Modeling vulnerability of protected areas to invasion by *Chromolaena odorata* under current and future climates

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Abstract. Invasive plant species and climate change are among the biggest threats to the ecological integrity of many ecosystems, including those of protected areas. Effective management of invasive plants requires information regarding their spatial distributions. Using maximum entropy, we modeled habitat suitability for an invasive plant species *Chromolaena odorata* under current and future climatic conditions (HadGEM2-ES and MIROC5) in protected areas of four West African countries (Benin, Côte d’Ivoire, Ghana, and Togo). Under current climatic conditions, approximately 73% of total land area within the protected areas was suitable for colonization by *C. odorata*. Under future climate projections, the total area of suitable habitats for this invasive plant was projected to decrease by 7–9% (HadGEM2-ES) and 12–14% (MIROC5). Country-specific patterns suggest that major protected areas in Côte d’Ivoire and Ghana will be more vulnerable to invasion by *C. odorata* than those in Benin and Togo under both current and future climatic scenarios. To maintain normal ecosystem functioning and provisioning of ecosystem services within the protected areas studied here, locations that have been identified as most vulnerable to invasion by *C. odorata* should be accorded proportionately higher priority when formulating appropriate management strategies.

Key words: *Chromolaena odorata*; climate change; HadGEM2-ES; maximum entropy; MIROC5; representative concentration pathways; risk assessment; Siam weed; West Africa.

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Introduction

Several hundred plant species have been introduced to biogeographic regions where they did not occur historically. A small percentage of them become invasive, with negative ecological and economic impacts to the regions they invade (Mack et al. 2000, Pimentel et al. 2005). The negative ecological impacts of invasive plants include losses of native biodiversity and disruption of normal ecosystem functioning (Mack et al. 2000, Pimentel et al. 2005). Invasive plants can have negative economic impacts when the displacement of native species disrupts the normal provisioning of economic services and can additionally be very costly to control (Pimentel et al. 2005).

The geographic distribution of a plant species is determined by complex interactions among a range of biotic and abiotic factors, including climate, soil properties, interactions with biotic agents, and dispersal limitation (Soberón 2007). Introductions of invasive plant species to new biogeographic regions has been attributed to human activities, including trade, travels, and recreation (Hulme 2009). With a recent intensifica-
tion in such activities, it is expected that alien plant species introductions will increase (Hulme 2009). Once introduced to a new biogeographic region, the range of an invasive plant species (i.e., the total land area that a plant can colonize) is determined by numerous factors, including the species’ residence time, the species’ rate of spread, the suitability of local climate, and the amount of suitable habitat available for its establishment, reproduction, and expansion (Foxcroft et al. 2007). Because climate is one of the major determinants of plant distributions, change in climatic conditions may influence range shifts (i.e., range expansion or contraction) in invasive plant species. This may have significant consequences for invaded ecosystems (Millennium Ecosystem Assessment 2005, Theoharides and Dukes 2007, Diez et al. 2012). Changes in temperature and precipitation can weaken biotic resistance of native plant communities to the establishment of alien species, potentially accelerating expansion of invasives (Diez et al. 2012). Alternatively, changes to current climatic conditions may render some areas less suitable and reduce the performance of certain invasive plants, leading to range contractions in those species (Taylor and Kumar 2013).

Protected areas are important for both conservation of biodiversity and provisioning of vital ecosystem services (Millennium Ecosystem Assessment 2005). However, the ecological integrity of protected areas globally is threatened by alien plant invaders and climate change (Millennium Ecosystem Assessment 2005, Foxcroft et al. 2007). Protected areas are similar to and are connected with their surroundings in many ways, with such surroundings serving as actual or potential sources of new or repeated introductions of invasive plants to the protected areas (Foxcroft et al. 2007). Spread of invasive plant species into and within the protected areas can occur through such natural means as dispersal by river water, birds, and mammals (Lonsdale and Lane 1994, Foxcroft et al. 2007). Human activities either inside or adjacent to the protected areas are another important pathway through which invasive plants can be introduced into the protected areas, with roads serving as a major pathway for introduction (Lonsdale and Lane 1994, Foxcroft et al. 2007). Despite the areas providing vital ecosystem services, management of protected areas is often allocated only limited resources (Foxcroft et al. 2007, 2011, Taylor and Kumar 2013). Therefore, prudent management regarding the threat of alien plant invasions requires information on the current and potential future distribution of invasive plants under changing climatic scenarios. Such information may enable the early detection and eradication of invasive plants from protected areas (Foxcroft et al. 2007, 2011, Taylor and Kumar 2013).

