BIODIVERSITY RESEARCH

Modelling ecological niches from low numbers of occurrences: assessment of the conservation status of poorly known viverrids (Mammalia, Carnivora) across two continents

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ABSTRACT

The conservation of poorly known species is difficult because of incomplete knowledge on their biology and distribution. We studied the contribution of two ecological niche modelling tools, the Genetic Algorithm for Rule-set Prediction (GARP) and maximum entropy (Maxent), in assessing potential ranges and distributional connectivity among 12 of the least known African and Asian viverrids. The level of agreement between GARP and Maxent predictions was low when < 15 occurrences were available, probably indicating a minimum number below that necessary to obtain models with good predictive power. Unexpectedly, our results suggested that Maxent extrapolated more than GARP in the context of small sample sizes. Predictions were overlapped with current land use and location of protected areas to estimate the conservation status of each species. Our analyses yielded range predictions generally contradicting with extents of occurrence established by the IUCN. We evidenced a high level of disturbance within predicted distributions in West and East Africa, Sumatra, and South-East Asia, and identified within West African degraded lowlands four relatively preserved areas that might be of prime importance for the conservation of rainforest taxa. Knowing whether these species of viverrids may survive in degraded or alternative habitats is of crucial importance for further conservation planning. The level of coverage of species suitable ranges by existing and proposed IUCN reserves was low, and we recommend that the total surface of protected areas be substantially increased on both continents.

Keywords

Ecological niche modelling, GARP, Maxent, protected areas, tropical forests, Viverridae

INTRODUCTION

Preservation of species requires not only detailed knowledge of their natural history and biology, but also information on the availability of suitable areas where species can survive; such knowledge can greatly aid in conservation planning. Recent developments in ecological niche modelling (ENM) have explored applications to diverse conservation issues, including suitable habitat and species range estimates (Chefaoui *et al.*, 2005; Gaubert *et al.*, 2006; Guisan *et al.*, 2006), protected area prioritization and network design (Margules & Austin, 1994; Rondinini *et al.*, 2005; Sánchez-Cordero *et al.*, 2005a), and effects of habitat disturbance on species distributions (Banks *et al.*, 2005; Sánchez-Cordero *et al.*, 2005b; Rhodes *et al.*, 2006).

The ecological niche can be defined as the set of environmental conditions (abiotic factors) under which a species is able to maintain viable populations without immigration (Grinnell, 1917, 1924). The challenge of identifying distributional areas for species requires two conditions to be met: favourable abiotic conditions and favourable biotic factors (e.g. presence of symbionts and mutualists, absence of serious parasites and predators); a third condition, geographical accessibility (landscape configuration, dispersal abilities of species), both at present and through history, is necessary for the actual presence of species (Soberón & Peterson, 2005).

A growing literature deals with methodological challenges specific to best ENM-based predictions of suitable areas (Peterson & Kluza, 2003; Guisan & Thuiller, 2005; Elith *et al.*,

2006) and identification of conservation priorities (Loiselle *et al.*, 2003). Included in this debate are ENM methods that apply specifically to presence-only records (Anderson *et al.*, 2003; Elith *et al.*, 2006; Phillips *et al.*, 2006), which remain the major source of occurrence data, and that are now widely available through networking of museum collections (Graham *et al.*, 2004). Presence-only records extracted from museum collections have several potential pitfalls that may affect the accuracy of ENM. First, it often remains impossible to consider zones lacking records as truly representing absence data, thus hampering application of binomial response models to reconstruct ecological niches (Anderson *et al.*, 2003; Elith *et al.*, 2006). Second, temporal correspondence between series of occurrence data and environmental variables like current land-cover classifications is often poor (Anderson & Martinez-Meyer, 2004; Gaubert *et al.*, 2006). Third, records may be geographically biased because of uneven sampling effort (absence of sampling strategy, sampling of easily accessible areas, spatial autocorrelation) (Reddy & Dávalos, 2003; Vaughan & Ormerod, 2003; Phillips *et al.*, 2006). Finally, accuracy of georeferencing of occurrence data may be challenged by erroneous or approximate locality attributions (e.g. Peterson *et al.*, 2004).

Poorly known species are usually represented by low numbers of museum records, a situation that is likely to challenge the accuracy of ENMs still further since (1) it exacerbates the drawbacks of presence-only data mentioned above, and (2) it may provide a biased or erroneous picture of suitable environments for the species (Phillips *et al.*, 2006). Methodological issues related to ENM based on low numbers of occurrences are of prime importance because poorly known species are likely to be the most frequent case, particularly among species of conservation concern. Stockwell & Peterson (2002) showed that the predictive success of ENM under reduced number of occurrences was dependent on choice of modelling methods and environmental variables, with machine-learning methods performing better. However, an empirical study on mammals of Guyana demonstrated that the combination of biased and/or small numbers of records with coarse geographical information – a condition met in most tropical regions – can yield large amounts of under-predicted areas and poorly fit models (Lim *et al.*, 2002). Recently, new statistical methods for obtaining predictions, such as maximum entropy (Phillips *et al.*, 2004, 2006) have been described as a promising tool for dealing with low numbers of occurrences (Pearson *et al.*, 2007).

