

Modeling co-occurrence between toxic prey and naïve predators in an incipient invasion

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Abstract Biological invasions can represent important threats to endemic species, including those within the invaders' food webs. The Asian common toad (*Duttaphrynus melanostictus*) was introduced to Madagascar in 2011. This introduction presents a potentially dangerous prey item to a relatively naïve, highly diverse endemic carnivore fauna. Using a multivariate niche modeling approach (background test), we assessed the predicted niche overlap between *D. melanostictus* and six endemic carnivores in eastern Madagascar. The overlap between this potential prey and predators was assessed on four environmental niche axes: temperature, precipitation, vegetation cover and elevation. Our

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results showed a mixture of niche overlap and divergence between *D. melanostictus* and the six carnivores for environmental axes tested. There was significant overlap with five of the carnivores on temperature and NDVI axes. On the precipitation axis, there was significant overlap between *D. melanostictus* with two species. Our results suggested that wide-ranging, locally rare carnivores may overlap extensively with *D. melanostictus*. The six carnivores that inhabit the eastern rainforest of Madagascar will likely share multiple, niche axes with this novel potential prey item. Species that eat the non-native common toad and are susceptible to its toxins are at conservation risk because their populations may not be robust enough to adapt quickly to this threat. We advocate closely monitoring these emerging interactions and suggest a preemptive conservation strategy for carnivores potentially at risk.

Keywords Asian common toad · Background test · Carnivores · Ecological niche models · Invasive alien species · Madagascar

Introduction

Biological invasions are a major driver of global environmental change and species loss (Crawford et al. 2010; Goodman 2012; Rebollar et al. 2014). They have led to biotic homogenization (Meyer et al. 2015; Wood et al. 2015), threats to native species (Cassey and Hogg 2015) and communities (Ehrenfeld 2010), and demand significant economic and human resources to manage (Inderjit 2005). Effective management of biological invasions requires explicit identification of the stage of invasion, since each is defined by different characteristics and therefore requires different control measures (Brown et al. 2008). The most effective strategy for controlling biological invasions is either prevention or early detection (Reaser et al. 2008). These management strategies rely on risk assessments of potential invasive alien species (IAS) that may be prohibitively expensive in certain circumstances, particularly for developing nations with high biodiversity (Faulkner et al. 2014). Furthermore, prevention requires a priori knowledge of which species are likely to invade and which regions are most susceptible to invasion. In the absence of preventative strategies, efforts to control IAS and mitigate impacts on native biota must rely on pre-invasion detection, prior to these species becoming widespread and dominant.

Two approaches have been used, separately and in combination, to predict species' invasive potential: (i) examine intrinsic factors, such as life history traits and niche properties (Thuiller et al. 2012; Ordonez 2014) or (ii) model extrinsic factors, such as climate and environmental variables (Thuiller et al. 2005; Godsoe and Case 2015). The latter strategy, which often uses correlative ecological niche models (ENM), is now common practice in invasion biology and provides a valuable framework for assessing the potential distribution of IAS (Thuiller et al. 2005). Projected distributions from ENMs give an approximation of the incipient invader's geographical range in the novel environment based on correlations between occurrence locations and abiotic environmental variables (Broennimann and Guisan 2008). Used in this way, ENMs provide the invader's predicted niche by matching environmental variables in the native and novel habitats under the critical assumption of niche conservatism (Broennimann et al. 2007). However, assessing niche overlap between two or more species using ENMs—as is necessary when assessing interactions between natives and non-natives—can be challenging from both conceptual and

statistical perspectives. This is mostly because environmental variables on which ENMs are based tend to be correlated with geographical location; ENMs may differ in their predicted niche solely because of different environmental characteristics of species' ranges (Costa et al. 2008), leading to possibly biased results. Consequently, any attempt to assess climatic niche overlap between natives and non-natives must account for the potential bias of spatial autocorrelation. Here, we aim to do so using a multivariate niche model (McCormack et al. 2010) to predict niche overlap on four environmental niche axes for an emerging predator–prey interaction.

The Asian common toad (*Duttaphrynus melanostictus*) was introduced to Madagascar in 2011. The first reported sighting was in the port city of Toamasina (Kolby 2014; Kull et al. 2014) and since then sightings have been mostly in urban areas and degraded forests in the humid eastern regions (Andreone 2014; Kolby 2014; Moore et al. 2015). However, this species may not remain confined to such habitats, as it has a wide geographic distribution across many environmental types in Asia (Srinivasulu and Das 2008). *Duttaphrynus melanostictus* releases a highly potent cardiotoxic toxin (unique to toads) from its parotoid gland when stressed (Chen and Kovarikova 1967). The introduction of *D. melanostictus* thus presents a potentially dangerous prey item to Malagasy communities who include frogs as part of their diet, as well as a relatively naïve, highly diverse endemic carnivore fauna that consume various amphibian species.