Potential range expansion (or contraction) of plant species under current and future climatic scenarios can be estimated using ecological niche models (ENMs; Elith et al. 2006, Elith and Leathwick 2009). Studies employing ENMs have drawn upon a host of species information, such as responses to climatic and soil conditions, and relate to that knowledge of current biogeographic distributions (Taylor and Kumar 2013). Ecological niche models use species occurrence data in conjunction with ecological data to achieve many objectives, such as estimating relative suitability of a habitat for a species in biogeographic regions where its presence either has or has not previously been detected, estimating changes in suitability of habitat over time with changing environmental conditions, and estimating the ecological niche of a species (Warren and Seifert 2011).

We used ENMs to model habitat suitability and potential future distribution of a globally important invasive plant species, *Chromolaena odorata* (L.) (King and H. E. Robins), under current and future climatic scenarios within the protected areas of four West African countries. *Chromolaena odorata* belongs to the genus *Chromolaena* DC, which comprises 129 species, all originating in South and Central America and the West Indies (King and Robinson 1970). Commonly called the Siam weed, *C. odorata* is a highly invasive species well known for its widespread distribution across five continents (Kriticos et al. 2005). The plant was reportedly first introduced to West Africa in the early 1960s, where it is currently a major weed across multiple ecological zones (Djietror 2012). Across the region, the plant has strong negative ecological impacts, particularly in forest reserves (Prasad et al. 1996, Djietror 2012, Uyi and Igbinosa 2013). For example, quick establishment of *C. odorata* prevents self-seeding of trees, hindering forest regeneration and development. Consequently, *C. odorata* is one of the biggest threats to native biodiversity in ecosystems of West Africa. Given the severity of the threat posed by *C. odorata*, forecasting its habitat suitability is therefore important for its management within protected areas of West Africa. Global and cross-continental models of habitat suitability and potential distribution have been previously constructed (Kriticos et al. 2005). However, land management is generally carried out at local or regional scales. Informing such management with ENMs requires the use of finer-scale maps detailing the specific regions of interest (Theoharides and Dukes 2007, Taylor and Kumar 2013). We used fine-scale data to construct ENMs for *C. odorata* that could be potentially more useful for land management purposes.

**Materials and Methods**

**Study area**

West Africa, the region of focus for this study, is located in the westernmost region of continental Africa and measures approximately 12.95 × 10^6 km². Sociopoliti-
cally, it comprises 16 countries (Benin, Burkina Faso, Côte d’Ivoire, Cape Verde, Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, Senegal, Sierra Leone, and Togo). The region is characterized by seven sub-climatic zones: humid, subhumid/humid, subhumid, subhumid/dry, semiarid, arid, and hyperarid (FAO 2007). The hyperarid and arid zones are characterized by a long dry season (up to nine months per year). The semiarid and subhumid/dry zones are marked by a single rainy season and receive most of their rainfall between July and September. The humid and subhumid zones are marked by two rainy seasons and two dry seasons. Depending on variations in local climate, the regional native vegetation is dominated by savanna mosaics, woodlands, moist forests, and rain forests. Temperatures in West Africa are expected to increase by more than 2°C by mid-21st century and by 3–6°C at the end of the 21st century. While rainfall projections are more uncertain, it is expected that there will be a 20% increase or decrease in precipitation by the mid- and late 21st century, relative to the late 20th century baseline (IPCC 2013).

Protected areas in the entire West Africa region provide support to the livelihood of millions. For example, non-timber forest products (NTFP) obtained from protected areas provide up to 40–50% of local household revenues annually (IUCN/PACO 2011). However, these protected areas are threatened with many alien, invasive plant species (CAB International 2004) and the adverse effects of climate change (IPCC 2013), and hence threaten millions of livelihoods. Due to limited availability of data for majority of the countries, our study assessed habitat suitability in only four countries from the region: Benin, Côte d’Ivoire, Ghana, and Togo. These four countries are all characterized by humid to subhumid/humid (4° N–7°30’ N), subhumid/dry (7°30’ N–11°5’ N), and semiarid (11°5’ N–12°25’ N) climates. The countries cover an area of 730,244 km², with ~20% (145,014 km²) under official conservation protection (see Fig.1; data available online).¹ Over 700 protected areas fall within the administrative territories of these four countries, cover a range of ecosystems (e.g., rain forests, moist forests, dry forests, and savannahs), and house a high diversity of native plants and animals.