Our study focused on one of the least known groups of carnivoran mammals, the Viverridae, and included two modelling approaches, genetic algorithms and maximum entropy, in the context of paucity of species records. The Viverridae consists of 13 genera and 35 species (Gaubert *et al.*, 2005a; Gaubert *et al.*, 2005b; Wozencraft, 2005), *c.* 50% of which are IUCN red-listed and/or poorly known (http://www. iucnredlist.org; Schreiber *et al.*, 1989). They represent small-to-medium-sized, nocturnal, solitary predators, often inhabiting inaccessible areas (Nowak, 1999). We focused on 12 species from tropical Africa and Asia, which have recently been assessed as of particular conservation concern – from Data Deficient to

Endangered – by the IUCN Global Mammal Assessment and the South-East Asian Mammal Databank joint projects (see Boitani *et al.*, 2006; www.iucn.org/en/projects/global_mamals.htm). The selected species have restricted known ranges, are represented by low numbers of occurrences, and are poorly known or unknown as to their natural history and basic biology: *Genetta abyssinica*, *Genetta bourloni*, *Genetta johnstoni*, *Genetta piscivora*, *Genetta poensis*, and *Poiana leightoni* in Africa, and *Cynogale bennetti*, *Diplogale hosei*, *Macrogalidia musschenbroekii*, *Paradoxurus jerdoni*, *Viverra civettina*, and *Viverra megaspila* in Asia. The aim of our study was to assess potential distributions of species and distributional connectivity between known points of occurrence to estimate current levels of protection for these viverrids.

METHODS

Input data

We compiled occurrence records for the 12 species of Viverridae from diverse sources, including detailed review of museum collections by P.G. and databases of information associated with collections (see Appendix S1 in Supplementary Material). Identifications within genus *Genetta* were based on morphological diagnoses and descriptions in Gaubert *et al.* (2005a, b). Published works were also used, but only when species-level identifications were deemed reliable (Table 1).

We obtained a total of 207 localities, with nine to 36 records per species (Table 1). We georeferenced localities using the following electronic resources: Atlas Mondial Encarta (Microsoft Corporation, 1998); Alexandria Digital Library Gazetteer (middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp); Global Gazetteer (www.fallingrain.com/world); and Google (Google, Mountain View, CA, USA). We also benefited from curators' knowledge concerning collection sites whenever possible.

To summarize environmental variation, we used the 19 'bioclimatic' variables based on the global climate data sets developed by Hijmans *et al.* (2005). These GIS data sets characterize global climates from 1950–2000 using average monthly weather station data and are available at different spatial resolutions. We chose the 2.5 arc-minutes (~ 4.5 km) resolution data set to match approximately the resolution in the occurrence data.

Ecological niche modelling

The environmental data and species occurrence data are used together in ENM with the aim of creating models of potential distributions of species. A recent survey of existing methods for ENM (also referred to as distribution modelling) by Elith *et al.* (2006) identified new tools (e.g. MARS, Maxent) that, under the assumptions made in that study, showed better performance than more widely used methods [e.g. DOMAIN, Genetic Algorithm for Rule-set Prediction (GARP)]. As such, we chose to apply a newer method, Maxent, and a more established method, GARP, to obtain predicted distributions for the 12 viverrid species.

Table 1 Summary of the 12 species of Viverridae used in this study

Species	IUCN status	Distribution	Number of occurrences	Sources
Africa				
Genetta abyssinica	DD	Ethiopian plateau and neighbouring plains	12	(Diaz Behrens & Van Rompaey, 2002; this study)
Genetta bourloni	DD*	Upper Guinean Block	18	(Gaubert, 2003a; this study)
Genetta johnstoni	VU*	Upper Guinean Block	17	(Kuhn, 1965; Gaubert *et al.*, 2002; this study)
Genetta piscivora	DD	North-eastern Democratic Republic of Congo	18	(Verheyen, 1962; Rahm, 1965; Hart & Timm, 1978; Kanyamibwa, 1999; this study)
Genetta poensis	DD*	Upper and Lower Guinean Blocks	9	(Gaubert, 2003a)
Poiana leightoni	DD	Upper Guinean Block	13	(Kuhn, 1965; Bourlière *et al.*, 1974; Taylor, 1989; this study)
Asia				
Cynogale bennettii	EN	South-East Asia, including Borneo and Sumatra	36	(Veron *et al.*, 2006)
Diplogale hosei	VU	Borneo	15	(Van Rompaey & Azlan, 2004; Yasuma, 2004; Wells *et al.*, 2005; this study)
Macrogalidia musschenbroekii	VU	Sulawesi	13	(Veron, 2001; Lee *et al.*, 2003; this study)
Paradoxurus jerdoni	LC*	Western Ghats (India)	24	(Rajamani *et al.*, 2002)
Viverra civettina	CR	Western Ghats (India)	9	(Rai & Kumar, 1993)
Viverra megaspila	VU*	South-East continental Asia	23	(Duckworth, 1994; Lynam *et al.*, 2005; this study)

*Status re-assessed in 2006 after the Small Carnivore Red List Workshop (IUCN Global Mammal Assessment project). *Paradoxurus jerdoni* was previously red-listed as Vulnerable (2006 IUCN Red List of Threatened Species: www.iucnredlist.org). IUCN status categories: CR, Critically Endangered; DD, Data Deficient; EN, Endangered; LC, Least Concern; VU, Vulnerable.

Maxent (Phillips *et al.*, 2006) is a maximum entropy-based machine-learning method used for making predictions when incomplete data are available. Maxent estimates the probability distribution for a species' occurrence that is most spread out given the constraints derived from the available data (Phillips *et al.*, 2004; Phillips *et al.*, 2006). The advantages of this technique include the possibility of using both categorical and continuous environmental data, detail of prediction due to the continuous nature of the resulting models (but see also Discussion), and speed and simplicity of the software implementation. We used the latest desktop version (Maxent 2.1; www.cs.princeton.edu/~schapire/maxent).

