A Conservation Strategy for the Amphibians of Madagascar	Monografie del Museo Regionale di Scienze Naturali di Torino, XLV (2008): pp. 397-410

David R. Vieites[1,2 *], Sandra Nieto-Román[2,3], Miguel Vences[4]

Towards understanding the spatial pattern of amphibian diversity in Madagascar

ABSTRACT

We summarize the current state of the exploration of the spatial pattern of the amphibian diversity in Madagascar based on a comprehensive database of specimen and locality data records for Malagasy amphibians, containing 2154 unique records. Data were gathered from museum voucher specimens, literature and from recent field work, and geo-referenced when possible. The recent increase in species descriptions and phylogenetic work challenged the validity of a considerable amount of species records, especially in cases where cryptic species are being discovered. Many of the records from literature or museums could not be precisely assigned to species in the light of novel taxonomic knowledge, and thus had to be discarded. Our analysis shows that for many species we have fewer than ten reliable records, with 130 species having only one or two records. Sampling effort has been traditionally biased towards protected areas, their surroundings and sites along major roads. We analyzed the potential effects of including unverified data on modeling species distribution of Malagasy amphibians, and we identify target areas for exploration to complete our knowledge of the biogeography of these organisms.

Key words: Amphibians, Distribution modelling, Locality records, Madagascar, Maxent.

INTRODUCTION

Madagascar harbors a large number of amphibian species, and is considered one of the hotspots for amphibian global diversity (Stuart et al., 2004). However, little is known about most of those species (Glaw & Vences, 1994). To develop an effective conservation strategy for the amphibians of Madagascar it is necessary to inventory all species (Vallan, 2000; Andreone et

[1] Museum of Vertebrate Zoology, Berkeley.
[2] Department of Integrative Biology, Berkeley.
[2] Departamento de Biología y Ecología Animal. Vigo.
[2] Technical University of Braunschweig.
* Corresponding author; web: vieites.berkeley.edu

al., 2005), solve their taxonomy, and define their distribution ranges. These three goals are linked, and work to achieve them is currently in progress. Inventories and rapid assessments have been carried out in many regions, mainly focused on protected areas (e.g., Andreone et al., 2000, 2001, 2003; Andreone & Randriamahazo, 1997; Nussbaum et al., 1999; Rakotomalala, 2002; Raselimanana et al., 2000; Raxworthy et al., 1996, 1998; Vences et al., 2002). The efforts to clarify the phylogenetic relationships of Malagasy amphibians, and the rate of discovery of new amphibian species in Madagascar, have never been as high as during the last decade (Glaw & Vences, 2006; Köhler et al., 2005; Vences et al., 2003), which is changing our current view on Madagascar's amphibian diversity and biogeography. Although many of the newly discovered species are genetically, bio-acoustically and morphologically different, many are difficult to distinguish by morphology from sibling species (Glaw et al., 2001; Köhler et al., 2005), their discovery questioning the validity of some species identifications in inventories and rapid assessments. The outcome is that the knowledge on the ranges of most species is changing rapidly, usually because of their splitting into several species. Together with true new discoveries of endemic taxa of restricted ranges (Glaw et al., 2006), these data claim for a revision of our assumptions on the spatial distribution of Madagascar's amphibian diversity (i.e. Andreone et al., 2005; Lees et al., 1999).

Clarifying the spatial distribution of the amphibian fauna in Madagascar is critical to understand the patterns of richness and endemism in space, and to define priority areas for conservation. Here, we analyze the current knowledge on the spatial distribution of Malagasy amphibians, explore the potential effects of the new discoveries in assessing potential distributions of species, and identify priority target regions for future field surveys.

MATERIAL AND METHODS

We assembled a comprehensive locality database for all the amphibian and reptile species of Madagascar. Locality data were gathered from different sources, including voucher specimen data from museum collections, own GPS readings from fieldwork, and literature. Almost all available literature was reviewed (see Vences et al., in press in this volume) and locality data, when available, were incorporated into the database. Many of the localities reported in the literature, or from old museum records, were too vague to be properly geo-referenced. For every geo-referenced locality we incorporated an uncertainty value following Chapman and Wieczorek (2006), allowing us to filter imprecise localities for GIS modeling analyses. These kinds of data are suitable to develop potential distribution models and biodiversity estimates for this fauna. Although dozens of records from different specimens, years or researchers, may be available for a species at a particular location, we considered them as duplicates for the purposes of this paper, only one species record per locality being considered.

