

Modeling the Effects of Anthropogenic Habitat Change on Savanna Snake Invasions into African Rainforest

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Abstract: We used a species-distribution modeling approach, ground-based climate data sets, and newly available remote-sensing data on vegetation from the MODIS and Quick Scatterometer sensors to investigate the combined effects of human-caused habitat alterations and climate on potential invasions of rainforest by 3 savanna snake species in Cameroon, Central Africa: the night adder (*Causus maculatus*), olympic lined snake (*Dromophis lineatus*), and African house snake (*Lamprophis fuliginosus*). Models with contemporary climate variables and localities from native savanna habitats showed that the current climate in undisturbed rainforest was unsuitable for any of the snake species due to high precipitation. Limited availability of thermally suitable nest sites and mismatches between important life-history events and prey availability are a likely explanation for the predicted exclusion from undisturbed rainforest. Models with only MODIS-derived vegetation variables and savanna localities predicted invasion in disturbed areas within the rainforest zone, which suggests that human removal of forest cover creates suitable microhabitats that facilitate invasions into rainforest. Models with a combination of contemporary climate, MODIS- and Quick Scatterometer-derived vegetation variables, and forest and savanna localities predicted extensive invasion into rainforest caused by rainforest loss. In contrast, a projection of the present-day species-climate envelope on future climate suggested a reduction in invasion potential within the rainforest zone as a consequence of predicted increases in precipitation. These results emphasize that the combined responses of deforestation and climate change will likely be complex in tropical rainforest systems.

Keywords: climate change, habitat fragmentation, invasion, rainforest, snakes, species-distribution modeling

Modelado de los Efectos del Cambio Antropogénico de Hábitat sobre las Invasiones de Serpientes de la Sabana al Bosque Lluvioso Africano

Resumen: Utilizamos un método de modelado de la distribución de especies, conjuntos de datos climáticos y datos de percepción remota de la vegetación recientemente disponibles de los sensores MODIS y Quick Scatterometer para investigar los efectos combinados de las alteraciones del hábitat y del clima causadas por humanos sobre invasiones potenciales de la selva lluviosa por tres especies de serpientes de sabana en Camerún, África Central: *Causus maculatus*, *Dromophis lineatus* y *Lamprophis fuliginosus*. Los modelos con variables climáticas y localidades contemporáneas de hábitats de sabana nativa mostraron que el clima actual en el bosque lluvioso no era adecuado para ninguna de las especies de serpiente debido a la elevada precipitación. La disponibilidad limitada de sitios de nidación térmicamente adecuados y la incompatibilidad entre eventos importantes de la historia de vida y la disponibilidad de presas son

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una explicación probable de la exclusión pronosticada. Los modelos sólo con variables de vegetación y localidades de sabana derivadas de MODIS pronosticaron la invasión de áreas perturbadas dentro de la zona de bosque lluvioso, lo cual sugiere que la remoción de la cobertura de bosque por humanos crea microhábitats adecuados que facilitan invasiones del bosque lluvioso. Los modelos con una combinación de clima contemporáneo, variables de vegetación y localidades de bosque y sabana derivados de MODIS y Quick Scatterometer pronosticaron una invasión extensiva del bosque lluvioso causado por la pérdida de bosque lluvioso. En contraste, una proyección de las especies-clima actuales envuelta en clima futuro sugirió una reducción en el potencial de invasión dentro de la zona de bosque lluvioso como una consecuencia de los incrementos de precipitación pronosticados. Estos resultados enfatizan que las respuestas combinadas de la deforestación y el cambio climático probablemente serán complejas en los sistemas de bosque lluvioso tropical.

Palabras Clave: bosque lluvioso, cambio climático, fragmentación de hábitat, invasión, modelado de la distribución de especies, serpientes

Introduction

Habitat destruction and fragmentation is a leading cause of biodiversity loss (Fahrig 2003; Hoffmeister et al. 2005), particularly in tropical rainforests, where species richness and rates of anthropogenic land conversion reach some of the highest levels of any ecosystem (Achard et al. 2002; Wright 2005). Although there has been considerable emphasis on the loss of rainforest species, less attention has been paid to the impacts of biological invasions (Wright 2005). Invasions are frequently mediated by habitat disturbance, facilitating dispersal into previously unsuitable habitats (Vitousek et al. 1997). Although invasive species typically refers to human-introduced non-native species, the term also describes the expansion of native species into adjacent biomes where they do not normally occur.

In addition to human-caused habitat loss, climate change may also alter habitats and animal and plant populations in profound ways (Parmesan 2006). Ranges of species are expected to shift as a function of their physiological tolerances (Parmesan 2006). Shifts in temperature are accompanied by changes in precipitation, which affects the distribution of vegetation (IPCC 2007). Populations unable to move or adapt quickly may face extinction (Parmesan 2006). Combined, impacts of habitat conversion and climate change are likely to have dramatic and complex effects. The combined effects of climate and habitat fragmentation on species distributions, however, are poorly understood, especially for tropical ecosystems.

Ectothermic species, such as snakes, are highly dependent on ambient thermal environments, which through their effects on body temperature influence physiology, locomotor performance, behavior, habitat use, and ultimately, fitness (Stevenson et al. 1985; Row & Blouin-Demers 2006). Because of this sensitivity, snakes are ideal for investigating the impacts of habitat alteration and climate warming. At a local scale rainforest fragmentation creates invasion opportunities for savanna species by producing clearings with more savanna-like thermal

attributes. These clearings also create edge effects that invaders can exploit: hotter, drier conditions persisting within fragments up to hundreds of meters from the rainforest-clearing boundary (Laurance et al. 2002) and increased microclimate heterogeneity (Camargo & Kapos 1995), which depend, in part, on edge structure (Camargo & Kapos 1995; Didham & Lawton 1999). Global warming alters temperature gradients and seasonality on a continental scale, which may lead to regional distribution shifts by temperature-sensitive species.