Since our sample sizes for all species were low, we used only the linear and, when $N > 10$, quadratic features (see Phillips *et al.*, 2004 for recommendations regarding sample sizes and features usage). We maintained all other parameters at default settings. The resulted cumulative probability distribution raster maps with pixel values of 0–100 were imported into ArcGIS as integers because most analyses in the desktop GIS environment work only with integer values. The main effect of importing the models as integer rasters (as opposed to floating point rasters) is that pixels with probability values between 0 and 1 are reassigned to a value of 0. However, because the species analysed here have restricted ranges, the most environmentally suitable areas are of interest, which generally correspond to high probability values (Phillips *et al.*, 2006), making values < 1 of little interest. We did not apply a particular threshold for each species, but rather retained all probability values > 0 for subsequent analyses.

The second ENM tool used in this study was GARP (Stockwell & Peters, 1999). GARP is a machine-learning method that builds ENMs based on non-random associations between known occurrence points for species and sets of raster GIS coverages describing the ecological landscape. Occurrence data are used in GARP as follows: 50% of the data points are set aside for an independent test of model quality ('extrinsic test data'), and 50% is used to develop the models ('training data'). The algorithm uses a fitness function to find rules that best describe the ecological requirements of species; these rules are created in an iterative process by applying methods chosen randomly from a set of four inferential tools (logistic regression, atomic rules, range rules, and bioclimatic rules). Rule quality is tested against the training data to maximize both significance and predictive accuracy, and a size-limited set of best rules is retained (Stockwell & Noble, 1992).

These models are subject to two types of errors: omission (known areas of presence predicted absent) and commission (areas of absence predicted present). These errors are inherent in any spatial predictions, but are used in GARP to separate between good and poor models (Anderson *et al.*, 2003). We used Desktop GARP version 1.1.6 available for download (www.lifemapper.org/desktopgarp), and followed Anderson *et al.* (2003) for choosing a subset of best models. We ran 200–500 models per species and retained only the 10 models in the lowest

10% of omission error values that showed least departure from median values of commission error. The 10 binary (presence–absence) predictions per species were summed in ArcGIS 9.1.

Owing to small sample sizes, no external testing was performed on the predictions obtained via ENM. We chose to use all available information to improve model building, and compared results obtained using the two different modelling methods.

Post-processing of predicted distributions

The two modelling techniques applied in this study have different architectures (Maxent – maximum entropy principle; GARP – genetic algorithm), so the outputs can be informative in unique ways. We investigated separately the maps produced with the two methods and compared them spatially (on a per-pixel basis) instead of applying numeric thresholds for this purpose. We took into consideration all pixels with values > 0 and ran a zonal statistics analysis under the Spatial Analyst extension of ArcGIS for pairs of predictions produced for each species, which calculates descriptive statistics (mean, median, standard deviation, minimum, maximum, range) of each pixel of one raster based on values of the other raster. We used the Maxent prediction as the zone raster and the GARP prediction as the zone field, meaning that for each Maxent value (integers from 0 to 100) we obtained the corresponding GARP model values.

Inclusion of land-cover information in the environmental data set and the modelling process is not feasible given temporal discords between the occurrence data and the landscape features. However, if information on habitat requirements is available, this information can be used to refine the 'raw', initial predictions by retaining only areas where the species were predicted present and the adequate land-cover type(s) is found. We used the year 2000 land-cover maps of Africa and south central Asia produced as part of the Global Land Cover mapping effort led by Global Vegetation Monitoring Unit (Bartholomé *et al.*, 2002; Stibig & Malingreau, 2003). These maps are derived from satellite data collected with the VEGETATION instrument on the SPOT-4 satellite (1-km spatial resolution), classifying land-cover types into 27 and 26 categories, respectively.

We selected and aggregated the appropriate categories for each species under two scenarios: a restrictive one under which we considered only 'natural' categories, and a moderate one under which we also admitted some degraded land-cover types where species were known to occur, hereafter LC1 and LC2. For African species, LC1 generally included closed evergreen lowland forest, submontane forest, swamp forest, mangroves, montane forest, savannah, closed deciduous forest, and deciduous woodland. The exception was *G. abyssinica*, with preference for deciduous shrubland with sparse trees, open deciduous shrubland, closed grassland, open grassland with sparse shrubs, open grassland, and sparse grassland. In LC2, we generally considered two additional categories: degraded evergreen lowland forest and mosaic forest/croplands; in *G. abyssinica*, we used croplands, croplands with open woody vegetation, and irrigated croplands.

For Asian species, we included in LC1: tropical and subtropical broadleaved, evergreen mountain forest; tropical lowland broadleaved evergreen forest; and tropical mixed deciduous and dry deciduous forests. In this group of species, the exception was *C. bennettii*, for which we excluded the last category but included swamp forests and woodlands. For LC2, we considered two additional categories: forest mosaics and degraded/fragmented forests, and mixed cropland and plantations; for *C. bennettii*, we excluded mixed cropland and plantations. The African and Asian LC1 and LC2 were used in ArcGIS to clip initial predicted distributions to correspond to distributions of currently suitable habitats.

Given widespread effects of historical limitations on dispersal abilities and distributions of species (Peterson *et al.*, 1999; Soberón & Peterson, 2005), we further reduced potential geographical ranges based on known species distributions, biogeographical boundaries (defined by unsuitable habitats considered impassable barriers), and historical evidence (i.e. locations of glacial refuges, estimates of divergence time of species compared to the timing of main biogeographical events). As such, we restricted *G. bourloni*, *G. johnstoni*, and *P. leightoni* to the Upper Guinean Block (Gaubert, 2003a,b; Gaubert *et al.*, 2005a), with the Dahomey Gap as the eastern boundary. *G. poensis* was restricted to the Upper and West Lower Guinean Blocks (Gaubert, 2003a); *G. piscivora* to the East Lower Guinean Block (Colyn & Gevaerts, 1986; Gaubert, 2003b); *G. abyssinica* to the high Ethiopian plateau and adjacent plains (Yalden *et al.*, 1996; Gaubert, 2003b); *C. bennettii* to Borneo, Sumatra and tropical south-eastern Asia (Veron *et al.*, 2006); *D. hosei* to Borneo (Van Rompaey & Azlan, 2004); *M. musschenbroekii* to Sulawesi (Lee *et al.*, 2003); *P. jerdoni* and *V. civettina* to the Western Ghats and adjacent areas (Rai & Kumar, 1993; Rajamani *et al.*, 2002); and *V. megaspila* to continental, tropical south-eastern Asia (Duckworth, 1994; Lynam *et al.*, 2005), with the high mountainous zone north-east of India as its western boundary.