In order to assess the potential effect of taxonomic uncertainty on predicting

Malagasy amphibian species' distributions, we performed a test with one of the commonest species in eastern rainforests. *Boophis luteus* is a medium-sized green arboreal frog that is found in primary and secondary rainforests across the central and southern part of the island (Glaw & Vences, 1994). The occurrence of *B. luteus* in northern parts of the island, like the Marojejy region, has not been confirmed although the species had been previously reported there (e.g., Blommers-Schlösser & Blanc, 1991). Several species were recently recognized from the *B. luteus* group (Andreone, 1993, 1996; Andreone et al., 1995; Glaw & Thiesmeier, 1993; Glaw & Vences, 2002). Recent genetic and bioacoustic analyses allowed us to confirm the presence of *B. luteus* in some localities and discriminate among other species of this group. As a result, some of the previous literature and museum records assigned to this species are now taxonomically unclear, because a reliable distinction of preserved specimens is impossible. Hence, we merged them under the name of "undetermined *Boophis luteus* complex". To test the effect of the inclusion of those records on predicting the potential distribution of the species, we performed two separate analyses with and without these uncertain locality records.

We used nineteen climatic variables from the WorldClim database version 1.4 (Hijmans et al., 2005), with potential evapotranspiration and percentage of forest cover in 2000, as predictors for the environmental niche models. The Worldclim dataset was created by interpolation of observed world weather station data, using a thin-plate smoothing spline and longitude, latitude and elevation as independent variables (Hutchinson, 1995), being the current version 1.4 more accurate than previous ones in some regions, because of the inclusion of more weather stations. The climatic variables employed in the models were annual mean temperature, mean diurnal temperature range, isothermality (monthly/annual temperature range), temperature seasonality (standard deviation across months), maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest, driest, warmest and coldest quarters, annual precipitation, precipitation of wettest and driest months, precipitation seasonality (coefficient of variation), and precipitation of wettest, driest, warmest and coldest quarters.

From all the environmental niche modeling methods currently available, we chose Maxent (version 2.3, Phillips et al., 2006), as it outperformed others in a recent cross-comparison analysis (Elith et al., 2006), and with small sample size datasets (Hernández et al., 2006). Maxent finds the distribution of maximum entropy subject to constraints imposed both by the observed distribution of the species, and the environmental conditions across the defined study area, and estimates the likelihood of a species being present. It computes a probability distribution across the defined study area, for which it requires presence and background absence data. As background pseudo-absence data, we randomly selected 10000 data points across Madagascar. Real absence data is not yet available for Madagascar, as detectability of many tropical amphibian species is very low. We run Maxent using 75% of the data for testing and 25% for training, with default values except the regularization multiplier value which was set to 0.25. The output predicted distributions are in cumulative format, in which the output value at a grid cell is the sum of the probabilities of all grid cells with no higher probability than the grid cell, times 100 (Phillips et al., 2006). Grid cell values can vary from zero (not suitable) to 100 (highly suitable). In order to evaluate the performance of the model, we calculated the area under the Receiver Operating Characteristic curve (AUC), which measures the ability of the model to discriminate between sites were the species is present versus sites were is absent (Hanley & McNeil, 1982). It ranges from 0 to 1, being AUC scores above 0.7 considered good model performance (Fielding & Bell, 1997).

RESULTS

Our database includes 452 spatially geo-referenced localities with 2154 unique valid amphibian records adequate for distribution modeling analyses. Most of these records were gathered from fieldwork developed during the last decade by MV, DRV and F. Glaw. About 700 additional unique records were discarded, being not suitable for such kind of analyses, because of the lack of precise geographic coordinates, or due to taxonomic uncertainty.