In equatorial Africa human population expansion, logging, agriculture, and firewood harvesting create open-canopy vegetation that structurally resembles savanna. Consequently, species that are typically restricted to savanna habitats now occur in disturbed areas within the rainforest zone (e.g., Thiollay 1986; Akani et al. 1999). In addition to these effects, Africa is predicted to be the continent most vulnerable to the effects of climate change (IPCC 2007). Determining invasion potential resulting from climate change or habitat destruction is important because invaders may displace or reduce densities of existing species (Case & Bolger 1991), cause extinction (Savidge 1987), and have deleterious ecosystem-level effects (Hoffmeister et al. 2005).

To generate present and future distribution models of 3 Central African snake species, which typically inhabit savanna but are also found in human-disturbed forest habitats, we integrated contemporary point-locality data and bioclimatic and satellite remote-sensing data in a species-distribution modeling framework. Species-distribution models use information on environmental variables at species localities to construct an environmental envelope that approximates a species' ecological niche, and then the models project the niche onto geographic space to predict distribution of a species.

Because our study species have not historically occurred in rainforest, we first tested the hypothesis that rainforest is climatically unsuitable for savanna snakes. We did this by building distribution models with only climate variables and snake localities from the savanna.

Next, we addressed the proposed mechanism underlying invasion, specifically, how human alteration of rainforest may create savanna-like habitats with suitable microclimates. To test this hypothesis, we built models that included only fine-scale remotely sensed data on vegetation from MODIS and savanna localities. Finally, to estimate the relative contributions of climate and vegetation in the predictions and to provide an assessment of invasion potential, we constructed models that included all environmental variables and all snake localities. Our specific objectives were to predict the contemporary distributions of the 3 snake species in Cameroon; assess the relative influence of vegetation cover and current climate on the snakes' ability to invade the rainforest zone; and explore how climate change might influence invasions.

Methods

Study Area and Species

We conducted our study in Cameroon, Central Africa, a country with dense rainforest in the south and savanna in the north (Fig. 1). Between these 2 biomes is an ecotone of rainforest fragments, gallery forest, and savanna (Letouzey 1968). There is substantial variation in level of anthropogenic disturbance, temperature, and precipitation regimes along the rainforest-savanna gradient, mak-

ing it an ideal setting to test the joint effects of forest fragmentation and climate change on species distributions.

We studied 3 snake species that are broadly distributed in the savanna. In the rainforest zone these species are found only in human-disturbed habitats, which suggests a recent invasion. We chose these species because available point-locality data sets were sufficiently large for modeling, their taxonomic status is reasonably certain and they are absent in undisturbed rainforest (Akani et al. 1999; Chippaux 1999; Sprawls et al. 2002) but have been recently observed in rainforest.

The night adder (*Causus maculatus*, 88 localities; Fig. 2) is a nocturnal viper found in savanna and human-disturbed regions of forest (e.g., gardens, plantations, and urban areas) and semidesert (Akani et al. 1999; Chippaux 1999; Sprawls et al. 2002). It preferentially feeds on amphibians and, as a result, uses wet microhabitats (Luiselli et al. 2004). Reproduction in this species is seasonal, with oviposition occurring most frequently at the beginning of the wet season, which coincides with the reproduction of its amphibian prey (Luiselli et al. 2004).

The olympic lined snake (*Dromophis lineatus*, 33 localities; Fig. 2) is a diurnally active, oviparous colubrid inhabiting moist savannas, damp grasslands, floodplains, lake shores, marsh edges, and plantations (Menzies 1966; Chippaux 1999; Sprawls et al. 2002). It feeds on amphibians and small mammals (Villiers 1975).

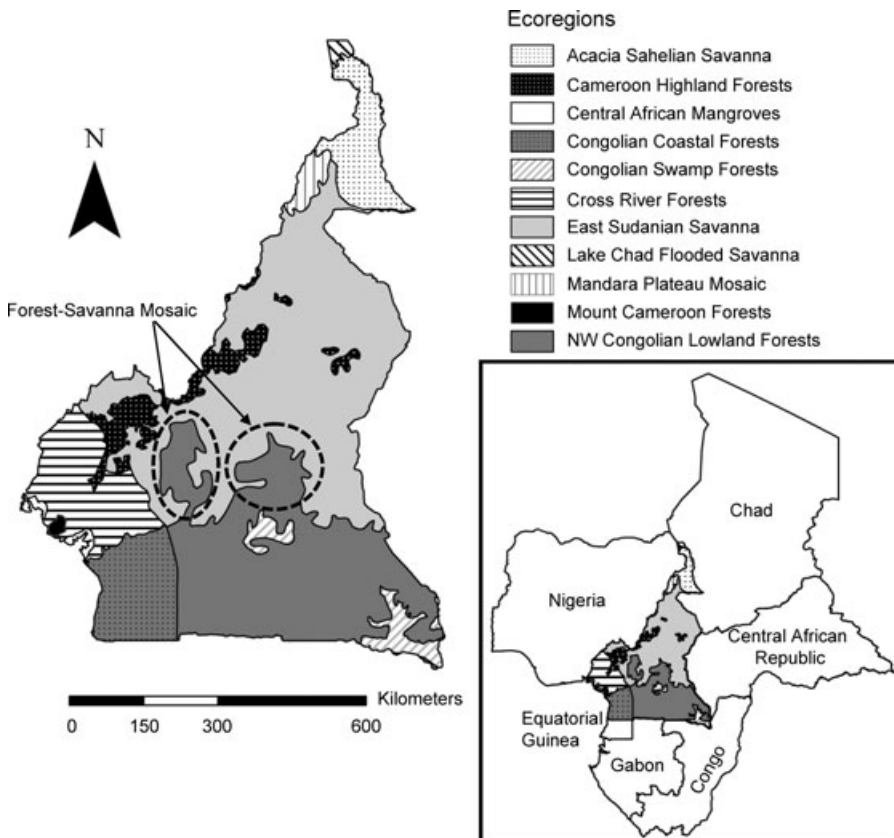


Figure 1. Ecoregions of Cameroon showing the distribution of rainforest and savanna habitats (from CARPE 1997).