Current reserves and conservation status

Our final goal was to assess the conservation status of potential distributions for the 12 species studied. For this purpose, we used a GIS layer of IUCN global protected areas (UNEP-WCMC, 2006). Based on information available, for each continent (African and Asian), we created one layer that included designated reserves only, and one that also included proposed reserves and reserves with no IUCN category assigned. We performed calculations in ArcGIS 9.1 in which we masked out the areas outside of designated or proposed reserves, which allowed for evaluation of extent of areas under protection and of areas for which no protection exists.

RESULTS

Maxent and GARP produced distributional predictions that were generally similar for each species. The zonal statistics between Maxent and GARP raster maps showed generally positive associations, but no consistent patterns across species (Fig. 1). Species with more occurrence data (e.g. *G. johnstoni*, *C. bennettii*) tend to show clearest relationships, i.e. high values of GARP only
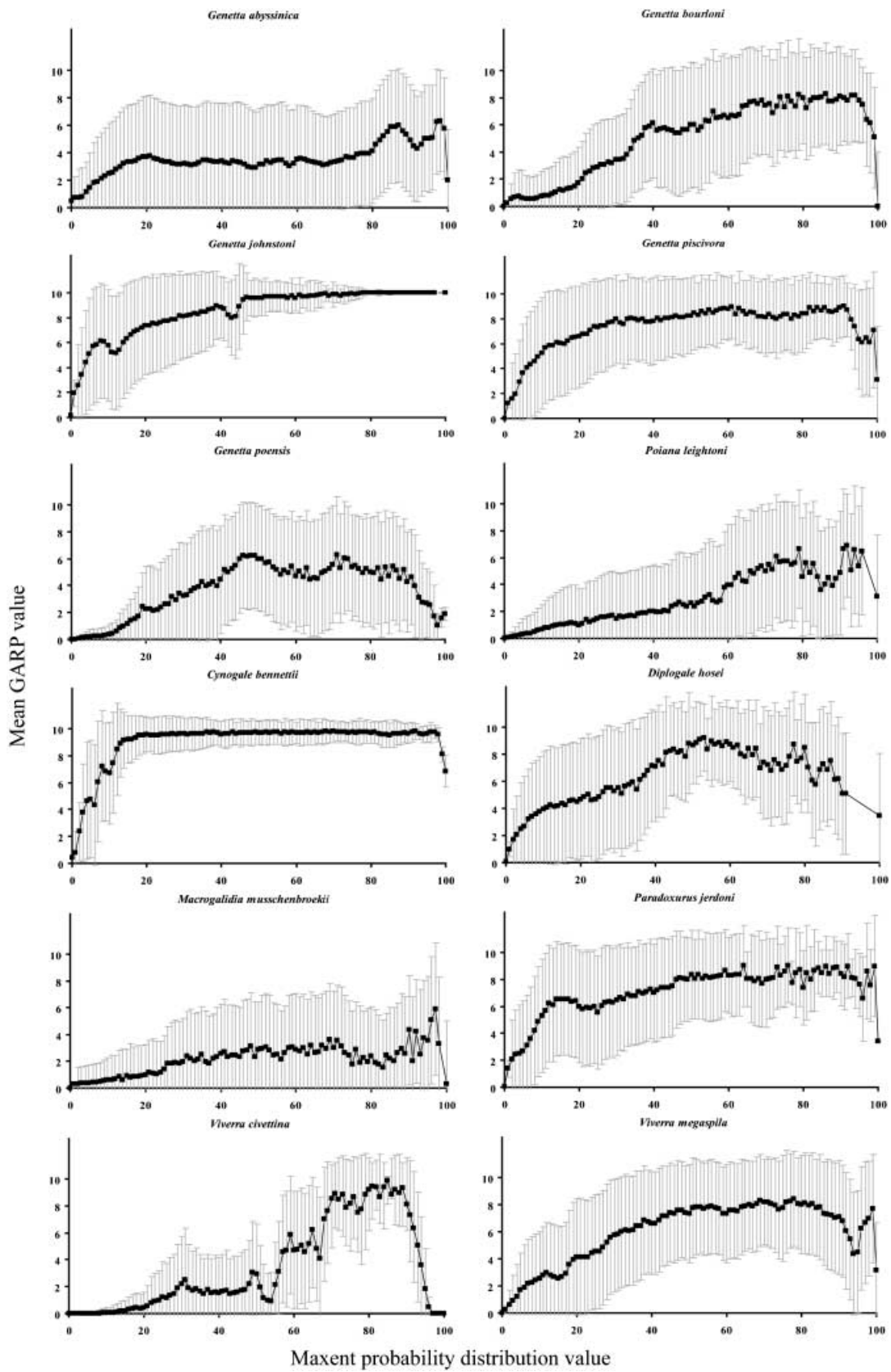
Figure 1 Maxent probability distribution values and GARP median values for six African species (upper panels) and six Asian species (lower panels). Standard deviation bars shown in grey.

at sites with high values of Maxent. GARP deviations from the mean were generally high for all Maxent probability values for most species studied, confirming the variability of GARP values for any given Maxent pixel value. Furthermore, high GARP values do not always correspond with high Maxent probabilities (see, in particular, *G. poensis*, *V. civettina*, and *M. musschenbroekii*); species showing this inconsistent behaviour had small occurrence data sets available (9, 9, and 13 points, respectively).