Modeling technique

A number of statistical methods are available for constructing species distribution models, which is typically done by estimating the probability of occurrence of a species at given geographic coordinates based on presence/absence (or presence only) and corresponding environmental data (Guisan and Zimmermann 2000). Maximum entropy (MaxEnt; version 3.3.3k; Princeton University, Princeton, New Jersey, USA) is one of the most powerful of such distribution-modeling tools among those employing climate envelope modeling (CEM) approaches. MaxEnt is a “machine learning” method, which provides highly informative biogeographical information and discrimination of suitable vs. unsuitable areas for a species (Philips et al. 2006). MaxEnt applies the principle of maximum entropy to a species’ presence-only data to estimate a set of functions that relate environmental variables to habitat suitability and estimate the species’ potential geographical distribution (Philips et al. 2006).

In brief, MaxEnt models a species’ distribution based on the principle described as follows. Assuming a set of presence records within an area of interest, Ω, where a species has been observed, let y = 1 be presence and $v$ be a vector of environmental predictors available in the area of interest (in the present study bioclimatic variables). Let background be defined as all possible locations within Ω. Define $f(v)$ as the probability density of predictors across Ω and $f_1(v)$ as the probability density of predictors across locations where the species is present within Ω. Using the presence and background data, MaxEnt estimates the probability of presence of the species conditioned to bioclimate and models $f_1(v)$ and $f(v)$ (Elith et al. 2011b) as

$$Pr(y = 1|v) = Pr(y = 1) \times \frac{f_1(v)}{f(v)}$$

where $Pr(y = 1|v)$ is the probability of presence of the species conditioned to bioclimate, and $Pr(y = 1)$, the proportion of occupied sites. While estimating $f_1(v)$, MaxEnt chooses the estimate that is the closest to $f(v)$. This maximizes the dispersedness entropy of $f_1(v)$. The model implicitly assumes a 50% chance of species being present in suitable areas. The raw outputs of the model are further transformed to logistic outputs to yield a better estimate of $Pr(y = 1|v)$. Elith et al. (2011b) provide further details and a comprehensive statistical explanation to ecologists on how MaxEnt functions.

Despite the well-recognized conceptual ambiguities and uncertainties about bioclimatic envelope modeling (see Schwartz 2012), MaxEnt remains a practical tool that allows assessment of the potential impact of climate change on the distribution of suitable habitats of plants and animals (i.e., their ecological niche, with the climatic dimension being considered; Elith et al. 2011b).

Data collection

Geographic coordinates (longitude and latitude) of location records of C. odorata were gathered from the Global Biodiversity Information Facility (data available online), peer-reviewed scientific papers, and extensive field survey in the study area.² Field data records came from the following climatic zones: humid, subhumid/

¹ http://protectedplanet.net
² http://www.gbif.org
humid, and subhumid. Overall, 163 records were obtained for *C. odorata* (see Table 1, Fig. 1).

Current (1950–2000) climate data and future climate projections (2050) were obtained from WorldClim, version 1.4 (available online). This data includes estimates for 19 bioclimatic variables and is derived from average monthly maximum and minimum temperature and precipitation data. All bioclimatic layers were interpolated from weather stations on a 2.5-minute grid (a spatial resolution of approximately 4.62 x 4.62 km in West Africa region) using the thin-plate smoothing splines approach. For projections of future climatic conditions, predictions from two models of the Coupled Model Intercomparison Project phase 5 (CMIP5) were used: the Met Office climate model (HadGEM2-ES) and the Model For Interdisciplinary Research On Climate Change (MIROC5). These models are among the most-used models currently available for simulating the global climate response to increasing greenhouse gas concentration. The projections were run under two of the four scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) in its Fifth Assessment Report (AR5): the mid-21st century representative concentration pathway (RCP) 4.5 and RCP 8.5. The other RCP scenarios were not used because RCPs trends for the study area do not diverge dramatically until the late century (IPCC 2013). By mid-21st century, RCP 4.5 projects temperatures to rise above industrial level by at least 1.4°C in West Africa, with atmospheric CO₂ reaching 500 ppm (IPCC 2013). Under the more extreme RCP 8.5 projections, temperatures are predicted to rise by 2°C and atmospheric CO₂ to reach over 550 ppm.