There are nine carnivores endemic to Madagascar, including *Cryptoprocta ferox* (fosa), *Eupleres goudotii* (falanouc), *Fossa fossana* (spotted fanaloka), *Galidia elegans* (ring-tailed vontsira), *Galidictis fasciata* (broad-striped vontsira), *Galidictis grandidieri* (Grandidier's vontsira), *Mungotictis decemlineata* (Northern bokiboky), *Salanoia concolor* (brown-tailed vontsira), and *Salanoia durrelli* (Durrell's vontsira). They have varying IUCN statuses, ranging from Least Concern (*Galidia elegans*) to Endangered (*Galidictis grandidieri*) and, as top predators, serve crucial ecosystem functions (Goodman 2012; Table 1). Certain species, such as *E. goudotii*, *F. fossana*, *G. fasciata* and *S. concolor* appear to confine their foraging to intact, primary forests, marshes and other aquatic habitats, and as specialists—for our purposes, defined solely by their environmental niche—tend to be restrictive in their habitat selection. They occupy a smaller or narrower range, depending on whether available habitats are threatened or resources are scarce (Gerber et al. 2012c; Farris et al. 2015b). In the case of *S. concolor* and *G. fasciata*, they are estimated to have a smaller initial population density compared to carnivores with wider environmental niches that are not restricted to intact forests (e.g., *C. ferox*, *G. elegans*). At least four of the nine are known to consume native frogs as part of their diet (Table 1), while no diet analysis has yet been conducted for the remaining two, *G. fasciata* and *S. concolor*.

There is currently a debate surrounding appropriate response to the introduction of *D. melanostictus* to Madagascar, where some have suggested immediate eradication (Kolby 2014), while others have cautioned against 'disproportionate countermeasures' without prior assessments (Mecke 2014). Moreover, Pearson's (2015) recent study suggests that *D. melanostictus* might occupy large swaths of Madagascar's eastern region, with the most likely invasion path predicted for areas within lowland and sub-humid forests in both northern and southern directions. This path will increase the probability of environmental niche overlap between the toad and Madagascar's endemic carnivores. The present study seeks to inform this debate by assessing the predicted niche overlap between this novel, toxic potential prey and native, endemic carnivores, a group that is likely to be directly affected by this incipient invasion.

Table 1 List of Madagascar's six endemic carnivores occupying eastern rainforest habitat, including diet, habitat preference, current IUCN classification, and body mass for each species

Species	Diet ^a	Habitat preference ^b	IUCN classification ^c	Body mass (kg) ^d
<i>Fosa Cryptoprocta ferox</i>	Bush pig, small carnivores, large and small bodied lemurs, shrews, tenrecs, rodents, birds, reptiles, frogs, crabs, invertebrates, domestic fowl	Contiguous dry and humid forest	Vulnerable	5.5–9.9
<i>Falanouc Eupleres goudotti</i>	Chameleons, frogs, earthworms, slugs, invertebrates	Contiguous humid forest, near marsh/aquatic areas	Endangered	1.5–4.6
<i>Spotted fanaloka Fossa fossana</i>	Tenrecs, rodents, reptiles, eels, frogs, crabs, centipedes, invertebrates	Contiguous humid forest, near marsh/aquatic areas	Vulnerable	1.3–2.1
<i>Ring-tail vontsira Galidia elegans</i>	Small bodied lemurs, tenrecs, rodents, birds, reptiles, frogs, fish, snails, crayfish, invertebrates, domestic fowl	Contiguous/degraded humid forests, near anthropogenic areas	Least concern	0.76–1.10
<i>Broad-stripe vontsira Galidictis fasciata</i>	No quantitative data available; rodents, reptiles, amphibians, invertebrates likely	Contiguous/degraded humid forest	Near threatened	0.6–1.0
<i>Brown-tail vontsira Salanoia concolor</i>	No quantitative data available; various invertebrates likely	Contiguous/degraded humid forest	Vulnerable	0.55–0.75