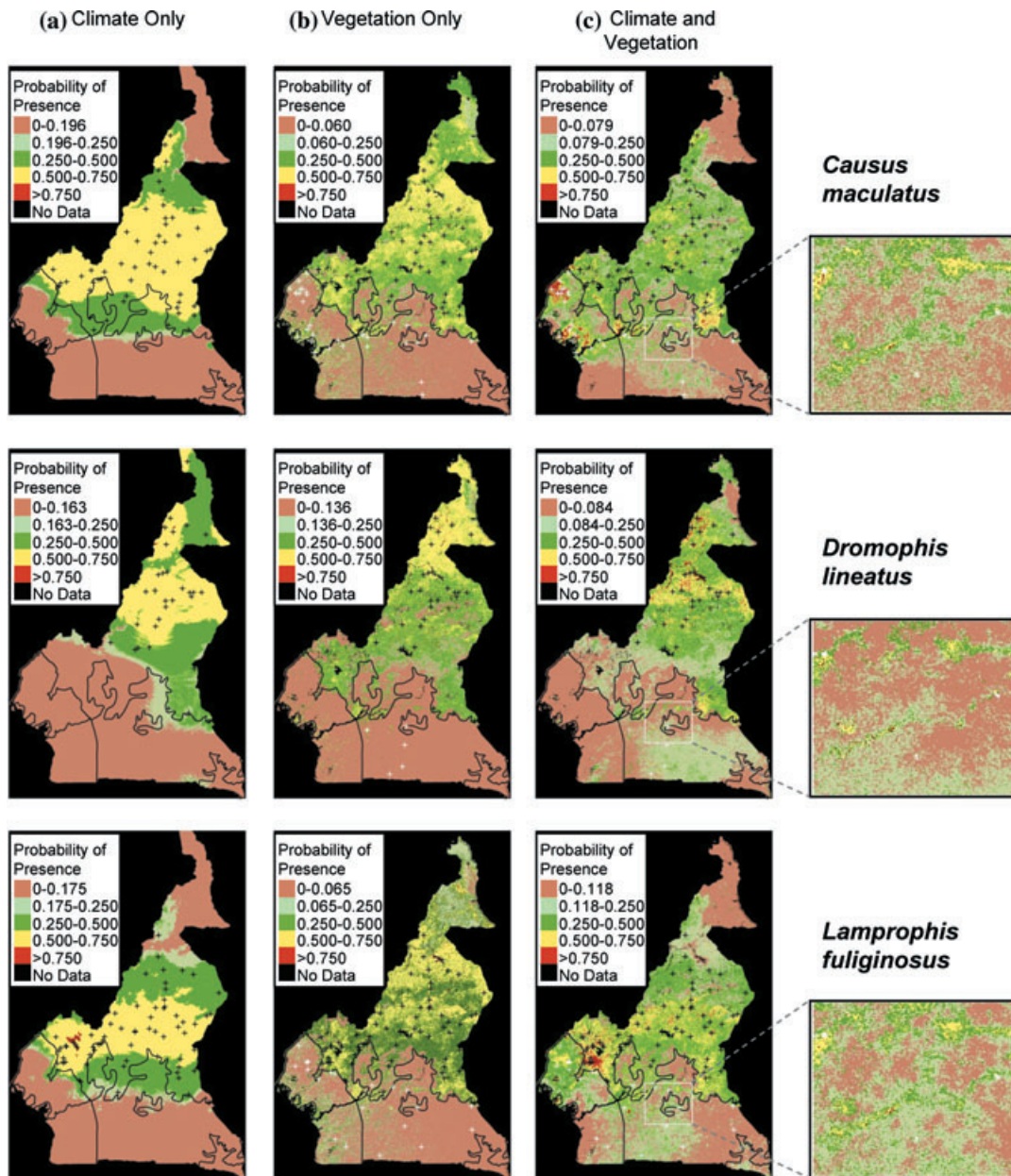


Figure 2. Point localities, probabilities of occurrence, and predicted distributions under present conditions for 3 snakes that are potentially invasive in Cameroon's rainforests. Color scale indicates probability of occurrence and thus invasion potential, with larger values indicating greater probability of occurrence. Areas with probability of occurrence larger than the balance threshold define a species likely distribution. Tan areas are those below the balance threshold. Distributions are derived from models with (a) climate and elevation variables and savanna points only, (b) fine-scale MODIS vegetation variables and savanna points only, and (c) climate, elevation, MODIS, and QSCAT variables and all point localities. Black and white crosses indicate localities in the savanna and rainforest, respectively. Black contour lines outline ecoregions within the rainforest (see Fig. 1). White squares in (c) indicate areas enlarged to the right. Within the enlargements, the area of high predicted probability of occurrence in the upper right corner is an area of extensive clearcutting, and the diagonal line running from the lower left corner represents clearing along the road between Yaoundé and Bertoua.