**Model validation**

For *C. odorata* presence data, duplicate records in each grid were removed to reduce sampling bias in favor of sites where sampling may be concentrated (Elith et al. 2006). Distribution of plants in the study area is known to be driven primarily by availability of soil moisture, total rainfall, air humidity, and the length of the dry season (Adomou et al. 2006). Thus, the initial subset of bioclimatic variables used incorporated only those that reflect water availability. Further variable selections were performed using the environmental niche modeling tools (ENMTs) to select least-correlated suitability predictor variables ($r < 0.70$; Elith et al. 2011a). A jackknife test was performed on the selected bioclimatic variables to determine variables that best contribute to the model prediction.

Model outputs were validated as follows. First, location record data were split into five folds and the model was fitted five times. For each model fitting, records corresponding to one of the five folds were used to evaluate the model, while those of the other folds were used for fitting the model. The five models were then cross-validated by averaging the results across all models. Model goodness-of-fit and predictive power

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**Table 1.** Source, number, type of record, and geographical location of *Chromolaena odorata* presence records used in the study.

| Source | Number and type of records | Geographical location |
|--------|----------------------------|-----------------------|
| Adebayo and Uyi (2010) | 20 and F | Nigeria |
| Djietror (2012) | 20 and F | Ghana |
| Prasad et al. (1996), B. Fandohan (personal observations) | 11 and F | Côte d’Ivoire |
| Prasad et al. (1996), B. Fandohan (personal observations) | 11 and F | Togo |
| B. Fandohan (personal observations) | 9 and F | Benin |
| Laboratoire des Sciences Forestière (LFS/FSA)† | 58 and F | Benin |
| Conservation International† | 2 and H, F | Côte d’Ivoire |
| Herbarium Senckenbergianum† | 1 and H | Côte d’Ivoire |
| Herbier CNRST/INERA† | 1 and H | Côte d’Ivoire |
| Tela Botanica† | 1 and H | Côte d’Ivoire |
| Prasad et al. (1996) | 6 and F | Liberia |
| Naturalis Biodiversity Center, Botany Leiden† | 6 and H | Côte d’Ivoire |
| Naturalis Biodiversity Center, Botany Wageningen† | 4 and H | Côte d’Ivoire |
| Conservation International† | 1 and F | Ghana |
| Naturalis Biodiversity Center, Botany Leiden† | 1 and H | Ghana |
| University of Legon, Ghana Herbarium† | 2 and H | Ghana |
| Conservation International† | 4 and F | Guinea |
| Naturalis Biodiversity Center, Botany Wageningen† | 1 and H | Guinea |
| Programme de Conservation de la Biodiversité du Mont Nimba† | 1 and H | Guinea |
| Conservation International† | 1 and F | Liberia |
| Naturalis Biodiversity Center, Botany Wageningen† | 1 and H | Liberia |
| Naturalis Biodiversity Center, Botany Wageningen† | 1 and H | Nigeria |
| Naturalis Biodiversity Center, Botany Wageningen† | 1 and H | Nigeria |

Note: Record types are H, herbarium record; F, field work record. † Occurrence data accessed through Global Biodiversity Information Facility (GBIF) data portal: www.gbif.org

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3 http://www.worldclim.org/
were assessed using the area under the receiver operating characteristic curve (ROC AUC) and the true skill statistic (TSS). The AUC is the probability that a randomly chosen presence location of the species will be ranked above a randomly chosen background point in terms of suitability. In practice, the AUC gives the probability that the predictive power of a model is better than random prediction (AUC = 0.5). A model with an AUC value close to one (AUC ≥ 0.75) is deemed to have a good fit. The TSS is a measure of the capacity of the model to accurately detect true presences (sensitivity) and true absences (specificity). A TSS ≤ 0 indicates a random prediction, while a value close to 1 (TSS > 0.5) suggests good predictive power (Allouche et al. 2006). The contribution of a given variable to the model was estimated using a jackknife test, by random permutation of the values of that variable among the model calibration points (both presence and background), and evaluation of the resulting decrease in AUC. A large decrease suggests heavy dependence of the model on that variable (Philips et al. 2006).