^a Sources for diet of carnivores include: Fosa—(Rasoloarison et al. 1995; Goodman et al. 1997, 2003c, 2012; Wright et al. 1997; Hawkins 1998; Britt et al. 2001; Hawkins and Racey 2005; Garbutt 2007); Falanouc—(Albignac et al. 1984; Dollar 1999; Goodman 2007; Goodman 2012); Spotted fanaloka—(Albignac 1972; Albignac et al. 1984; Goodman and Pidgeon 1999; Goodman 2003c, 2012; Kerridge et al. 2003; Garbutt 2007); Ring-tail vontsira—(Albignac 1972; Dunham 1998; Goodman and Pidgeon 1999; Britt and Virkaitis 2003; Goodman 2003a, 2012; Garbutt 2007); Broad-stripe vontsira—(Goodman 2003b, 2012); Brown-tail vontsira—(Britt and Virkaitis 2003; Goodman 2012)

^b Sources for carnivore habitat preference include: (Gerber et al. 2012c; Goodman 2012; Farris et al. 2014)

^c IUCN (2016)

^d Carnivore weights taken from: (Goodman and Pidgeon 1999; Goodman 2003a, b, c, 2012; Kerridge et al. 2003; Garbutt 2007; Lühns and Kappeler 2013)

First, we predicted the degree of niche overlap between environmental niches for *D. melanostictus* and the carnivores using a multivariate niche modeling approach. We expected this relationship to be modulated by different factors, such as abundance or microhabitat differences (e.g., site-specific temperature or forest cover). Therefore, differences in niche overlap with *D. melanostictus* were predicted to arise between species with narrow ranges and restricted climatic niches and those with wide ranges and less restricted climatic niches. For instance, we predicted *G. fasciata* and *S. concolor* to show little niche overlap with *D. melanostictus*; meanwhile *C. ferox*, *E. goudotii*, *F. fossana*, *G. elegans* should show high niche overlap with *D. melanostictus*. Secondly, in an effort to understand whether environmental specialization affects overlap with *D. melanostictus*, we calculated the spatial niche breadth of each carnivore species. We then determined the degree of association between niche breadth and niche overlap with *D. melanostictus*. For this question, we relied on ENM-generated predicted distributions to calculate niche breadth and niche overlap. Specialization has been shown to increase extinction risk in terrestrial wildlife, including carnivores (Cardillo et al. 2004), birds (Julliard et al. 2006) and mammals (Fisher et al. 2003). However, we had no a priori predictions about which carnivores—those with restricted or less restricted niche breadth—would significantly overlap with *D. melanostictus*.

Methods

Study system and taxa

Madagascar is well-known for possessing high levels of animal and plant endemism (Goodman and Benstead 2005). To date, 292 amphibian species have been named in Madagascar (Perl et al. 2014), with new species still being described (Rosa et al. 2014). Although rich in amphibians, most of which are endemic and resulting from five different radiation events (Crottini et al. 2012), Madagascar has no native species of true toads (Bufonidae) (Glaw and Vences 2007). This distinction is shared with only three other countries: Australia, New Guinea and New Zealand. The endemic *Dyscophus antongili* (tomato frog; Microhylidae) and *Mantella aurantiaca* (golden mantella; Ranidae) are both known to produce toxins (Glaw and Vences 2007).

We focused on the six native carnivore species known to occupy the eastern rainforest region of Madagascar (Fig. 1; Table 1; Goodman 2012). The largest is *C. ferox*, an opportunistic, wide-ranging species that has the most diverse diet of Madagascar's carnivores; while *E. goudotii* is a wide-ranging carnivore that is thought to be restricted to marsh and wetland environments where it feeds primarily on earthworms and various aquatic species, including amphibians (Hawkins 2003; Garbutt 2007; Goodman 2012). The wide-ranging *F. fossana* appears to prefer contiguous forest near streams where it feeds primarily on aquatic species, including amphibians (Kerridge et al. 2003; Goodman 2012). *Galidia elegans* is common throughout degraded forests and near anthropogenic areas where its diet resembles that of the generalist *C. ferox* (Goodman 2003a, 2012). *Galidictis fasciata* appears to be particularly sensitive to degradation and human encroachment, though little is currently known about this carnivore, including its diet (Goodman 2003b, 2012). Finally, *S. concolor* has the most restrictive range of these eastern carnivores, with observations ranging between Betampona Strict Reserve in the south and Makira Natural Park in the north. There is also a lack of baseline data on this carnivore, including knowledge of its diet across its range (Farris et al. 2012; Goodman 2012).