Figure 1 shows the spatial distribution of localities, and the number of species recorded in each locality. The geo-referenced localities with amphibian data associated were distributed all across the island, mainly in the eastern rainforests (Fig. 1). However, most of them were within National Parks, other protected areas, their surroundings or close to the roads connecting them with major towns. The most densely sampled areas were the protected areas of Mantadia-Analamazaotra, Ranomafana, Andringitra, Andohalela, Nosy-Be, Montagne d'Ambre and their surroundings. Many of the localities sampled are close to the roads that connect Antananarivo with Andasibe, Antananarivo with Fianarantsoa-Ranomafana, or Fianarantsoa with Toliara, where almost every locality is by the road. Large areas of natural habitat remain to be explored, mainly between national parks in eastern Madagascar. These include a large portion of rainforest between Mantadia-Analamazaotra and Masoala, from where very few localities with records exist, and 11 small reserves across the island for which no confirmed amphibian records have been published.

The number of species recorded per locality was higher in reserves than in other areas. In 87% of the localities, fewer than ten species were recorded. In some areas, many of the localities were very close to each other but not all species occurring in the general area were recorded from each of these localities, resulting in relatively low numbers of species per locality. The mean number of species per locality was 4.6 ± 5.7 (mean ± SD). The total number of valid records per species is shown in figure 2. The mean number of locality records per species was 6.5 ± 8.7 (mean ± SD), and only 16.7% of species had more than 10 locality records. More than half of the species had fewer than 5 records (55.4%), most of the unique records corresponding to recently described species.

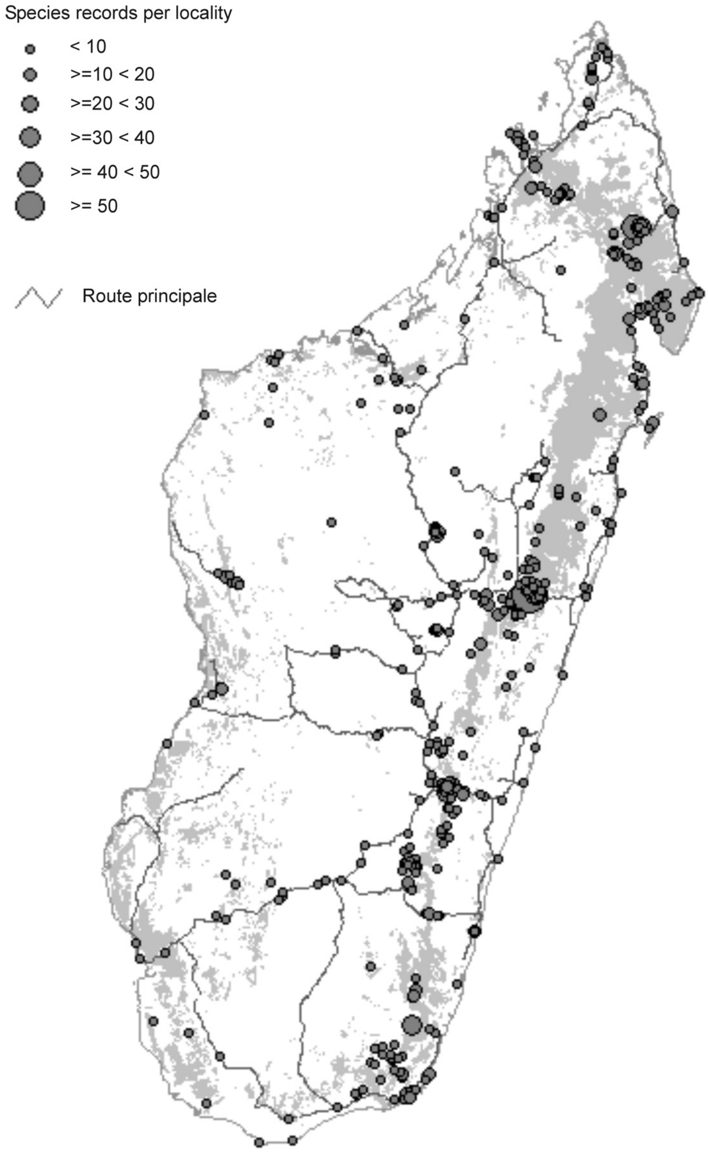

Fig. 1. Plot of the number of individual and non-duplicated geo-referenced species records per locality in our database. Circle size is proportional to the number of records. Grey represents remaining rainforest where most of amphibian diversity occurs. Major roads (Routes principales) are depicted.