Mapping current and future suitable habitats within the protected areas

Suitable habitats for C. odorata under current and future climatic conditions generated with MaxEnt were mapped using ArcGIS 9.3 (Environmental System Research Institute, Redlands, California, USA). The logistic probability distributions generated by the model were used to measure the level of habitat suitability across the study area. The 10th percentile training
logistic threshold was used as the threshold value, and all areas with an occurrence probability below that value were deemed unsuitable for the species (Scheldeman and van Zonneveld 2010). Occurrence probabilities higher than the 10th percentile were deemed suitable. To assess vulnerability of the protected areas to invasion by *C. odorata*, current and future habitat suitability maps were overlain with the protected areas network (PAN) map of the study area, which was extracted from the global protected areas network within the world database of protected areas (see footnote 1). Percentages of potential habitat suitability within the PAN were estimated using the spatial analysis toolset in ArcGIS. On the basis of the potential habitat suitability maps obtained, amounts of presently nonvulnerable areas projected to become vulnerable and vice versa by the year 2050 were estimated.

Table 2. Contribution of predictor variables to the model (permutation importance).

| Variables | Definition                        | Contribution (%) |
|-----------|-----------------------------------|------------------|
| bio 17    | Precipitation in driest quarter   | 77.6             |
| bio 12    | Annual precipitation              | 17.6             |
| bio 4     | Seasonal temperature variation    | 4.7              |

Results

Representative bioclimatic variables and model validation

Three least-correlated bioclimatic variables were selected as predictors in the models: precipitation of the driest quarter, annual precipitation, and temperature seasonality (Table 2). Precipitation of the driest quarter and annual precipitation were the best predictors. Precipitation of the driest quarter had the highest gain of all bioclimatic variables when fitted in the model in isolation. Omitting this variable decreases the gain considerably, indicating that it is also the most uniquely informative variable (jackknife test; Fig. 2a). The models showed good predictive ability with a mean cross-validated AUC of 0.863 ± 0.012 (mean ± SD; Fig. 2b) and a mean TSS value of 0.60 ± 0.095. The 10th percentile training logistic threshold value for discriminating suitability level was 0.36. *Chromolaena odorata* showed preference for humid climates with habitat suitability declining in areas with low precipitation of driest quarter (bio 17). Habitat suitability decreased in areas with bio 17 lower than 200 mm and declined steeply below 100 mm (Fig. 3a). Relatively high seasonal temperature variations (bio 4) seemed to restrict the range of the species, with habitat suitability increasing in areas with bio 4 lower than 2°C (Fig. 3b). Similarly, habitat suitability was higher in areas with annual precipitation (bio 12) of above 1000 mm (Fig. 3c).

![Fig. 2.](image)

Fig. 2. (a) Results of a jackknife test for regularized training gain for *Chromolaena* and (b) cross-validated areas under the receiver operating characteristic curve (AUC). Sensitivity is defined as 1 – (omission rate).
Overall model outputs

Approximately 73% of land within the protected areas networks in the four countries was suitable for *C. odorata* under current climatic conditions (Figs. 4 and 5a; between 4° N–10°23’ N latitudes). These areas were confined to the humid and subhumid/humid zones, as well as the lower part of the subhumid/dry zone. Suitable areas were projected to decline by 7–14% under future climatic conditions projected for the year 2050 (Figs. 4 and 5b–e). Decreases in suitable areas were overall greater under MIROC5 projections than under HadGEM2-ES projections. The loss in suitable areas under RCP 4.5 was projected to be slightly lower than under RCP 8.5 projections for model HadGEM2-ES, while the opposite trend was observed for model MIROC5 (Fig. 4). The future distribution of suitable habitats for *C. odorata* was projected to be confined to latitudes lower than 10° N under HadGEM2-ES and 9°30’ N for MIROC5.