Restricting the ENMs to LC1 reduced the initial GARP predictions by 25–75% and Maxent predictions by 11–64% for the 12 species studied. With LC2, predictions increased by as little as 10% (GARP) and 11% (Maxent), and as much as 78% (GARP) and 83% (Maxent). The minimal increase with inclusion of LC2 was observed for *G. piscivora* for which two categories of degraded landscape were added: degraded evergreen lowland forest and mosaic forests/cropland; the maximal increase was observed for *M. musschenbroekii* for which forest mosaic/degraded/fragmented forest and mixed cropland/plantations categories were added.

Potential geographical ranges for the West African species (*G. bourloni*, *G. johnstoni*, *G. poensis, P. leightoni*) evidenced islands of closed evergreen forests as favourable habitats isolated by degraded evergreen lowland forest cover (Fig. 2). *G. johnstoni* had a larger potential geographical range, including northern deciduous woodlands. *G. piscivora* had a continuous predicted range within the closed evergreen lowland and submontane forests of the Congo basin. As for *G. abyssinica* in East Africa, open/sparse grasslands in Eritrea and surrounding countries, and deciduous shrubland – montane forest in western Ethiopia were depicted as suitable areas, geographically isolated by croplands. The two Asian species found in Borneo (*C. bennettii* and *D. hosei*) had their potential geographical ranges covering the evergreen lowland and montane forests of the island; the distribution of these suitable areas for *C. bennettii* (including in addition swamp forests) appeared fragmented in Sumatra and South-East Asia, and did not include the historical records mentioned from northern Thailand and Vietnam. The potential range of *V. megaspila* in South-East Asia covered a wide spectrum of habitats (evergreen lowland and montane forests, mixed and dry deciduous forests) but was fragmented by cropland. Among the two Indian species, *V. civettina* had its potential geographical range covered by evergreen lowland and montane forests along the south-western coast (Kerala), whereas *P. jerdoni* had a range also broadened to the east (North Tamil Nadu–South Karnataka), including mixed and dry deciduous forests. As for *M. musschenbroekii*, notable discrepancy between outputs of the two models (see above) made any interpretation hazardous.

As expected, the degree of coverage of species predicted ranges by existing reserves was small under both modelling techniques (Fig. 3). Depending on the species, only 4–18% of the areas predicted present is currently protected. Considering areas overlapping with proposed reserves added only a small area, but was noteworthy for two Asian viverrids (*C. bennettii, D. hosei*; Fig. 3), suggesting that some species would benefit from establishment of these proposed reserves. Nevertheless, the importance of these potential reserves becomes evident for

all species when compared with the extent of areas coinciding with current reserves (Fig. 3): proposed reserves may cover small sections of species distributions, but they increase the overall degree of protection considerably.

We observed differences between the two types of models in extent of the predicted distributions and consequently, but to a smaller degree, in extent of areas under protection (Fig. 3). We attribute these differences again to the small occurrence data sets for some species: for instance, the largest discrepancies between the two models were recorded for *V. civettina* (nine localities; GARP original prediction represented 6% of the size of Maxent prediction; percentage increased to 8% when LC1 and LC2 were included), and *M. musschenbroekii* (13 localities; GARP prediction equalled 2.5% of Maxent prediction but increased to 25% after LC1 and LC2 were included).

DISCUSSION

GARP and Maxent applied to low number of occurrences

GARP has been successfully tested and used for the past several years in various fields of research (Peterson & Vieglais, 2001; Costa *et al.*, 2002; Raxworthy *et al.*, 2003) mainly because of its power to generalize or extrapolate, a quality needed when species' ecological niches are reconstructed from incomplete occurrence and environmental data. In previous comparisons, GARP has not performed as well as other algorithms (e.g. Maxent) in discriminating between presences and absences (Elith *et al.*, 2006), although trade-offs exist between the ability to achieve such discrimination and the ability to extrapolate predictions into broad, unsampled areas (A. T. Peterson *et al.*, in press). Maxent was recently introduced as a tool for ENM (Phillips *et al.*, 2004). One of the appealing characteristics of this tool is the continuous output, which offers finer levels of distinction in terms of degree of suitability for a species. However, it is not yet clear how significant are the differences between various probability distribution values (Phillips *et al.*, 2006); as such, the user is left with the difficult task of selecting the appropriate threshold, below which the model may loose predictive power and become too general.

