus specificity values as thresholds (Liu *et al.* 2005, Botero-Delgadillo *et al.* 2015). Note that specificity values defined by MAXENT use predicted area, rather than true commission (Phillips *et al.* 2006).We used a partitioning procedure (Maxent jackknife test) to take into account the co-linearity between spatially related variables. This allows the 'pure' effect of each variable/variable set to be separated from joint effects that cannot unambiguously be attributed to one variable/variable set or another due to spatial collinearity. This procedure entailed the calculation of incremental improvement in performance of a model with a particular variable/variable set compared with the equivalent model without that variable/variable set. We also calculated model performance for each variable/variable set when used in isolation. The estimated contributions were based upon the test gain.

Finally, we calculated total surface of suitable area for the species according to Maxent models in the whole study area and in the species extent of occurrence (EOO), that is, the, the area within the Minimum Convex Polygon, MCP, including all known locations of the species. For this task, model predictions were transformed into binary

maps (i.e. presence/absence) using as thresholds the 10 percentile training presence and the maximum sensitivity plus specificity values (Liu *et al.* 2005, Botero-Delgadillo *et al.* 2015).

Results

Occurrence patterns and accessibility

Probability of occurrence near roads and rivers was greater than that expected from a spatially random distribution (Table 2), indicating that the distribution of occurrence points was skewed towards more accessible areas (Fig. 2). Among accessibility variables, distance to secondary roads showed both the highest model performance when used in isolation and the highest pure contribution in multivariate models (Figs 3a, c).

Occurrence patterns and habitat

Among habitat variables, distance to palms followed by land use composition at the landscape level (~1km) showed the highest model performance when used in isolation (Fig. 3a). Interestingly, the presence of forest at a local scale (~30 m) was a poor predictor when used in isolation. In contrast, pure contribution of this variable was high when used in combination with the other habitat variables (Figs 3b). This is because probability of occurrence increased with the presence of forest at a local scale (~30m resolution) only when forest patch size was low and thus surrounded by other habitat

types at the landscape scale (Fig. 2). That is, occurrence probability increased in forest islands dominated by palms.

Partitioning the effect of habitat and accessibility

The predictive model including both habitat and accessibility variables was more accurate than the model which only considered habitat (Table 2). However, the magnitude of these differences was low and model predictions were similar (Fig 4). Habitat variables showed the highest pure contribution to the habitat+access model (76.2%) according to Maxent jackknife test, indicating that their main effect was not related to their spatial covariation with accessibility. However, some degree of spatial covariation between both variable sets was found (joint contribution of habitat and accessibility variables: 22.3%, Supplementary Information, Appendix 2). This was mainly related to covariation of landuses at the landscape scale with distance to secondary roads (note the reduction in pure effect of these two variables in the habitat+access model, Fig. 3d). Broadly, the presence of forest at the landscape scale (used as a measure of continuous forest) was more common with increasing distance from secondary roads (Supplementary Information, Appendix 2).

According to the habitat+access model, suitable habitats occupied 29,183 km^2 or 56,064 km^2 in the whole study area, when using the 10 percentile training presence or the maximum sensitivity plus specificity thresholds. This value was reduced to 12,347 km^2 or 19,249 (10 percentile and maximum sensitivity plus specificity thresholds, respectively) when only considering the area within the actual known distribution range of the species (i.e., that included in the MCP containing all occurrence points).

Discussion

The spatial distribution of species represents the cumulative effects of many different factors that are often difficult to separate. Sampling bias towards more accessible areas is a common phenomenon in biodiversity databases, but models based on such databases rarely take them into account in model predictions (Yackulic *et al.* 2013). When accessibility bias allows covering enough environmental variability to disentangle the pure contribution of habitat variables on observed patterns (Ferrer-Paris *et al.* 2014), results of SDMs could be used confidently. However, in other situations, the difficulty in determining which factors ultimately determine observed species distributions makes the usefulness of SDMs controversial. Therefore, future effort should be dedicated to quantifying the extent of different sources of sampling bias in datasets used in habitat modelling as well as exploring the consequences of such bias on model predictions. Partitioning methods, such as those present in this study, can help clarify the proportion of the total variance that might be accounted for by uncertainty due to joint effects of different variable sets.