Country-specific trends

The extent of suitable *C. odorata* habitat within the focal protected areas under current and future climatic conditions is depicted in Table 3. The models estimated the percentage of land within protected areas suitable for *C. odorata* under current vs. future climate conditions to be 15% (vs. 8%, 8%, 1%, and 4%, respectively, for HadGEM2-ES and MIROC5 under RCP 4.5 and 8.5) in Benin, 94% (vs. 88%, 87%, 83%, and 86%, respectively) in Côte d’Ivoire, 75% (vs. 71%, 67%, 59%, and 56%, respectively) in Ghana, and 62% (vs. 25%, 25%, 25%, and 23%, respectively) in Togo (Table 3). This suggests that a significant proportion of the total protected land areas in Côte d’Ivoire, Ghana, and Togo (62–94%) may be currently vulnerable to colonization by *C. odorata*. Conversely, a much smaller proportion (15%) of land within the protected areas of Benin is currently vulnerable to *C. odorata* establishment. In Côte d’Ivoire and Ghana, a high proportion (88–94% and 75–95%) of these areas were projected to remain vulnerable by 2050 under RCP 4.5 and RCP 8.5 for the two climate models. In Togo, however, vulnerable areas were projected to undergo a 60–62% decrease. The greatest decrease in suitable habitat was projected for Benin, with *C. odorata* losing 50% of its suitable habitat under the HadGEM2-ES model and 75–91% under MIROC5. In Benin, losses
of suitable area were similar for RCPs 4.5 and 8.5 under HadGEM2-ES, while they were quite different under MIROC5, with a greater loss projected under RCP 4.5. The same trends were observed in Côte d’Ivoire, with lower differences between RCPs. In Ghana, losses of suitable habitat were projected to be greater under RCP 4.5 than under RCP 8.5 for both HadGEM2-ES and MIROC5. Projected changes for Togo revealed little differences between RCPs and climate models.

Discussion

Climate change may accelerate range expansions by invasive plant species into, and within, protected areas (Foxcroft et al. 2011). Here, we used MaxEnt to model potential habitat suitability for Chromolaena odorata within the protected areas of four West African countries under current and future (2050) climatic conditions as projected by HadGEM2-ES and MIROC5 models for RCP 4.5 and RCP 8.5 projections. Most of the protected area networks of the four countries were projected to be greater under RCP 4.5 than under RCP 8.5 for both HadGEM2-ES and MIROC5. Projected changes for Togo revealed little differences between RCPs and climate models.

MIROC5 model (e.g., a decrease in habitat suitability was projected to be greater under RCP 4.5 than under RCP 8.5 in some areas, while the reverse was true in others). These spatial differences in climate projections could be attributed to local differences in the magnitude of climate change as projected by each climate model and representative concentration pathway. Historical climate change events are congruent with such local differences. For example, a local drying of the West African climate (referred to as the Dahomey Gap, after the former name of Benin, “Dahomey”) is known to have occurred during the late Holocene (5000 yr BP) and affected only Benin, Togo, and a small part of Ghana (Salzmann and Hoelzmann 2005).

Protected areas found to be vulnerable to invasion by C. odorata in this study are some of the most important ecosystems among the last refuges for wild mammals in West Africa. Many of these mammals are already listed on the International Union for Conservation of Nature (IUCN) Red List (e.g., Loxodonta africana, Panthera pardus, Panthera leo, Cercopithecus erythrogaster subsp. erythrogaster). Furthermore, these ecosystems host many highly endemic and/or extremely rare plant species, some with a distribution range smaller than 100 km² (e.g., Byttneria dahomensis, Diaphananthe suborbicularis, Byttneria ivorensis, Suregada ivorensis, Zanthoxylum psammophilum, Clerodendrum sassafras, Dichapetalum dictyospernum, and Cola umbratilis; Poorter et al. 2004). Besides being important for biodiversity conservation, these ecosystems generate large amounts of revenue through tourism and non-timber forest products for the countries in this region. Hence, widespread invasion by C. odorata could negatively impact provisioning of ecosystem services in this region.