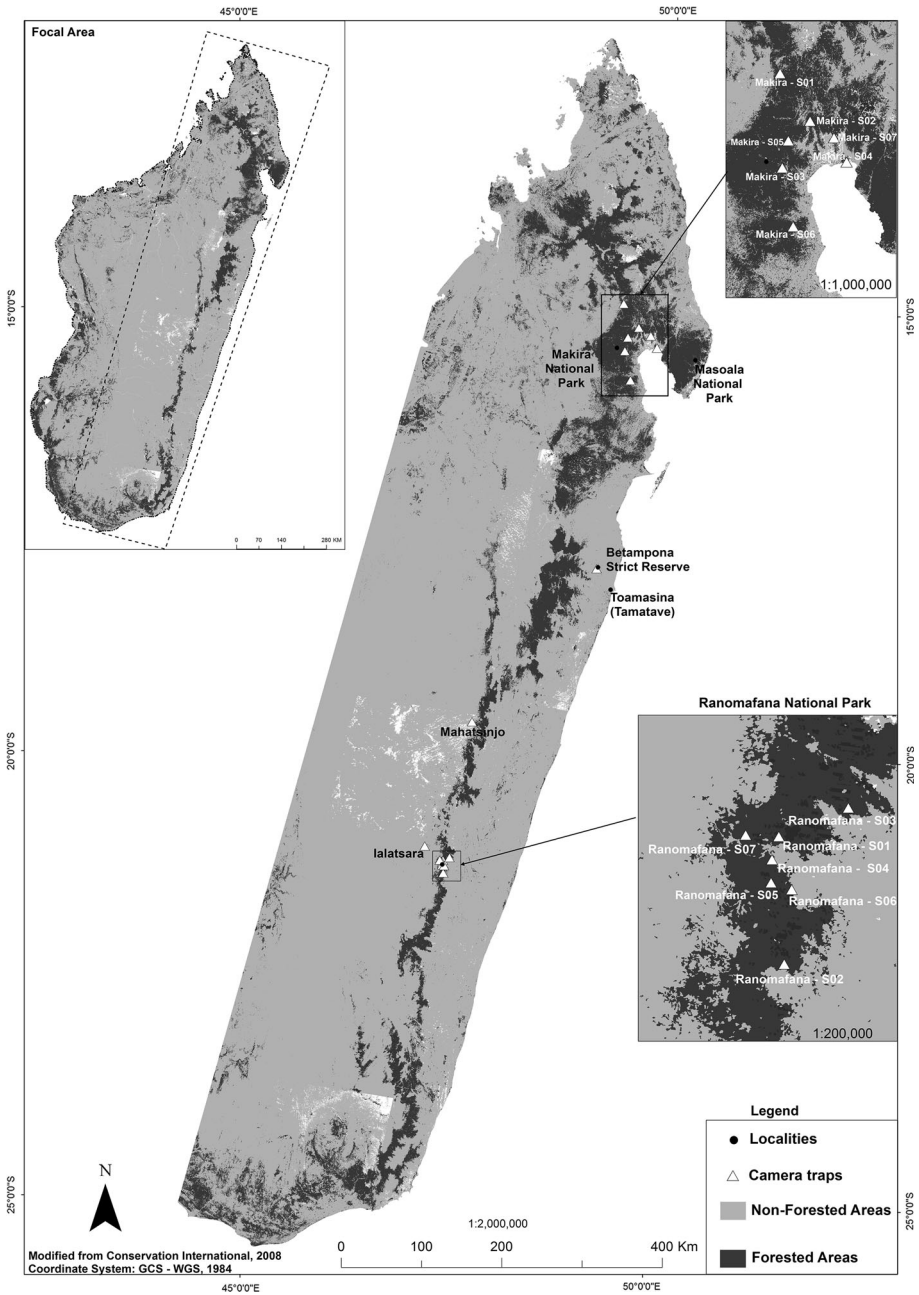


Fig. 1 Site map showing area of focus for the study area in eastern Madagascar, highlighting Masoala, Betampona and Ranomafana National Park (carnivore occurrences from camera traps) and the point source of introduction for *Duttaphrynus melanostictus* (Toamasina). Coordinate system GCS–WGS, 1984