Our study revealed the contrasting importance of habitat characteristics and habitat accessibility in the spatial distribution of a Critically Endangered and still poorly-known species inhabiting tropical South America. As with other bird species (Kadmon *et al.* 2004, Reddy and Dávalos 2003), occurrence probability of the blue-throated macaw decreased with the distance to human pathways (mostly to secondary roads). This pattern may result from different, not mutually exclusive processes. It could reflect biases in bird surveys towards more accessible areas and a poorer coverage of the most remote ones, but it could also result from ecological processes since distributions of species may respond negatively as well as positively to landscape humanization. (e.g.,

Carrete *et al.* 2009, Ferrer-Sánchez and Rodríguez-Estrella 2016, Cardador *et al.* 2016). For this species, all known breeding sites are within private and highly managed cattle ranches, and recent occurrence models obtained at a smaller spatial scale showed that, contrarily to other sympatric macawss (blue-and-yellow *Ara ararauna* and red-and-green *Ara chloropterus*), the blue-throated macaw does not appear to avoid human settlements (Berkunsky *et al.* 2016). This might suggest that blue-throated macaws prefer more human-altered areas and/or that they are displaced towards those areas by stronger congeneric competitors (see discussion below). However, since all sampled locations (not only presences but also absences) were skewed towards more accessible areas (see Appendix 3 in Supplementary Information), we could not separate the effects of habitat selection from sampling bias in observed patterns. In any case, the bias in the spatial distribution of occurrences in relation to secondary roads did not mask the independent contribution of most environmental factors on observed patterns (with the exception of forest at the landscape scale), probably because road and river networks are distributed throughout the entire study site, reaching areas in most of the sampled habitat types (Kadmon *et al.* 2004, Leitão *et al.* 2011).

Although the good fit of a model does not necessarily imply causation, our explanatory models suggest that the most suitable areas for this species are forest islands containing palms, which is consistent with the previously described association of the species with these habitats (Herrera and Hennessey 2007, Yamashita and De Barros 1997). According to our models, the amount of suitable habitat for the species is predicted to be between 29,183 km^2 and 56,064 km^2. These estimates are closer to the upper limit of the variability range described for the species (9,236 - 61,500 km2) (Herzog *et al.* 2012). Predicted suitable habitat appears to be very large in comparison with the distribution of known records of the species. Clearly, factors beyond these

measured environmental variables are currently constraining the spatial distribution of the species.

Our SDMs may inform a deeper analysis of the conservation status, threats and potential for the recovery of this species. The critical status of this bird is attributed to habitat loss and trapping for the pet-trade (BirdLife International 2015). Population viability analyses suggest that further or even small annual increases in habitat loss (2 %) and trapping (3 %) would significantly increase its extinction risk over the next 50 years (Bouzat and Strem 2012). The habitat loss hypothesis is challenged by our SDMs, which show the current extent of suitable habitat for the species could currently hold a much larger, healthier population; in fact, congeneric macaws are present in the same region at high densities (Berkunsky *et al.* 2015, 2016). Regarding the wild-bird trade hypothesis, trade on the most attractive parrot species (including macaws) has been related to their population decline and current threatened status (Tella and Hiraldo 2014). However, legal international export of wild parrots was banned in Bolivia in 1984 (BirdLife International 2015), and trade in blue-throated macaws does not appear to have been any more intensive relative to other Bolivian species since that time. For example, international trade in red-fronted macaws (*Ara rubrogenys*), an Endangered species also endemic to Bolivia, was more intense than trade in blue-throated macaws in recent decades (www.cites.org), and current domestic trade in blue-throated macaws is negligible compared to the very high rates of red-fronted macaws annually poached and traded (Tella *et al.* 2013, Pires *et al.* 2016). Despite that, the current population of red-fronted macaws (Tella *et al.* 2013) is at least three times higher than the estimated for blue-throated macaws, and the breeding population of blue-throated macaw seems not being recovering (Berkunsky *et al.* 2014). However, in contrast to birds captured for the pet trade that usually involve young individuals (but see Pires *et al*. 2016), adult