The African house snake (*Lamprophis fuliginosus*, 86 localities; Fig. 2) is a nocturnal, oviparous colubrid inhabiting savanna and mosaics of forest and human-created savanna ("derived savanna"). It is highly tol-

erant of urban land use and cultivation. It preferentially feeds on small mammals (Akani et al. 1999; Chippaux 1999; Sprawls et al. 2002; Luiselli et al. 2005).

Because lower temperatures under the canopy might pose less of a physiological constraint to nocturnal species—whose peak activity times coincide with the coolest part of the diurnal cycle—we hypothesized that *C. maculatus* and *L. fuliginosus* would display greater invasion potential than *D. lineatus*. Rainforest habitats contain greater per-area abundance of amphibian prey than savanna, but intensive human land use leads to elevated rodent densities. Thus, we did not attempt to make a priori predictions with respect to invasion potential on the basis of dietary preferences. Here, we defined invasion as the penetration of areas within the rainforest zone.

All locality data were compiled during a recent countrywide survey of reptiles by a Cameroon-based project (CAMHERP) and will be in a forthcoming atlas of the reptiles of Cameroon. Our data points (spanning 1998–2003) included GPS-referenced sites of reptiles captured by CAMHERP herpetologists and those collected by local field assistants in villages, surrounding forest, and on farms. Although there may be some bias in collection toward inhabited areas, this would actually underestimate invasion areas. Because localities in the rainforest would only be associated with extreme levels of vegetation clearing proximal to human settlement and not other disturbed forest habitats, models would underpredict invasions of disturbed habitats farther from inhabited areas. Area coverage included most 0.5° grid cells within country boundaries.

Environmental Data

We obtained data on 19 bioclimatic variables from WorldClim (version 1.4; Hijmans et al. 2005) gridded to 1-km resolution and selected a subset to capture major variation in annual means and seasonality of temperature and precipitation that likely serve as limiting factors for reptiles. Specifically, we selected annual mean temperature, temperature mean diurnal range, temperature seasonality, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest quarter, and precipitation of the driest quarter. Future projections of these climate layers were also obtained from WorldClim and stem from a simulation of the CCM3 general circulation model under doubling of CO₂ (Govindasamy et al. 2003). Depending on the emission scenario, a doubling of CO₂ may be reached anytime from the middle to the end of this century (IPCC 2007).

Remote-sensing data provided measurements of variables such as topography, tree cover, vegetation density (e.g., leaf area), and seasonality. To quantify spatial and temporal vegetation patterns, we used the monthly 1-km leaf area index (LAI) data derived from MODIS reflectance over a 5-year period (2000–2004; Myneni et al. 2002). To further reduce effects of persistent cloud cover and natural interannual variability in the data, we created

monthly climatologies by averaging the 5 years of data. We then used these composites to generate 2 vegetation variables: annual maximum LAI and LAI annual seasonality (difference between annual maximum and minimum months). As an additional fine-scale metric of land cover, we used the MODIS-derived vegetation continuous field (VCF) product as a measure of the percentage of tree canopy cover at 1-km resolution (Hansen et al. 2002). The VCF came from 2001 MODIS data and separated open, fragmented, and deforested areas from those of intact old-growth forests. We also generated monthly composites of global Quick Scatterometer (QSCAT; Long et al. 2001) microwave measurements for 2001 and processed them to produce 2 variables: annual mean (QMEAN) and standard deviation of radar backscatter (QSD). The QSCAT data layers were reaggregated from their 2.25-km native resolution to 1 km to match the resolution of the other predictor variables. The QSCAT radar measurements are sensitive to surface roughness, surface moisture, leaf water content, and other seasonal attributes, such as deciduousness of vegetation. They also have the added advantage of being unbiased by cloud cover. Finally, we included elevation data at 1-km resolution from the Shuttle Radar Topography Mission (SRTM).

Covariance among environmental variables may limit interpretation with respect to which variables best explain predicted distributions. To assess covariance among the 13 environmental variables, we computed a cross-correlation matrix with 1000 random points sampled throughout the study area. Only 7 of 78 bivariate correlations had values of $r > 0.75$, which suggests the selected variables carry a considerable amount of unique information. The model algorithm we used (Maxent) is largely insensitive to covariance among variables (S. Phillips, personal communication).

Species-Distribution Modeling

We modeled species distributions with Maxent (version 3.0), a recently developed general-purpose algorithm for presence-only data (Phillips et al. 2006). In a recent, comprehensive, intermodel comparative study, Maxent ranked among the highest performers (Elith et al. 2006). Other researchers prefer biophysical models for predicting reptile distributions (Kearney & Porter 2004). Although such approaches are useful for deriving hypotheses pertaining to mechanisms through which thermal constraints limit distributions (Kearney & Porter 2004; Crozier & Dwyer 2006), they require extensive species-specific information on physiological responses to ambient climate. Such data are lacking for most tropical species, including ours. Furthermore, biophysical models focus on the fundamental niche and do not account for nonclimatic influences, such as interspecific interactions, unless physiological parameters are supplemented with information on relevant biotic features such as

community composition. In contrast, correlative models derived from environmental envelopes (such as Maxent) can capture biotic and abiotic effects and at large spatial scales are suitable for making predictions concerning the likely effects of climate change (Pearson & Dawson 2003). Although distributions of ectotherms may be limited by the thermal environment, there is also abundant evidence for biotic interactions of large effect in tropical snakes (Madsen & Shine 2000; Luiselli 2006; Madsen et al. 2006). Because we focused on distributions at a countrywide scale and wished to incorporate all potentially significant factors influencing invasions, an environmental-envelope modeling approach was implemented.