Although there is intermodel variation in projected climate change for West Africa, the region has been facing increases in frequency and intensity of drought since 1950 (IPCC 2013). A recent evaluation of the
downscaling performance of many climate models (i.e., representation of basic aspects of the observed climate at a regional scale), including HadGEM and MIROC models, suggested that the former model outperforms the latter model and several others (Brands et al. 2013). Thus, it is plausible that projections by MIROC5 are less accurate than projections by HadGEM2-ES. However, the declines in suitable land area projected in this study do not account for any potential plastic responses by C. odorata to changes in the climatic conditions. Under these circumstances, the protected areas networks could be at a higher risk of invasion.

Soil was not included as a predictor variable in this study, despite its well-documented importance in influencing distribution of many plant species. Inclusion of soil data in models that estimate habitat suitability of a plant species has been recommended when the scale of the study is below 2000 km (Pearson and Dawson 2003).

**Fig. 5.** Projected vulnerability to *Chromolaena odorata* mapped under current and future (HadGEM2-ES and MIROC5 for RCPs 4.5 and 8.5) climatic conditions. Areas labeled suitable are vulnerable, while areas labeled unsuitable are non-vulnerable. Panel (a) is current climatic conditions, (b and c) are RCPs 4.5 and 8.5 for HadGEM2-ES, respectively, and (d and e) are RCPs 4.5 and 8.5 for MIROC5, respectively.
Table 3. Potential habitat suitability for *Chromolaena odorata* within the protected areas of four countries in West Africa under current and future climatic conditions (HadGEM2-ES, MIROC5, RCP 4.5, and RCP 8.5).

| Country and habitat suitability | Area (km²) | (%) | Current | HadGEM2-ES | MIROC5 | RCP 4.5 | RCP 8.5 | RCP 4.5 | RCP 8.5 | RCP 4.5 | RCP 8.5 |
|--------------------------------|------------|-----|---------|------------|--------|---------|---------|---------|---------|---------|---------|
|                                 |            |     | RCP 4.5 | RCP 8.5    |        |         |         |         |         |         |         |
| Benin                           |            |     |         |            |        |         |         |         |         |         |         |
| Suitable                        | 4119.47    | 15.15 | 2070.41 | 384.20     |        |         |         |         |         |         |         |
| Unsuitable                      | 23073.30   | 84.85 | 2122.36 | 26808.57   |        |         |         |         |         |         |         |
| Subtotal                        | 27192.77   |       | 27192.77| 27192.77   |        |         |         |         |         |         |         |
| Côte-d’Ivoire                   |            |     |         |            |        |         |         |         |         |         |         |
| Suitable                        | 70671.31   | 93.58 | 66423.77| 62752.54   |        |         |         |         |         |         |         |
| Unsuitable                      | 4845.18    | 6.42 | 9092.71 | 12763.95   |        |         |         |         |         |         |         |
| Subtotal                        | 75516.49   |       | 75516.49| 75516.49   |        |         |         |         |         |         |         |
| Ghana                           |            |     |         |            |        |         |         |         |         |         |         |
| Suitable                        | 26829.91   | 74.82 | 25591.94| 21152.30   |        |         |         |         |         |         |         |
| Unsuitable                      | 9028.68    | 25.18 | 10266.66| 14706.29   |        |         |         |         |         |         |         |
| Subtotal                        | 35858.59   |       | 35858.59| 35858.59   |        |         |         |         |         |         |         |
| Togo                            |            |     |         |            |        |         |         |         |         |         |         |
| Suitable                        | 4012.75    | 62.25 | 1622.17 | 1579.49    |        |         |         |         |         |         |         |
| Unsuitable                      | 2433.26    | 37.75 | 4823.83 | 4866.52    |        |         |         |         |         |         |         |
| Subtotal                        | 6466.01    |       | 6466.01 | 6466.01    |        |         |         |         |         |         |         |
| Total                           | 145013.85  |       | 145013.85| 145013.85  |        |         |         |         |         |         |         |

† Trends depict change (%) in suitable land area under future climatic conditions. Trends indicating a percentage decrease in suitable habitat imply a corresponding increase in unsuitable habitat and vice versa.

Even though soil properties may help to better project range distribution of a species under current climate (Taylor and Kumar 2013), the accuracy of such projections made under future climate scenarios may be limited. Such models would assume that soil properties do not vary with a change in climate, which in reality is unlikely to be the case (Allen et al. 2011). It remains a challenge to predict future properties of soils in response to changes in climatic variables (Wixon and Balser 2009). Nevertheless, in the current study area, *C. odorata* is observed on a wide range of soils (from sandy to clay) as reflected by previous reports regarding its distribution (see Prasad et al. 1996), except for hydroorphic soils with a permanent water table. Thus, soil is unlikely to be a strong determinant of *C. odorata* distribution.