macaws were hunted in the Beni region for making traditional headdresses. Population viability analyses indicate that the blue-throated macaw, as many other long-lived species, is highly sensitive to adult mortality (Bouzat and Strem 2012) and thus the species could have been largely affected by this activity. However, this activity has been largely reduced nowadays and is not likely to be the main cause impeding the recovery of the species (BirdLife International 2015, M. Herrera, com. pers.).

Other less considered factors such as low breeding performance or other abiotic/biotic constraints (e.g., microhabitat selection or interspecific interactions) could be maintaining the population at low-density, thus limiting the access and use of all suitable habitats. In this regard, it is known that only an average of 4.3 nestlings per year fledged from all known nests (n=19) despite of intense management for improving breeding success (Berkunsky *et al.* 2014). The entire population may be already too small and scattered through such a large region that behavioural, demographic and/or genetic-related Allee effects (Courchamp *et al.* 1999, Tella 2001) might currently impede the species' recovery. On the other hand, key ecological factors acting at a smaller scale not measured in this study, such as the number of tree cavities for breeding, the size and habitat deterioration of the forest islands, or food availability (palm fruits) could also be related (Berkunsky *et al.* 2015, Yamashita and De Barros 1997). Additionally, other factors such as interspecific interactions might also be important. Previous studies on the region have shown that the occurrence of a rich community of parrots depends upon local abundance of tree cavities in forest patches (Berkunsky *et al.* 2015), which suggests that interspecific competition might be high. Blue-throated macaws share their preference for nesting in large cavities of dead palms and trees with the larger-bodied blue-and-yellow macaw and red-and-green macaw (J.A. Díaz unpubl. data). Observations conducted in another Amazonian region showed that

blue-and-yellow nesting macaws engage in frequent intra- and inter-specific agonistic interactions in an area of up to 100 m around the nest, causing even infanticide and nesting failures (Renton 2004). Interference competition of nesting macaws may thus exclude potential breeders, effectively limiting nest availability where palm cavities are clumped in space (Renton 2004), as it is the case of palm forest islands where blue-throated and blue-and-yellow macaws coexist (Berkunsky *et al.* 2015). As blue-and-yellow macaws are larger, more aggressive, and far more abundant (Berkunsky *et al.* 2014, J.A. Díaz unpubl. data), they might be limiting the access to reproduction of blue-throated macaws even after the supplementation of artificial nests (see also Renton 2014). This may explain why the breeding population has not increased after a long-term program of nest-site provisioning within the species' breeding areas (Berkunsky *et al.* 2014). More specific studies are needed to determine whether and to what extent microhabitat selection (including food availability across the annual cycle) and interspecific interactions may be limiting the actual abundance and distribution of this Critically Endangered species.

Finally, population numbers and distribution range of the species could be actually larger than those recorded here, but limited surveys in less accessible areas limit our current knowledge. Future monitoring programs could directly benefit from results of SDMs provided in this study, which can be iteratively refined (as more observational data is collected), for conducting new surveys in the best suitable habitat patches. As a first step, new surveys should prioritize collecting empirical data in more remote (less accessible) areas and better distributed with respect to landuse composition at a landscape scale (particularly with better representation of continuous forest). Additionally, our SDMs should also help for an optimal design of potential reintroduction or population reinforcement programs that are projected for the species

(BirdLife International 2015). Such programs may benefit from validated estimates of the occurrence and distribution of true optimal habitats for the species (White *et al.* 2014), and a misunderstanding of these fundamentals may lead to inappropriate conservation management efforts. Refining SDMs with new surveys would aid in the optimal selection of release sites based both on habitat suitability and distance – connectivity- to the patches currently occupied by the species. This SDM-based approach could also help to increase the success of a number of translocation projects of parrots (White *et al.* 2012) and many other animal taxa (Pérez *et al.* 2012). Importantly, new studies should also consider finer habitat-demographic linkages, beyond species occurrences, since habitat-related choices made by individuals may be in some occasions decoupled from fitness outcomes (e.g., Cardador *et al.* 2015).