For each species, we built 3 different species-distribution models for present-day conditions. First, to test the hypothesis that undisturbed rainforest is climatically unsuitable for our focal species, we built models with only bioclimatic variables and elevation. We included elevation because it captures steep elevation-associated climatic gradients. To characterize the climatic envelope of the noninvasive range of our species, we restricted this analysis to localities from (1) savanna, (2) the northernmost margin of the forest-savanna mosaic containing natural savanna vegetation, and (3) Cameroon Highland forests, which contain a mixture of shrub, woodland, and savanna vegetation and thus have natural habitat for our focal species (Fig. 1). Our climate data were relatively coarse and did not allow us to quantify the microclimates our study species presumably use in the rainforest. But, given historical correlations between climate and vegetation cover at regional scales (in the absence of substantial habitat alteration by humans), we used climate data to validate the known, historical exclusion of our study species from the rainforest. This test was complementary to the second test that only had vegetation variables and savanna localities (see below) because it allowed us to rule out invasions facilitated by suitable macroclimates in the rainforest zone.

Second, to test the hypothesis that large-scale human alteration and fragmentation of rainforest has made it more suitable for invasions, we built a set of models with only the MODIS remote-sensing variables. These variables are suitable to identify rainforest alterations at spatial scales on the order of 1 km (close to their original resolution), but cannot discern deforestation pattern at smaller scales. If the mechanism that underlies invasion is the creation of more savanna-like habitat and microclimates (Vitt et al. 1998; Foley et al. 2005), then localities within the savanna should predict invasion within the rainforest biome. In other words, we used the remotely sensed variables as surrogates for microclimatic variation in the affected rainforest zone. As with the first set of models, we excluded rainforest localities, but included them in a second step to evaluate how well the models predicted distributions in rainforest.

Finally, in a third set of models, we used all available information on climate, elevation, and vegetation to quantify the relative contributions of climate and vegetation and to determine the extent of current snake distributions. Because we wanted to characterize the environmental envelope of both the native and invasive distributions, we included rainforest localities. However, because the climate variables are interpolated surfaces, they have extremely coarse effective resolution (due to the low density of the station network) and thus do not capture microclimatic variation. Thus, inclusion of rainforest sample points introduced a bias in the species-climate relationship: models inferred that rainforest climates are suitable and overpredicted invasion potential in the rainforest zone. However, failure of our vegetation variables to detect areas of small-scale deforestation that are potentially suitable habitat for savanna snakes would lead to underprediction of invasion potential. With these considerations in mind, our models defined reasonable approximations of invasion potential. To reduce some of the potential bias, we included QSCAT variables, which have a 2.25-km nominal resolution. These data were slightly coarser than the MODIS variables, but have proven effective in distinguishing rainforest from savanna biomes (Buermann et al. 2008). Furthermore, because QSCAT measurements are sensitive to canopy moisture and roughness, they captured aspects of climate at finer resolution than the bioclimatic variables. They also reduced potential overprediction resulting from edge effects: presences in pixels of high rainforest cover estimated by MODIS that result from close proximity to other pixels with low vegetation cover.

To explore how future climate change may influence invasion potential, we projected the present-day climate-species relationship onto future estimates of temperature and precipitation data that stem from the CCM3 CO₂ doubling scenario (Govindasamy et al. 2003). In this experiment, we only included climate variables because we did not know how vegetation would change in the future. We excluded elevation because of its confounding association with contemporary climate. To identify which climate variables were most important in the projection of the species' responses to a doubling of CO₂, we ran sensitivity analyses in which the climate variables were held constant except for the variable of interest and visually compared climate-change maps with model predictions. To evaluate potential problems with predictions due to climate shifts outside current climate space, we examined Maxent output maps that identify areas of "clamping," where Maxent reduces projected future climate variables to their present maximum within the study area, if they are projected to exceed it. Although future climate projections (and particularly those for precipitation) contain uncertainty (Neelin et al. 2006), the CCM3-based projected increases in temperature and precipitation over our study region are largely consistent

with projections derived from ensemble means of 22 different climate models (IPCC 2007).

We tested spatial accuracy of the predictions with threshold-dependent (omission and predicted area) and threshold-independent (area under the receiver operator curve [AUC]) measures following Phillips et al. (2006). We created 10 random data partitions, with 60% of the point localities assigned for training and 40% for testing. We performed threshold-independent tests through the Accumetric Test Performance Analysis toolbox (Vida 1993). To facilitate threshold-dependent tests, we evaluated model performance at the balance threshold, which balances intrinsic (training) omission, proportional predicted area, and cumulative threshold, and, hence, minimizes over- and underprediction (Phillips 2005). For the models in which only vegetation variables and savanna localities were used, we also estimated how well the models predicted rainforest localities by calculating omission error at the balance threshold and across all thresholds (in terms of test AUC). Here we used the average predicted probability of presence within a 5-km radius to account for imprecision in georeferencing of locality and remote-sensing data. We defined the rainforest zone according to ecoregion boundaries (Fig. 1) and considered areas within that zone with predicted probabilities of occurrence above the balance threshold to constitute the invasion area; increasing probabilities of species occurrence indicated greater invasion potential.

Results

Distribution models for all species performed well. The probability of predicting a species absent when it was actually present (test omission error) was generally low at the balance threshold (Table 1). At that threshold all but one model performed significantly better than random at the 0.05 level, and all models were significant at the 0.10 level (Table 1). Across all thresholds (thresh-

old independent), all model performances were highly significant ($p < 0.005$; on the basis of test AUC against random). Test AUC values were generally close to training AUC except for the climate-only simulations in which there was a tendency for the models to overfit. In general, these test results from 10 partitions indicated the models were powerful in discriminating suitable from unsuitable habitats.