The potential distribution models for *Boophis luteus* and for the *B. luteus* species complex are depicted in figure 3. The AUC values for 25% testing data were very high in both cases (0.864 and 0.932 respectively), suggesting the models performed well to predict the distributions. When only confirmed records were used to predict the distribution of *B. luteus* (Fig. 2 C), the model suggested the most suitable areas for the species are in the eastern rainforests south of Zahamena and some central areas. Isalo is predicted, although with low suitability. Some over-prediction occurred in areas like Marojejy or Masoala but not further north and with low suitability values. When all confirmed and non-confirmed data were included (Fig. 2 D), the species is still predicted in the same areas, but the range extending further north and suggesting a continuous distribution from Andohahela to Marojejy, and also in Montagne d'Ambre. The distribution range obtained from the Global Amphibian Assessment (Fig. 2 B, IUCN, 2006) is a coarse representation of the species range, with less detail and a ca. 200 km extension further north compared with the model. This extension corresponds to two localities in which the species has been cited but for which we have no data to confirm the records (Fig. 2 A).

DISCUSSION

Taxonomy in progress and identification verifiability

Over 240 species of amphibians have been formally described in Madagascar so far, about one third of them during the last decade (Köhler et al., 2005). However, from molecular, bioacoustic and morphological data, our database currently contains about 126 additional species more that need formal description. This suggests an increment of 54% respect to the current number, a higher increase than during the last decade, and there are many additional taxa that probably have to be added to this list. These new discoveries enlighten the patterns of amphibian richness and endemism on the island. This previously unrecognized diversity challenges our ability to properly identify these taxa in the field. Identifications based on morphology or colorations are unreliable (as we further discuss in another chapter in this volume). Molecular techniques have proven to be of much help in identifying Malagasy amphibian species and seem to be more successful than any other approach (Thomas et al., 2005, Vences et al., 2005). However, there is no doubt that a combination of methods is needed to ascertain the identification of amphibians in Madagascar. Fieldwork, specimen vouchers, call recordings and tissues for DNA sequencing analyses are vital for filling the gaps in species taxonomy and identification, because many more species are expected to be discovered from poorly surveyed areas.

Current efforts are in progress to clarify the taxonomy of Malagasy amphibians, while we are learning more about the distribution of these species on the island. New species descriptions, large unexplored areas, and low number of records per species is a common situation in tropical areas, which