Supplementary Material

The supplementary materials for this article can be found at journals.cambridge.org/bci

Acknowledgements

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Table 1. Variable description and information sources. All variables were derived at 10 arcseconds (~30m) resolution.

Variable	Description	Source
Habitat		
Forest	Categorical variable with two levels, describing the presence of forest	Global Landcover Facility 2010
Palms	Minimum Euclidian distance to habitat categories including palm species, used as a proxy of food availability	Superintendencia Agraria 2007, Bolivia (Cobertura de Uso Actual de la Tierra 2007)
Landscape	Categorical variable with 6 levels, describing the dominant habitat at 1km^2 radius: cultivated land, forest, grassland, shrubland, wetlands and water and urban areas.	Global Landcover Facility 2010
Accessibility		
Rivers	Minimum Euclidian distance to rivers	Sistema de Informacion Territorial de Apoyo a la Producción, Bolivia (SITAP 2009)
Main roads	Minimum Euclidian distance to main roads	Administración Boliviana de Carreteras 2008
Secondary roads	Minimum Euclidian distance to secondary roads	Administración Boliviana de Carreteras 2008

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Table 2. Model performance of Maxent models based on different sets of variables using AUC, TSS and Test gain values. Note that for each set of variables, AUC, TSS and test gain (TG) values are averaged values across 10 replicate models calibrated using different randomly selected subsamples of total data (N = 79 records). Model significance was tested using threshold-dependent binomial probability tests, using the 10 percentile training presence (10p TP) and the maximum sensitivity plus specificity values (MSPS) as thresholds. The number of significant replicate models is provided.

Variable sets	AUC	TSS	TG	10p TP	MSPS
Habitat	0.88	0.65	1.50	all p<0.01	all p<0.01
Accessibility	0.70	0.33	0.36	all p<0.01	all p<0.01
Habitat+Accessibility	0.89	0.66	1.52	all p<0.01	all p<0.01

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Figure captions

Figure 1. Study area.

Figure 2. Partial response curves illustrating the relationships between probability of occurrence of the blue-throated macaw and our set of environmental and accessibility variables. These curves show how the shape of the response changes for a particular variable, while all other variables are held at their mean sample value. Mean response curve of the 10 replicate Maxent runs (red) and standard deviation (blue, two shades for categorical variables) are shown.

Figure 3. Performance of environmental and accessibility variables in univariate models (a) and independent contribution (b–d) of individual variables to multivariate models using different combinations of variables. Mean variable contributions and their standard deviations are calculated based on 10 replicate runs. The model contributions are based on test gain from Maxent.

Figure 4. Predicted distributions of the blue-throated macaw in Bolivia. Predicted distributions are based on Maxent models using occurrence data (dots, N=79) and different sets of variables: habitat, accessibility and habitat+accessibility. Note that models developed for each set of variables were calibrated using 10 different randomly selected subsamples of total data. Averaged predictions are shown.