For all 3 species, with the exception of minor incursions, models derived exclusively from climate and elevation variables did not predict invasions into the rainforest zone (Fig. 2a). This suggests that, when undisturbed, rainforest is climatically unsuitable. In the predictions for *C. maculatus* and *D. lineatus*, precipitation of the driest quarter (PDQ) was the most important variable. This variable exhibited greater values in the rainforest zone, particularly near the coast, and had a negative relationship with habitat suitability. Elevation was most important for *L. fuliginosus* (Table 2) and had a positive relationship with habitat suitability. This was due to higher temperature and lower rainfall on the Adamaoua plateau, which makes up a large portion of the savanna in Cameroon. For *C. maculatus* and *L. fuliginosus*, lower temperature diurnal range in the rainforest also limited invasion potential.

Models that included only MODIS vegetation variables and savanna localities showed extensive areas of invasion within the rainforest zone for *C. maculatus* and *L. fuliginosus* and to a much lesser extent for *D. lineatus* (Fig. 2). For all species tree cover was the most important variable (Table 2). Habitat suitability was negatively correlated with tree cover, and predictions of invasion in rainforest along major roadways and near urban centers were consistent with our hypothesis that human removal of rainforest vegetation facilitates invasion by creation of savanna-like microhabitats in the rainforest zone. For predicted probabilities of occurrence at known rainforest localities, omission error rates derived from the balance threshold were variable: 15%, 80%, and 50% for

Table 1. Species-distribution model summary statistics and results from threshold-dependent and threshold-independent significance tests with 10 data partitions for 3 snake species.*

Species	Predicted area	Test omission rate	Training AUC	Test AUC
<i>Causus maculatus</i>				
climate only	0.567 (0.010)	0.065 (0.017)	0.788 (0.005)	0.693 (0.010)
vegetation only	0.577 (0.011)	0.036 (0.011)	0.803 (0.006)	0.789 (0.009)
climate and vegetation	0.668 (0.031)	0.057 (0.013)	0.848 (0.004)	0.748 (0.006)
<i>Dromophis lineatus</i>				
climate only	0.476 (0.011)	0.142 (0.028)	0.878 (0.005)	0.776 (0.012)
vegetation only	0.473 (0.012)	0.020 (0.020)	0.849 (0.007)	0.847 (0.014)
climate and vegetation	0.569 (0.027)	0.078 (0.020)	0.896 (0.007)	0.826 (0.011)
<i>Lamprophis fuliginosus</i>				
climate only	0.556 (0.015)	0.044 (0.011)	0.826 (0.003)	0.781 (0.008)
vegetation only	0.571 (0.015)	0.039 (0.014)	0.830 (0.003)	0.802 (0.006)
climate and vegetation	0.423 (0.007)	0.086 (0.014)	0.904 (0.003)	0.833 (0.007)

*Estimates are means (SE) from 10 random partitions of the data.

Table 2. Relative contributions (%) of environmental variables to Maxent models of the distribution of 3 snake species.

Model scenario	Variables ^a												
	SRTM	BIO1	BIO2	BIO4	BIO6	BIO12	BIO16	BIO17	MAX	MAX-MIN	VCF	QMEAN	QSD
Climate only													
<i>C. maculatus</i>	0.0	14.8	18.2	22.3	0.1	3.2	0.0	41.5 ^b	—	—	—	—	—
<i>D. lineatus</i>	1.0	6.8	19.2	4.7	0.8	0.3	0.0	67.2 ^b	—	—	—	—	—
<i>L. fuliginosus</i>	38.6 ^b	0.0	15.6	25.4	0.0	7.5	2.4	10.4	—	—	—	—	—
Vegetation only													
<i>C. maculatus</i>	—	—	—	—	—	—	—	—	12.3	0.0	87.7 ^b	—	—
<i>D. lineatus</i>	—	—	—	—	—	—	—	—	29.7	3.8	66.4 ^b	—	—
<i>L. fuliginosus</i>	—	—	—	—	—	—	—	—	33.7	5.1	61.2 ^b	—	—
Climate and vegetation													
<i>C. maculatus</i>	8.1	1.6	2.0	4.6	5.3	4.9	16.5	12.7	3.6	2.5	20.6 ^b	0.4	17.2
<i>D. lineatus</i>	1.8	3.2	4.4	6.4	1.4	10.8	0.0	18.9	17.4	5.0	28.6 ^b	0.0	2.2
<i>L. fuliginosus</i>	3.0	4.8	5.8	0.4	0.1	14.7	1.8	12.9	8.1	2.9	22.6 ^b	2.9	20.1

^aAbbreviations: SRTM, elevation; BIO1, annual mean temperature; BIO2, temperature mean diurnal range; BIO4, temperature seasonality; BIO6, minimum temperature of the coldest month; BIO12, annual precipitation; BIO16, precipitation of the wettest quarter; BIO17, precipitation of the driest quarter; MAX, annual maximum LAI; MAX-MIN, annual LAI seasonality; VCF, percent tree cover; QMEAN, annual mean of radar backscatter; and QSD, standard deviation of radar backscatter.

^bVariable contributing most to the model.

C. maculatus, *D. lineatus*, and *L. fuliginosus*, respectively. The relatively high omission errors for the latter 2 species were to some extent due to our choice of a conservative threshold, but also resulted from remote-sensing data not capturing smaller-scale deforestation that facilitates invasion. Even so, threshold-dependent (at balance threshold) and threshold-independent tests with rainforest point localities and predicted area restricted to the rainforest zone indicated that the predictions were significantly better than random for *C. maculatus* (both tests, $p < 0.001$; AUC = 0.754) and *L. fuliginosus* (both tests, $p < 0.001$; AUC = 0.637). For *D. lineatus*, both tests were marginally nonsignificant ($p = 0.133$; AUC = 0.643), likely due to the small sample size ($n = 5$) for test localities.