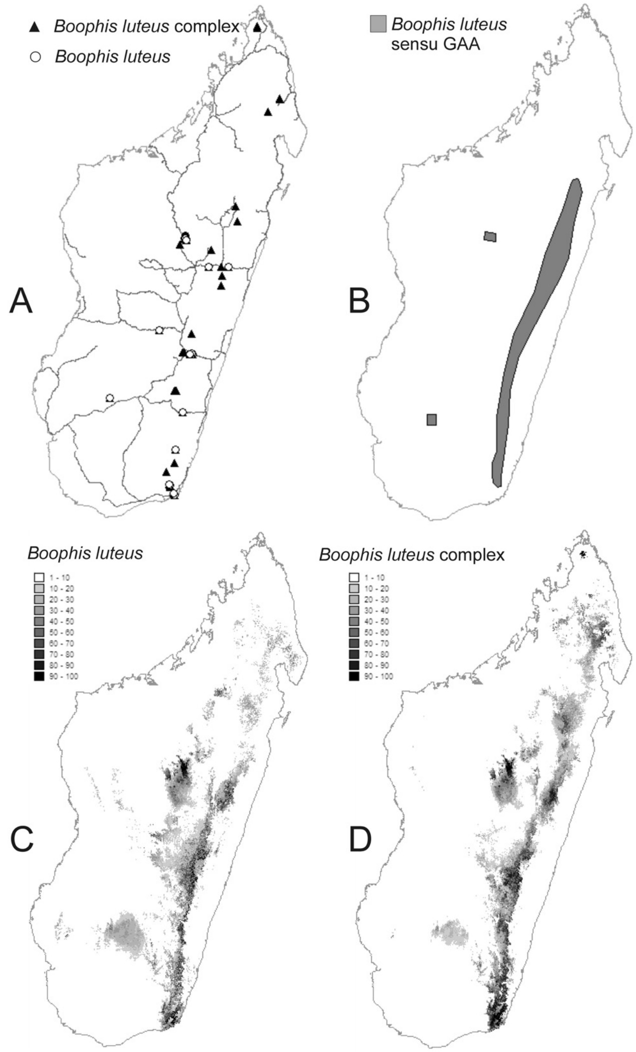

Fig. 2. Locality records and distribution models for *Boophis luteus*. (A) White circles represent the confirmed records for this species in Madagascar, while black triangles represent unconfirmed records previously assigned to the species. (B) Distribution of *B. luteus* according to the Global Amphibian Assessment based on expert opinion. (C) Potential distribution model for *B. luteus* using confirmed records only. Suitability values per grid cell go from cero (not suitable, light grey) to 100 (very suitable, black) (D) Potential distribution model for *B. luteus* complex including confirmed and unconfirmed records.

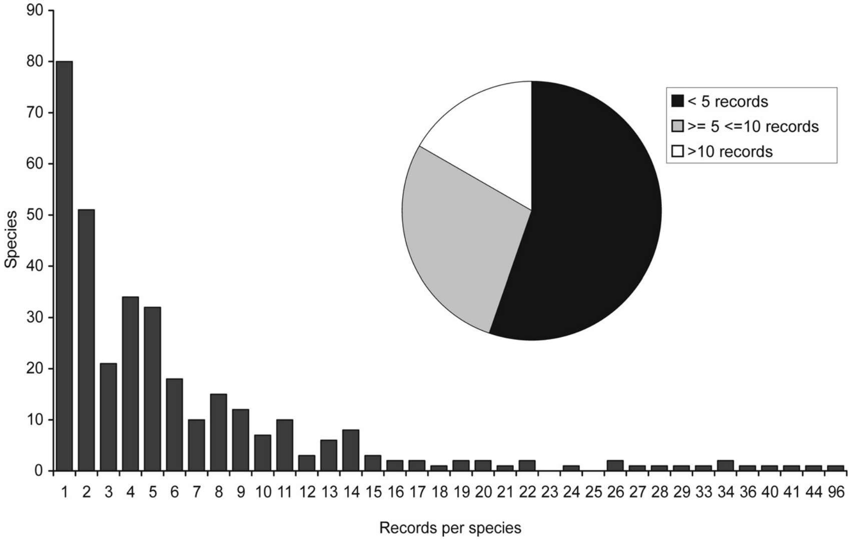

Fig. 3. Histogram showing the number of reliable locality records per species of Malagasy amphibians compiled in our database.

difficult species' distribution modeling and conservation planning. Different kinds of distribution data (i.e. point locality, geographic ranges), usually have associated commission and omission errors (Rondini et al., 2006), which can influence conservation planning. As we have shown in the case of a common species like *Boophis luteus*, any attempt to model species distributions using non-validated records can lead to seriously wrong predictions and needs to be strictly avoided. If problems are already detected with common and well-known species, we expect considerable difficulties for the more poorly known species.

Current pattern of amphibian diversity

The geographic pattern of amphibian diversity in Madagascar is poorly understood. Few biodiversity analyses have been done to analyze the spatial pattern of Malagasy amphibian diversity based on previous data (Lees, 1996; Lees et al., 1999; Andreone et al., 2005). New discoveries and sampling effort can bias these analyses, as some areas, like Mantadia or Ranomafana National Parks, received much more attention than others, which resulted in a higher number of species recorded per locality (Fig. 3). Modeling the distribution of the species may be a way to circumvent the problems caused by the biased distribution of sampling efforts across the island.

For many species we do not have enough information to directly assess their distribution ranges, hence to perform accurate biodiversity, hotspot or endemism analyses. The number of records per species is low, mainly due to two reasons. First, many areas have been extensively sampled, while others still need to be surveyed. Large areas in the East, North and West parts of the island likely hold high species diversity which requires confirmation through sampling. Exploration of these areas will lead to the discovery of new species and to range expansions for many species, but in many cases access to these areas is not easy.