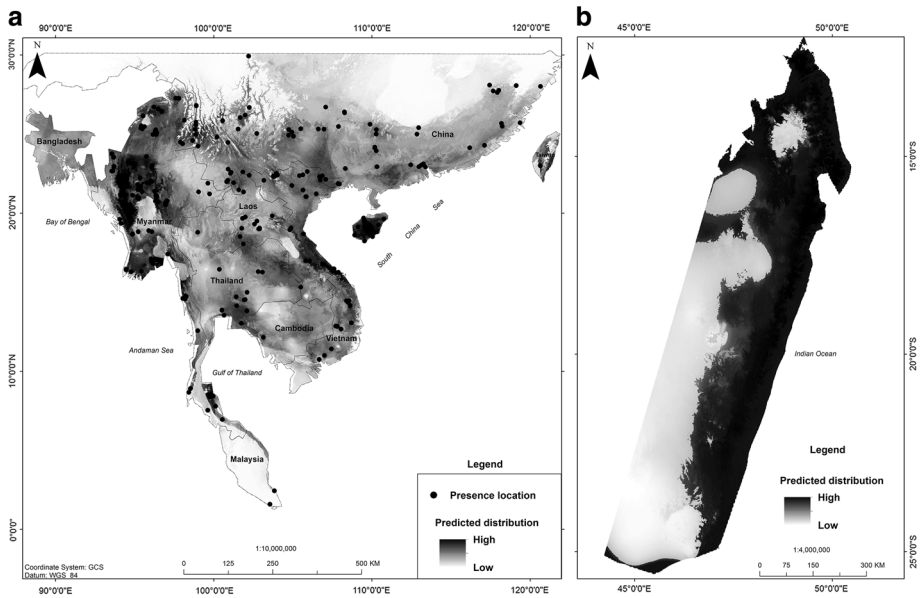


Fig. 2 Predicted distributions for *Duttaphrynus melanostictus* in Asia (native range) and Madagascar (non-native range). **a** Predicted distribution showing occurrence points (circles) used to parameterize model ($N = 426$); mean AUC = 0.925. **b** Predicted distribution for *D. melanostictus* in Madagascar. Model constructed using amphibians, mammals and plants as the background target-groups; mean AUC = 0.984. Darker areas show higher predicted occurrence, lighter areas show lower predictions. Ecological niche models constructed using fivefold cross-validation and Maxent regulation value = 2.0. Coordinate system GCS-WGS, 1984

Species occurrence points for *D. melanostictus* and carnivores

Species occurrence points for the *D. melanostictus* were downloaded from Global Biodiversity Information Facility (GBIF: <http://www.gbif.org/>). *Duttaphrynus melanostictus* has a very broad distribution, ranging from the Maldives to Indonesia; we restricted records to those falling within the core of its known native range to ensure that ENMs were constructed using presence locations from populations at equilibrium with their environments (Van Dijk et al. 2004). After removing duplicate records (occurrences falling within the same grid cell at $\sim 1 \text{ km}^2$), there were 426 presence locations for *D. melanostictus* (Fig. 2).

From 2008 to 2014, presence locations for the six carnivores were collected from camera traps. A total of 198 cameras were deployed across degraded and non-degraded forests and non-forest matrix areas within three eastern rainforest regions in Madagascar: the Masoala-Makira landscape (Farris et al. 2015a), Betampona Strict Reserve (Rasambainarivo, unpublished data), and the Ranomafana region (Gerber et al. 2012b, c) (Fig. 1). Across the Masoala National Park (240,000 ha) and Makira Natural Park (372,470 ha) landscape in NE Madagascar, we surveyed seven sites, ranging from 21–1400 m in elevation, across both degraded and non-degraded forest and located within ($n = 4$) and bordering ($n = 3$) protected areas (Farris et al. 2015b). Within the Betampona Strict Reserve (29,200 ha), we surveyed one site from 138–535 m in elevation, which included both degraded and non-degraded forests (Rasambainarivo, unpublished data). We surveyed two sites (primary and selectively logged) within the Ranomafana National Park (39,900 ha) from 559–1396 m elevation; one fragmented site (<2.5 km from intact forest)

within the Mahatsinjo; Tsinjoarivo Protected Area (a highly fragmented site with 19 fragments less than 7 ha, eight fragments of 10–40 ha and one fragment of 192 ha) from 1342–1643 m elevation; and one fragmented site (>15 km from intact forest) within the Ialatsara Forest Station (~2000 ha) from 1300–1500 m elevation. In addition, we also used camera trap data collected by the Tropical Ecology Assessment and Monitoring (TEAM) Network (Jansen et al. 2014) undertaken by the Centre ValBio research team at Ranomafana National Park. We used data collected in 2010 from three primary rainforest sites within the protected area; these sites did not overlap with two aforementioned surveys within Ranomafana National Park.

At each study site we established camera grids, consisting of 10–31 camera stations per grid which ran for an average (\pm SD) of 61 ± 9 days per site, thus providing 400–1570 trap nights per survey (Gerber 2011; Rasambanarivo unpublished data; Farris 2014). At each camera station we placed two digital (Reconyx PC85 & HC500, Wisconsin, USA; Moultrie D50, D55, MCG12597, & M-880 Alabama, USA; Cuddeback IR, Wisconsin, USA) and/or film-loaded (DeerCam DC300) remote sensing cameras on opposing sides of existing human (0.5–2.0 m wide) and wildlife (<0.5 m wide) trails and spaced camera stations approximately 500–600 m apart. We offset cameras to prevent mutual flash interference and checked cameras every 5–10 days to change batteries, memory cards and/or film, and to ensure proper functioning. We placed cameras 20–30 cm off the ground and allowed them to run for 24 h. At Masoala-Makira and Betampona camera survey grids, no bait or lure was used; however, bait was used at the Ranomafana camera survey grids, but it was found to have no influence on density, maximum movement distances, or activity patterns of carnivores (Gerber et al. 2012a). For all taxa, we restricted the analyses to the eastern escarpment (Fig. 1).