Models incorporating climate and remote-sensing (including QSCAT) variables in conjunction with all point localities predicted an invasion front extending deep into the Northwest Congolian Lowland Forest for all species (Fig. 2c). Present-day patterns of species distribution within the rainforest zone were determined by a combination of vegetation variables. This is clearly visible in the pixellated distribution of higher-suitability values within the rainforest (Fig. 2c), which contrasts with the smooth, clinal variation of the coarser bioclimatic variables (Fig. 2a). In addition, even though the coarser-resolution QSCAT and climate variables partially obscured the effect of fine-scale vegetation patterns, increased habitat suitability due to anthropogenic reduction of forest cover was still apparent along the major transportation corridor between the cities of Yaoundé and Bertoua and in an area of past rainforest clearcutting (Fig. 2c, see enlargement). Predicted distributions of *C. maculatus* and *L. fuliginosus* also extended into the

Cross River Forest, and *L. fuliginosus* showed the greatest propensity for invading the Congolian Coastal Forest (Fig. 2c). For all species, tree cover contributed most to the overall model (Table 2). For *C. maculatus* and *L. fuliginosus*, QSD explained proportions of the model comparable to tree cover (Table 2). Differential levels of invasion potential among the three species supported the hypothesis that nocturnal species exhibit greater invasion potential: extent of invaded areas in the rainforest zone (on the basis of balance threshold) were 133,267 km², 103,467 km², and 148,319 km² for *C. maculatus* (nocturnal), *D. lineatus* (diurnal), and *L. fuliginosus* (nocturnal), respectively. The importance of rainforest alteration was not confounded by climate because within the rainforest zone, correlations between climate and vegetation (including QSCAT) variables were extremely weak (mean absolute value of bivariate correlations at 1000 random points within rainforest, r (SE) = 0.148 (0.018)).

The reduction of invasion potential within the Congolian Coastal Forest relative to models built only with vegetation variables was due to climatic constraints. Percent contributions of variables to models, combined with sensitivity analyses that excluded bioclimatic and QSCAT variables in a stepwise fashion, demonstrated that for *C. maculatus* this pattern was driven by greater PDQ, for *D. lineatus* by larger values for all precipitation variables combined, and for *L. fuliginosus* predominantly by lower temperature diurnal range and by higher PDQ. These comprehensive models suggest that human alteration of vegetation facilitates savanna snake invasions, but that climatic constraints may limit these invasions in portions of the rainforest biome.

Future climate change was predicted to cause a reduction in habitat suitability in the rainforest zone for

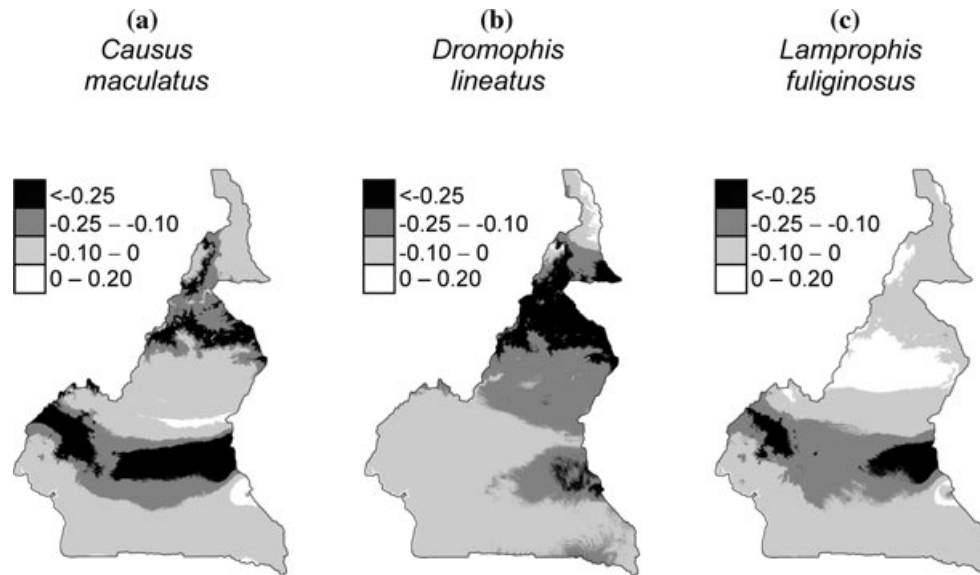


Figure 3. Changes in predicted probability of occurrence of (a-c) 3 snake species as a result of climate change predicted by the CCM3 global circulation model under a doubling of CO_2 . Future distributions were generated through projecting the present-day climate-species relationship derived from savanna points and climate layers only onto the future climate. Map values equal the difference between the future and present predicted distributions (see Fig. 2a), with negative and positive values indicating areas of decreasing and increasing probability of occurrence, respectively.

all species largely because of the projected trend toward wetter conditions (Fig. 3). These changes were most dramatic for *C. maculatus* and *L. fuliginosus*, rendering substantial areas of the rainforest-savanna ecotone and lower savanna climatically unsuitable. Increase in PDQ was an important driver of reductions of habitat suitability for these 2 species. Decreasing temperature diurnal range and a more spatially variable pattern of change in precipitation of the wettest quarter also contributed to suitability reductions for *C. maculatus* and *L. fuliginosus*, respectively. The smaller reductions in suitability predicted for *D. lineatus* were not clearly explained by any single variable, which suggests small changes in several variables were the cause. We did not observe any clamping effects, which indicates projection of future climate outside of the current climate space did not occur.