Pearson *et al.* (2007) addressed the threshold issue in the context of small samples available for ENM. The acceptable threshold value depends on the type of question asked: if the interest is in observing general distributional patterns, then a 'liberal' threshold is suitable (i.e. over-predicting is informative). However, when conservation applications are of principal interest, a 'conservative' threshold is more adequate (i.e. over-predicting is not desirable). In the context of very low sample sizes (as low as five records), a fixed Maxent probability value of 10 was shown by Pearson *et al.* (2007) to significantly recover all known presences. In the same context, a lower Maxent value (below that associated with the inclusion of any one of the known presence records) was useful in revealing unconfirmed but potentially important distributional areas. In our study, a Maxent probability value of 10 generally ensured the inclusion
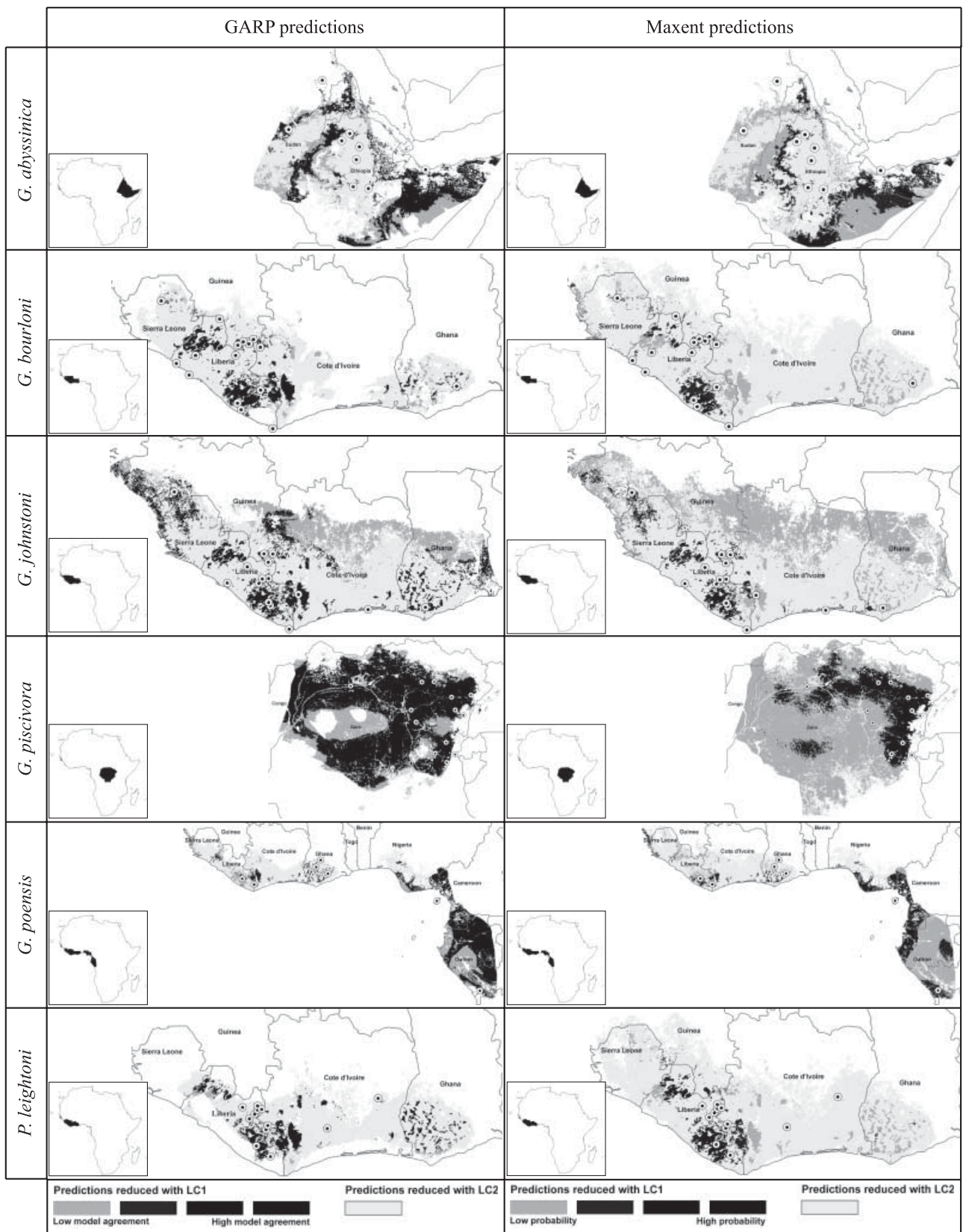
Figure 2 Species predicted distributions. Strong model agreement (GARP) and high probability distribution values (Maxent) are shown in darker colour under restricted land-cover scenario (LC1). Lightest grey shows the predictions under moderate land-cover scenario (LC2).
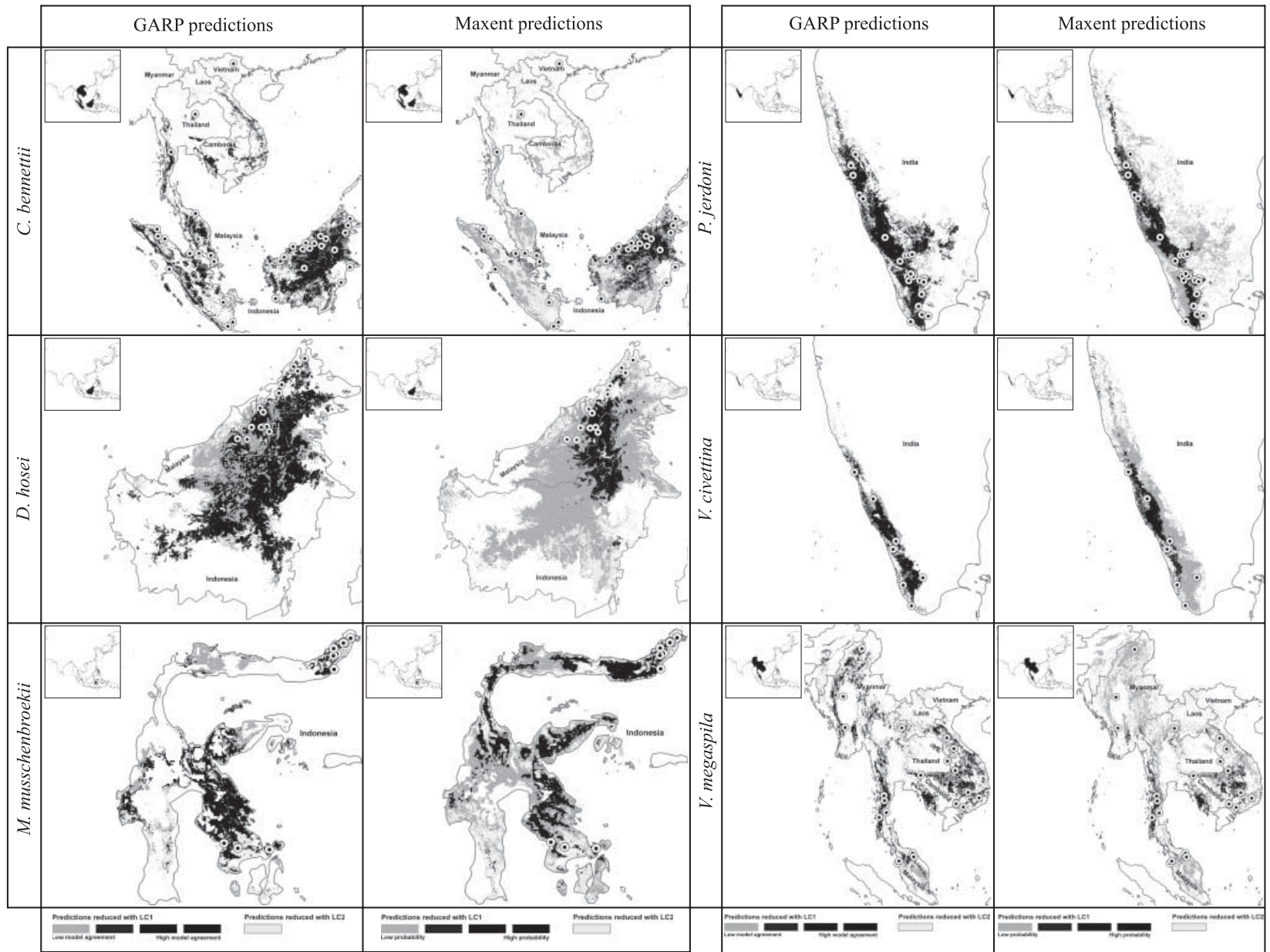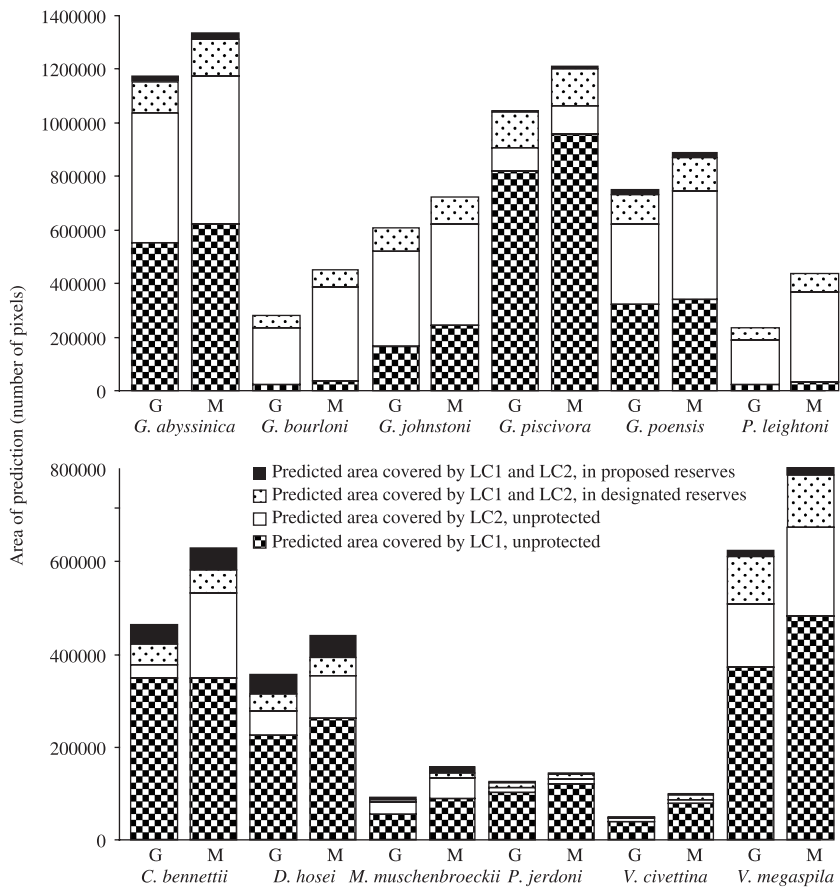
	GARP predictions	Maxent predictions		GARP predictions	Maxent predictions