44   Figure 1.

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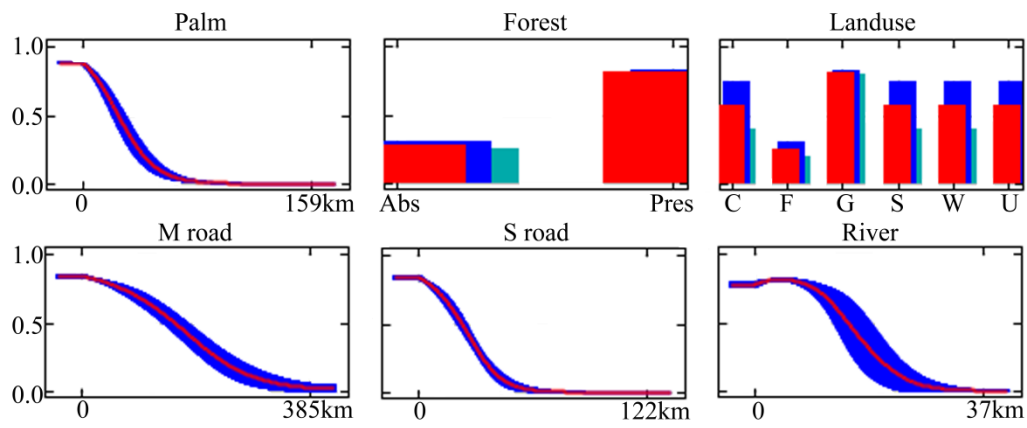0   500 1,000   2,000 Km

69   Figure 2.

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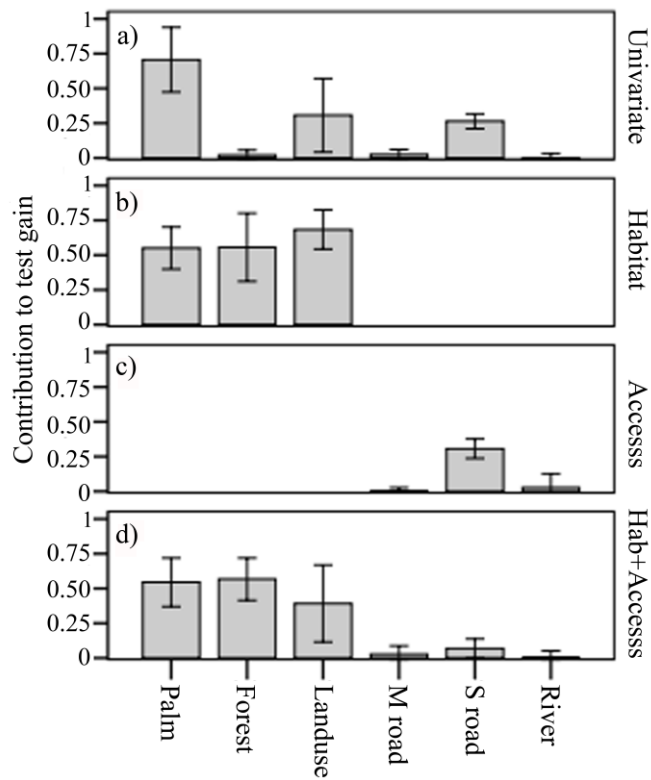
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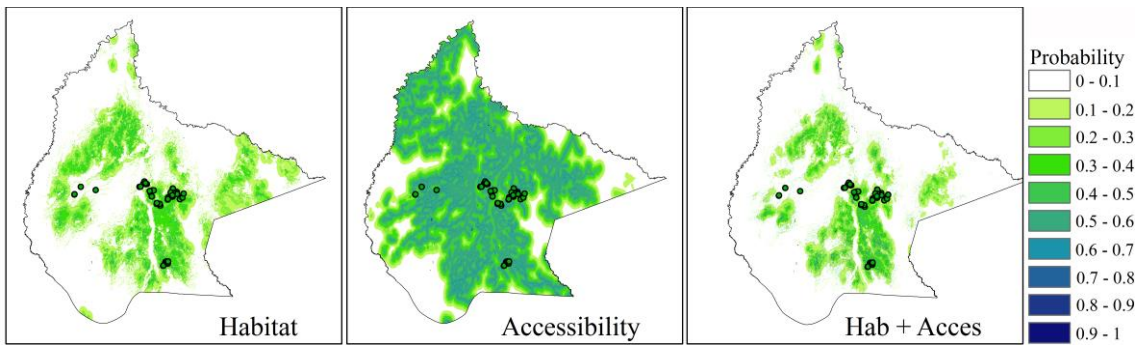97

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104   Figure 4.

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