Environmental variables

We used 21 environmental variables for Asia and Madagascar in our ENMs. These included 19 climate variables (Online Resource 1), an elevation layer and the Normalized Difference Vegetation Index (NDVI). Climate variables were obtained from WorldClim database at ca. 1-km resolution and described temperature and precipitation means, seasonality and biologically limiting extremes (Hijmans et al. 2005). The elevation variable was also obtained from WorldClim (Hijmans et al. 2005). We used NDVI to provide information about vegetation cover within our study regions. The NDVI datasets for Madagascar and Asia were downloaded from Copernicus Global Land Service—SPOT vegetation (VGT) portal: (<http://land.copernicus.vgt.vito.be/PDF/portal/Application.html#Home>). SPOT-VGT products are a compilation of satellite imagery data strips acquired in a 10-day maximum vegetation composite circle at a spatial resolution of 1-km. The composites covering Madagascar were acquired on 13 April 2014, and those covering Asia/Oceania were acquired on 25 May 2014. All images were georeferenced to the Geographic Coordinate System and WGS84 ellipsoid. SPOT-VGT sensors have higher revisit periods (more recent), improved radiometric sensitivity (discriminatory ability), reduced geometric distortions (Gobron et al. 2000) and four spectral bands in the visible to near infrared region of the electromagnetic spectrum. Elsewhere they have been determined to have high similarities in inter-annual trends based on phenological parameters and seasonal amplitude with MODIS (Yin et al. 2012). The 21 environmental variables were all resampled to the same resolution (exactly 1-km).

Ecological niche models (ENMs)

Ecological niche models were developed with Maxent software v.3.3. Maxent uses presence-only records to estimate the probability of occurrence for a species, which can then be used to discriminate suitable and unsuitable habitats (Phillips et al. 2006). We used Maxent, as opposed to other ENMs (e.g., BIOCLIM, Boosted Regression Trees, DOMAIN) because: (i) it has been shown to perform well in comparison to other methods (Elith et al. 2006; Pittman and Brown 2011); (ii) techniques can be adopted to improve its overall performance (e.g., target-group background to correct for sampling bias and adjusting regularization multiplier to produce better model fit); and (iii) occurrence records for *D. melanostictus* and carnivores were presence-only.

Occurrence records for *D. melanostictus* were downloaded from GBIF and 21 environmental variables were used to generate ENMs. For *D. melanostictus*, the model was trained for its native habitat in Asia and projected to Madagascar. Since many GBIF occurrence records are taken from herbaria and museums, they may exhibit spatial bias in sampling effort (Reddy and Dávalos 2003). We used target-group background, rather than random background to account for this potential sampling bias in occurrence records (Phillips et al. 2009). The target-group background approach suggests that choosing background data with the same sample selection bias as the occurrence records is likely to increase predictive performance of ENMs (Searcy and Shaffer 2014). We used amphibians, mammals and plants as the target-group, since occurrence records for species within those taxa would have been sampled with a similar bias as *D. melanostictus*. These occurrence records for target-groups were obtained from GBIF. Ecological niche models for carnivores' predicted range were constructed in Madagascar. We developed models for *D. melanostictus* and carnivores using fivefold cross-validation and assessed model performance on the held-out (i.e., test) folds. Receiver-operating characteristic curves (ROC) were constructed for each fold and the area under the curve (AUC) was used to compare model performance (Fielding and Bell 1997). For each fold, we calculated the test omission rate by generating binary predictions using equal sensitivity and specificity and used a one-tail binomial test to assess whether the observed omission rate was greater than expected compared to a random prediction (Anderson et al. 2002). We adjusted regularization multipliers from the default for each species based on preliminary tests that sought to maximize AUC values and minimize overfitting (difference between calibration and evaluation AUC) (Radosavljevic and Anderson 2014). Therefore, we set the Maxent regularization to 2.0 for *D. melanostictus*, as well as for *E. goudotii*, *G. fasciata* and *S. concolor* and the default value of 1.0 for *C. ferox*, *f. fossana* and *G. elegans*. We relied on the default settings for other model parameters. The ENMs developed (for carnivores and toad) were a necessary pre-requisite for quantifying niche breadth and niche overlap, as well as the predicted distribution of *D. melanostictus* in Madagascar and Asia. We have provided the details of those results in supplementary materials (Online Resource 2, 3).