Ecological niche modelling of poorly known viverrids

Figure 2 *Continued*

Figure 3 Extent of areas predicted present by GARP (G) and Maxent (M), which overlap with restricted land-cover layer (LC1), moderate land-cover layer (LC2), and designated and proposed reserves. African species are shown in upper panel and Asian species in lower panel.

in the prediction of all known records for most species studied (nine out of 12); the lowest Maxent values of 2 and 3 were necessary in the case of *D. hosei* (14 records) and *C. bennettii* (36 records), respectively.

Our study yielded results that were somewhat different from our initial expectations. We had anticipated that GARP predictions would be broader than Maxent models, as Maxent tends to overfit models (Phillips *et al.*, 2004), especially with small sample sizes. However, with the default Maxent regularization value, Maxent model predictions were broader than those of GARP, the opposite of expectations. It seems that, in this study, Maxent extrapolated more than GARP (Fig. 3), a similar result, to some extent, with that of Pearson *et al.* (2007) study.

For Asian species with < 15 localities, GARP raw predictions with values > 0 covered only 2.5–6% of the extent of areas predicted present by Maxent (values ≥ 1; maps not shown). Even using the 'lowest presence threshold' (LPT, i.e. the predicted level at which all known occurrences are predicted present; see Pearson *et al.*, 2007), the discrepancies were still large. For example, although *G. poensis* had the highest LPT (30%) of all of the species, the GARP 'raw' prediction still represented only 31% of the extent of the area predicted by the Maxent model. For Asian species with < 15 localities, correspondence between the two models (Figs 1 & 2) was poor. We could attribute this result to reaching the minimum number of occurrence points, below that necessary to obtain models with good predictive

power. Pearson *et al.* (2007) used a jackknife procedure to show that Maxent performed better than GARP when small occurrence datasets are available, smaller than the ones we used in our study. However, due to the differences (e.g. geographical scale of the study, sample sizes) between Pearson *et al.* (2007) study and the present one, we cannot conclude that the discrepancies we observed are a result of GARP failing to produce informative predictions using < 15 localities. For those African and Asian species for which we had ≥ 15 localities, correspondence between the two models generally improved. Given that we had no localities available for external testing of models, we cannot say for sure which of the two methods performed better, although this was not the aim of our study. In general, both methods produced similar results regarding overall distributional patterns; however, the means by which they achieved that were quite different. Oddly, the highest Maxent values generally corresponded to lower GARP values for almost all species' predicted distributions (Fig. 2). This association reflects the broader areas generally predicted by GARP, and the broader spectrum of predictions provided by Maxent models. Although these differences do not necessarily indicate differences in quality, they do reflect very real differences in the nuts and bolts of the two methods that must be taken into account in any comparative applications. Finally, although we took precautions in assembling the occurrence data set so as to minimize potential taxonomic or geographical errors, outliers caused by

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misidentifications or faulty geographical references could influence model outputs, particularly for species with low numbers of known occurrences; as such, our findings are vulnerable to some degree of error and uncertainty.

Ecological niche modelling, present landscapes, and conservation status of the Viverridae

The use of ENM methods including land use yielded range predictions generally contradicting with the extents of recognized occurrence (i.e. the limits of the areas where species can be found; see Rondinini *et al.*, 2005) recently redefined for the 12 species of viverrids studied herein (Boitani *et al.*, 2006; P.G., pers. obs.). Notably, northern Laos and Vietnam were not predicted as suitable areas for *V. megaspila*, whereas some northern latitudes in Cambodia and Vietnam were estimated as suitable for *C. bennettii* (Fig. 2). In the latter case, our results confirmed that northernmost mentions from Vietnam and China (Veron *et al.*, 2006) were likely ecological 'outliers'. Overall, ENM predictions yielded more fragmented extents of suitable areas for African species than extents of occurrences, whereas they generally tended to estimate more range connectivity among Asian species. Discrepancies between the two range assessment outputs was notably due to the fact that our analysis took into account current land use, and showed that a fair proportion of historical records were now located in unsuitable (degraded) habitats, especially in West and East Africa.

Five out of six African viverrids showed a large extent of suitable areas (30–80%) currently covered by degraded evergreen lowland forest (West Africa) and croplands (East Africa) that may prevent connectivity between populations. In West Africa, four islands of forest might be of prime importance for conservation of rainforest taxa; they are located in (1) eastern Liberia – south-western Ivory Coast (including Sapo, Cestos Sehhkwehn, and Tai National Parks); (2) north-western Liberia (Lofa Mano National Park); (3) south-western Ghana (Bia National Park and Ankasa Reserve); and (4) at the boundary of south-eastern Guinea (Mt. Nimba National Park, Ziama and Diéké forest reserves). In East Africa, the suitable range estimated for *G. abyssinica* also suffered from great fragmentation, with most of the historical records now situated in croplands. Conversely, *G. piscivora* appeared to be the least affected species in terms of habitat disturbance, with a relatively continuous distributional area within the Congo basin. Greater distributional connectivity between points of occurrence was suggested for Asian species, thanks to relative preservation of vegetation cover, notably in south-western India (*P. jerdoni* and *V. civettina*) and Borneo (*C. bennettii* and *D. hosei*; the latter species showing a suitable range significantly wider than extent of recognized occurrences). However, fragmentation of suitable areas by crop cover was also evidenced in Sumatra (*C. bennettii*) and South-East Asia (*C. bennettii* and *V. megaspila*). The question of whether or not these viverrids may survive in degraded or alternative habitats is thus a crucial issue. These animals generally have restricted distributions, so options in choosing prime habitats for preservation are limited. Although the biology of most of the viverrids studied herein remains poorly known, it is likely that specialized species (including *G. johnstoni, G. piscivora, G. poensis, P. leightoni, C. bennettii, D. hosei,* and *M. musschenbroekii*) are more sensitive to habitat disturbance (e.g. Heydon & Ghaffar, 1997).

The level of coverage of species ranges by existing reserves was low (Fig. 3). The situation was similar for the proposed reserves (UNEP-WCMC, 2006), but since these represent a significant fraction of the extent of present reserve network (notably in Borneo), they would improve the degree of protection in Africa and Asia of the 12 species of viverrids studied. Great extents of the areas identified as suitable through ENM have no protection, so we follow Schreiber *et al.* (1989) in making the obvious recommendation that protected areas should be augmented to conserve these small Carnivores. Given the high degree of isolation of suitable forested habitats in West Africa and absence of proposed future reserves, this sub-region should be given highest priority in terms of conservation planning.

The outputs – sometimes inconclusive – of suitable ranges that we made available should be taken as a preliminary, indicative step towards the better understanding of the distribution and ecology of those species of viverrids. Field studies are needed to test and improve further our models, refine and obtain data on the ecology of the species, and test hypotheses of distributions. Our study showed that ENM methods reached limitations when confronted with too-small numbers of occurrence points. In this case, model-based environmental stratifications (Araújo & Guisan, 2006) may be an effective solution to orientate sampling effort necessary to complement occurrence data presently available and improve niche modelling.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 List of the records of the 12 species of Viverridae used for ecological niche modelling.

This material is available as part of the online article from:
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