Second, the new taxonomic developments are showing that what we thought to be one species often is in fact a complex of several species. Hence, all the previous records for that species have to be re-evaluated and distributed among the "new" taxa. In some cases this is possible but in others not, resulting in a high number of records that can be assigned to species groups but not precisely to any species. As a consequence it is not possible to model several species due to limited records after taxonomic revisions. Ten records is usually considered a low number to perform distribution modeling, and five would be an absolute minimum (Hernández et al., 2006), giving suitability estimates that will be helpful to locate areas environmentally similar to those where the species is actually present, but may be not representing the real distribution of the species. Less than five records are available for more than half of the species of Malagasy amphibians, and about 30% of the species have between 5 and 10 records, making the modeling of the distribution of these species difficult without more data. One approach that can be followed in such cases is to model clades defined through molecular phylogenies, instead of species units.

Inventories are needed in new areas to complete the distribution range of many species, and increase the number of records per species, which would allow for more accurate modeling analyses. However, models based on limited records are still useful as they often overpredict species occurrences leading us to priority sites for conducting surveys for those species (Raxworthy et al., 2003).

Target regions for future inventory work.

A preliminary test of models for species with more than 5 records, with a detailed analysis of the distribution of localities from figure 1 and remnant natural habitats, suggested several target regions which merit further surveys in the near future. From North to South they would be the remaining habitat corridors between Tsaratanana and Ankarana, and Tsaratanana and Marojejy, which have been poorly explored and likely sustain contact zones between biogeographic regions. The Masoala peninsula has only been partially explored thus far, and from collaborative molecular work with F. Andreone it is clear now that many of the taxa from this area are undescribed new species. Between roughly Marojejy and Mantadia there are ca. 500 km of rainforest which have been poorly explored, with only few records from Zahamena and Ambatovaky in the middle and no published records thus far from the large new Makira Reserve. This area could hold a huge diversity of species and multiple potential geographic range expansions of southern and northern species need to be confirmed there. The corridors Mantadía-Ranomafana and Ranomafana-Andringitra need further exploration because few confirmed records are available from the areas in between these biodiversity hotspots. In the South, Andohahela has been extensively sampled, but the area from Midongy du Sud to Andringitra needs further work, and the whole Anosy and Vohimena chains urgently need to be inventoried using also bioaocustic and molecular methods. Huge range extensions have been discovered by sampling low elevation localities in the east coast, and more work is needed to assess the diversity of species present in low elevations also outside primary habitats. In the West, species distribution modeling suggests range extensions for many species between Ankarafantsika and Manongarivo. Although the diversity of amphibian species in the West will be lower than in the eastern rainforests, many of the western species are locally endemic to highly threatened forest fragments.

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RÉSUMÉ

Vers la compréhension des patterns spatiaux de la diversité pour les amphibiens de Madagascar.

Nous résumons le statut curent de l'exploration des patterns spatiaux pour la diversité des amphibiens à Madagascar, en se basant sur une base de données complet des spécimens et des localités de collecte, avec 2154 records uniques. Les données ont eté récoltés pour les spécimens de musée, de la littérature et le travail de terrain récent, et géoréferencés quand possible. L'augmentation récente dans le taux de description d'espèces et de travaux phylogénétiques ont mis en doute une bonne quantité de données de présence des espèces, puisque plusieurs espèces cryptique ont été décrites. Beaucoup parmi les données bibliographique ou muséologiques peuvent pas être assignés aux espèces sur la base de la nouvelle connaissance taxinomiques, et pourtant on du être éliminés. Notre analyse montre que pour plusieurs taxons nous avons moins de dix données fiables, avec 130 espèces avec moins de 2 données. L'effort d'échantillonnage a été traditionnellement orienté vers les aires protégées ou leurs entours, ou sur des sites a coté des routes principales. Nous avons pourtant analysé les effets potentiels de considérer des données non-vérifiés pour modéliser la distribution des espèces, avec l'identification de aires-cible pour compléter notre connaissance de la biogéographie de ces organismes.

Mots clés: Amphibiens, Données de localité, Madagascar, Maxent, Modélisation de la distribution.

David R. Vieites
Museum of Vertebrate Zoology, 3101 Valley Life Sciences Building.
Department of Integrative Biology
3060 Valley Life Sciences Building
University of California
Berkeley, CA 94720-3160, USA
Email vieites@berkeley.edu

Sandra Nieto-Román
Departamento de Biología y Ecología Animal
Campus Lagoas Marcosende
Universidad de Vigo. 36200. Vigo, Spain

Miguel Vences
Zoological Institute, Technical University of Braunschweig, Spielmannstr
8, 38106 Braunschweig, Germany

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