Quantifying niche similarity and overlap

We used a multivariate background test described by McCormack et al. (2010) to quantify the predicted niche overlap between each carnivore and *D. melanostictus*. Unlike some other niche overlap methods (e.g., identity test; Warren et al. 2008, 2010), the background test does not summarize environmental data into a single value, allowing each niche axis to be examined separately. The background test was used to answer the following: will

environmental niches in the predicted invaded area be more or less similar to that found in the native habitat of *D. melanostictus*, and will that lead to high or low predicted niche overlap with Madagascar's carnivores?

Values for the 21 environmental variables were drawn from observed occurrence points for the carnivores and *D. melanostictus*. The common toad's predicted invasion distribution within Madagascar (see "ENMs" section for details) was used for the 'observed' occurrence points and 500 points were randomly chosen within that area. A total of 500 background points were randomly drawn for both carnivores and *D. melanostictus* using ArcGIS v10.1 (ESRI 2012). Carnivores' background points were drawn from their known geographical ranges within Madagascar (Farris et al. 2012; Goodman 2012) and constrained by the vegetation layer (i.e., NDVI), since viable populations for these species were known to only occur in forested habitats. Background points for *D. melanostictus* were drawn from a 1-km buffer surrounding observed occurrences from within its native range (Fig. 2).

The 19 bioclimatic variables were strongly correlated (i.e., $-0.85 > R > 0.85$). To prevent these correlations from biasing results toward detecting only processes associated with temperature or precipitation, we used a principle components analysis (PCA) to derive two independent, uncorrelated climate axes: temperature and precipitation (see Online Resource 1). These climate axes were derived by performing a PCA on the 11 most commonly used temperature variables and eight most commonly used precipitation variables in niche modeling, respectively (Online Resource 1). We extracted scores from the first PCA axis for each species to represent independent temperature and precipitation axes. These two derived climate axes, along with elevation and NDVI, were used as environmental variables in the background tests. This approach allowed a comparison between background environmental variables for *D. melanostictus* and the six carnivores, where all taxa were analyzed across their complete environmental niche breadth.

On each of the four axes, niche overlap was tested against a null model of background divergence by comparing observed mean differences to the differences in mean background values. The null hypothesis is that the mean divergence in background environments is equal to mean divergence in observed niche (on each niche axis assessed). The carnivores' niches were compared to that of *D. melanostictus* and were considered similar (overlap) if the observed value falls below the 95 % CI of the null distribution (i.e., differences between background points are less than differences between the observed occurrence points). We used a two-tailed test to determine significance and performed 1000 bootstrapped replications. These analyses were performed using scripts in R 3.0.3 (R Development Core Team 2012).

Quantifying observed niche breadth and niche overlap

Both estimates of niche breadth and overlap were based on outputs from Maxent-generated ENMs. The degree of habitat specialization was quantified by measuring the niche breadth for each carnivore, which was estimated from predicted suitability values from ENMs. We quantified niche breadth with Levins' (1968) inverse concentration metric, which was scaled such that 0 is minimum and 1 is maximum possible niche breadth over the modeled landscape (Nakazato et al. 2010). We performed a Pearson's correlation between observed niche overlap and niche breadth to determine if habitat specialization influenced the likelihood that environmental niches of carnivores and *D. melanostictus* might converge. Niche overlap between carnivores and *D. melanostictus* was estimated using Schoener's *D* and Hellinger's *I* (Warren et al. 2008), both of which range from 0 (no overlap) to 1

(complete overlap). Niche overlap and niche breadth measurements were implemented in *ENMtools* (Warren et al. 2010) and the correlation was performed in R 3.0.3 (R Development Core Team 2012).