Discussion

Deforestation and the effects of climate change are dramatically transforming ecosystems worldwide. The rapidity and pervasiveness of these impacts requires a better understanding of how they operate in concert, yet few researchers have taken such an approach. To our knowledge ours is the first study that attempts to simultaneously examine the effects of habitat alteration and future climate change for equatorial African reptiles. Our results show that human disturbance is creating favorable condition for the invasion of 3 snakes into the rainforest zone.

In contrast, predictions of future climate change indicate rainfall will increase in the rainforest zone, which will likely inhibit invasions. Thus, the effects of deforestation and climate change are complex and potentially opposing forces on invasion dynamics.

Our models provide evidence that human alterations of vegetation are leading to invasions within the rainforest. First, models with savanna occurrences and climate variables supported our hypothesis that the rainforest zone is climatically unsuitable. This suggests that for invasion to occur in the rainforest, a release from climatic constraints is necessary. Second, models with savanna occurrences and vegetation variables supported our hypothesis that human alteration of rainforest vegetation facilitates invasions. These models predicted invasions within the rainforest and identified areas of anthropogenic habitat modification (along roadways and in logged and urbanized areas) as suitable habitat. Third, models including all environmental variables predicted extensive invasion areas within the rainforest zone. Vegetation variables were the drivers of invasions, and models predicted fine-scale, pixellated invasion patterns in rainforest despite the smoothing effects of climate and QSCAT variables. This was due to the dominant influence of satellite-based fine-scale data on tree cover, which indicated snake species were more likely to occur in areas with limited canopy cover resulting from land conversion.

Habitat suitability does not guarantee occupancy because invasions also depend on dispersal success

(Peterson 2003). Nevertheless, given the extensive amount of disturbance that has already occurred and the large and increasing road network (Nolte et al. 2001), dispersal is unlikely to be a limiting factor. In light of this and the potential sources of under- and overprediction mentioned above, we believe our models represent reasonable approximations of where species will invade.

Human-mediated increases in habitat suitability may be due to increased insolation in more open habitats created by rainforest removal. This would lead to thermal conditions at potential nest sites being more similar to those in savanna. For nocturnal reptiles warmer nest sites can be a limiting resource in areas where dense canopy cover reduces nest-site temperatures (Pringle et al. 2003). Thus, although we found greater invasion potential for nocturnal than diurnal species (consistent with our hypothesis that nocturnal species have lower thermal sensitivity), this pattern may actually be due to land-use-facilitated increases in the availability of thermally suitable daytime refugia.

Because we constructed models that both isolated and combined climate and vegetation variables, we were able to determine how unsuitable climate might partially constrain invasions driven by anthropogenic alteration of rainforest. Within the Congolian Coastal Forest, prevailing wet conditions limited invasions relative to those predicted by models that included only vegetation variables. The greater predicted invasion areas in the Northwest Congolian Lowland Forest relative to the Congolian Coastal Forest suggest that, as one moves away from the coast, climates become more suitable and human effects on vegetation overcome the constraints imposed by the rainforest macroclimate.

Invasions may also be constrained by seasonal differences between the rainforest and savanna. In Cameroon rainforest is characterized by a short rainy season followed by a long one; the single and shorter savanna wet season lags months behind the onset of the wet season in rainforest. Oviparous tropical reptiles time reproduction to coincide with optimal nest moisture conditions and to avoid lethal waterlogging of eggs (Brown & Shine 2006). Timing may also be linked to prey availability because precipitation-regulated abundance of prey influences demographic, reproductive, and ecological characteristics of tropical snakes (Madsen & Shine 2000; Brown et al. 2002; Madsen et al. 2006). In particular, oviposition in *C. maculatus* is timed to coincide with reproduction of amphibian prey at the beginning of the wet season (Luiselli et al. 2004). If oviposition in the savanna corresponds to a period of relatively wetter conditions in the rainforest, invaders may deposit eggs when moisture levels are too high and produce offspring after the peak in prey availability has passed. Such maladaptive timing might substantially reduce reproductive success (Parmesan 2006).

For each of the 3 species, projected changes in future climates led to decreased habitat suitability in the

rainforest zone due to a trend toward increased precipitation and tended to counteracted invasions caused by deforestation. Although savanna ectotherms would be expected to be able to take advantage of future temperature increases in the rainforest, our results suggest the benefits from warming may be outweighed by the negative consequences of increased precipitation. Analogous to present-day exclusions from coastal areas noted earlier, the wetter conditions in the future may accentuate the temporal mismatch between important life-history traits and features of the biotic environment and may limit the availability of dry sites for oviposition. Conclusions with respect to future climate projections should, nevertheless, be regarded as tentative because there remains substantial uncertainty concerning patterns of future precipitation change (IPCC 2007). Furthermore, because future projections did not include vegetation variables and because human removal of rainforest is ongoing, whether an actual reduction in invasion potential due to climate change would occur is unclear.

Conclusions

As rainforest habitats of Central Africa continue to be degraded, snake species currently found in disturbed and savanna habitats are predicted to invade the rainforest zone. Because invading snake species may have severe impacts on native vertebrate populations (Savidge 1987; Case & Bolger 1991), conservation strategies for equatorial Africa should take into account the possibility of these invasions. Our models predict that future climate change will counteract the effects of rainforest removal and reduce invasion potential, due to projected increases in precipitation in the rainforest. Thus, climate change may actually mediate the effects of human removal of rainforest, which illustrates how anthropogenic habitat alteration and climate change are likely to have complex impacts on biodiversity. Nevertheless, because there is substantial uncertainty associated with projecting precipitation trends in tropical Africa, better predictions of future precipitation and analyses that incorporate such uncertainty are crucial. Additional studies are also needed to identify the outcome of interactions between bioclimatic variables that drive broad-scale species distributions, microhabitat variation due to human alterations of rainforest, and population-level processes that determine persistence of species within the invaded range.

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