Our projected future distribution of suitable habitats for *C. odorata* in Benin, Ghana, and Togo did not extend far beyond climatic ranges of that of current presence observations (Prasad et al. 1996, Djettror 2012; unpublished data). However, in Côte d’Ivoire, where presence of *C. odorata* was reported to be below latitude 8° N (Prasad et al. 1996; unpublished data), the models showed that suitable habitats extend beyond latitude 10° N in the subhumid/dry zone. In the humid zone (4° N–6° 25’ N; Fig. 1), most of the protected areas (e.g., Tai National Park, Côte d’Ivoire; Kakum Park, Ghana) were found to be vulnerable to invasion by *C. odorata* under both current and future climatic conditions. Also under current and future climate conditions, the following major national reserve and parks within the subhumid/humid and subhumid/dry climates (6°25’ N–7° 30’ N; Fig. 1) were projected to be vulnerable to invasion by *C. odorata*: Comoé National Park (Côte d’Ivoire), Digya and Bui National Parks, Yerada and Yakombo Forest Reserves (Ghana), Fazao Malfakassa Park (Togo), and Mont Kouffé, and Lama Forest Reserves (Benin). Some of these reserves are already well known to be invaded by the species (e.g., Lama Forest Reserve in Benin, Tai National Park in Côte d’Ivoire; see Prasad et al. 1996). At the border between the subhumid/dry and the semiarid climatic zones (10°30’ N–11°3’ N; Fig. 1), the Pendjari and W Benin National Parks (Benin), the Red Volta Park (Ghana), and de Keran Park (Togo) were found not to be vulnerable to invasion by *C. odorata*.

There have been concerns about uncertainties regarding MaxEnt parameters and driving forces (Merow et al. 2014). In the present study, *k*-fold cross-validation was used to account for uncertainties associated with the model. While this method may yield good evaluation-of-fit model metrics, it has the disadvantages that only part of the data are used to fit the model and that obtaining test data that are spatially independent from training data is challenging (Merow et al. 2014). This may result in overestimation of model performance and underestimation of standard error of prediction over the *k*-fold runs. In addition, a fundamental limitation of presence-only-based models is that the proportion of occupied sites, Pr(*y* = 1), cannot be determined exactly from occurrence-only data. To handle this issue, MaxEnt implicitly assumes a 50% chance of species being present in suitable areas. This assumption is arbitrary and
influences model outputs (Merow et al. 2014). Thus, it has been suggested that whenever possible, the latter probability should be approximated using information on sampling effort. Such information was not available for C. odorata. Other computationally more demanding and reportedly more efficient methods for assessing uncertainties and model driving forces (e.g., point process regression models, global sensitivity and uncertainty analysis) are currently being explored for use in MaxEnt and may be considered in future studies. Despite these limitations of MaxEnt, visual inspection of model outputs indicated that the model was able to predict suitability beyond the occurrence records’ range. Similarly, the predicted suitable areas were not biologically unrealistic.

Eradication of invasive plant species that have established over a large area is rarely feasible as management option (Myers et al. 2000). Hence, management strategies that aim at preventing new introductions and further spread of invasive species are considered a more cost-effective method for dealing with alien invaders (Leung et al. 2002). An important approach to preventing new introductions is predicting habitat suitability for the invasive species and its potential future geographic distribution. The habitat suitability models we report here have identified areas that are suitable or unsuitable for C. odorata under current and future climatic conditions within the protected areas of four West African countries. This identification can inform prioritization of management activities aimed at preventing new introductions and establishments of this alien invader, and thus, sustain healthy ecosystems in the protected areas. In West Africa, efforts to manage C. odorata have not been successful, perhaps due to improper planning and implementation of management strategies (Djetior 2012). Some potentially effective management measures that could be implemented to contain this invader within the protected areas, include raising awareness among local communities on the negative impacts of this plant and the risks associated with introducing it to new locations. Legislation restricting movement of this plant between different locations also needs to be enacted.

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