Results

Niche similarity between *D. melanostictus* and carnivores

Overall, results showed strong support for niche overlap between the non-native Asian common toad, *D. melanostictus* and the six endemic carnivores within Madagascar’s eastern rainforest. However, the degree of overlap varied depending on the environmental niche axes considered. The multivariate background test showed a mixture of niche overlap and divergence between *D. melanostictus* and the six carnivores. On the precipitation axis, there was significant overlap between *D. melanostictus* with *C. ferox* and with *G. fasciata*, but no predicted overlap with *E. goudoutii*, *F. fossana*, *G. elegans*, or *S. concolor* (Table 2). There was significant overlap between *D. melanostictus* and five of the carnivores (except *G. fasciata*) on the temperature axis (Table 2). In addition, all carnivores except *C. ferox* showed significant niche overlap with *D. melanostictus* on the NDVI niche

Table 2 Results for observed niche overlap (for Schoener’s *D* and Hellingers *I*, niche breadth and background test between six native carnivores and *D. melanostictus*

	<i>Cryptoprocta ferox</i>	<i>Eupleres goudotii</i>	<i>Fossa fossana</i>	<i>Galidia elegans</i>	<i>Galidictis fasciata</i>	<i>Salanoia concolor</i>
Niche overlap						
D	0.24	0.22	0.26	0.26	0.30	0.28
I	0.54	0.48	0.54	0.54	0.58	0.55
Niche breadth						
	0.05	0.13	0.04	0.07	0.15	0.11
Background test ^a						
Precipitation ^b						
Axis	1.4 (O) (2.4, 3.0)	2.3 (D) (1.4, 2.0)	0.88 (D) (0.06, 0.64)	0.76 (null) (0.67, 1.2)	1.2 (O) (1.4, 2.0)	3.4 (D) (1.7, 2.3)
Temperature ^b						
Axis	2.5 (O) (3.4, 4.1)	1.7 (O) (2.2, 2.9)	3.2 (O) (16.4, 17.0)	3.4 (O) (15.8, 16.5)	2.8 (D) (1.6, 2.2)	0.28 (O) (1.0, 1.8)
NDVI	0.18 (null) (0.17, 0.22)	0.18 (O) (0.23, 0.27)	0.17 (O) (0.22, 0.27)	0.16 (O) (0.19, 0.24)	0.15 (O) (0.22, 0.26)	0.17 (O) (0.24, 0.29)
Elevation	310.0 (null) (217.5, 355.2)	193.8 (O) (380.6, 516.9)	423.0 (null) (343.6, 473.7)	474.3 (null) (430.7, 562.4)	401.0 (null) (383.3, 522.0)	19.20 (O) (33.50, 161.6)

^a Background test shows predicted niche overlap between *Duttaphrynus melanostictus* and six carnivores in Madagascar. Values are based on mean differences between *D. melanostictus* and each species for each variable (and PCA axes). Bold values indicate significant niche overlap (O) or divergence (D) compared to the null model of background divergence between *D. melanostictus* and each species’ respective ranges. The 95 % confidence intervals (CI) from 1000 bootstrapped replicates are shown in parentheses. NDVI refers to Normalized Difference Vegetation Index

^b The climate variables were obtained from WorldClim (Hijmans et al. 2005); we used a principle components analysis (PCA) to derive two independent, uncorrelated climate axes based on 19 climate measures related to precipitation and temperature (see Online Resource 1)

axis (Table 2). Results for elevation were equivocal: *E. goudoutii* and *S. concolor* were predicted to overlap with *D. melanostictus* on that niche axis, while the remaining species were not significantly different from null expectations (Table 2). The first PCA axes explained the greatest amount of variation for each species: *D. melanostictus* = 0.78 and 0.87; *C. ferox* = 0.97 and 0.95; *F. fossana* = 0.96 and 0.92; *E. goudoutii* = 0.98 and 0.85; *G. elegans* = 0.96 and 0.91; *G. fasciata* = 0.95 and 0.93; *S. concolor* = 0.97 and 0.97 for temperature and precipitation, respectively.

There was a significant positive correlation between niche overlap and breadth, where species with broad geographical distributions and less restricted climatic niches also had high overlap with *D. melanostictus*. Results were similar for Schoener's *D* ($R = 0.932$, $t_{0.05, 4} = 4.38$, $P = 0.007$; Table 2) and Hellingers *I* ($R = 0.862$, $t_{0.05, 4} = 2.97$, $P = 0.027$; Table 2). Contrary to expectations, *G. fasciata* and *S. concolor* had among the largest niche breadths (Table 2).

Discussion

Niche similarity and overlap: background test

This study helps to predict the extent of an incipient invasion in a top biodiversity hotspot and suggests considerable niche overlap between naïve native predators and a non-native toxic prey. The potential spread of the Asian common toad, *D. melanostictus*, across Madagascar's eastern rainforest presents an additional threat to the six endemic carnivore species occupying these forests and represents a pressing management issue demanding targeted control efforts. Our finding that *D. melanostictus* and five of six carnivores in this study are predicted to overlap along the temperature axis is consistent with the conclusion that carnivores and this non-native toad are likely to have similar climatic niche characteristics (Online Resource 2, 3 and Pearson 2015), particularly due to the similar temperature regimes between the eastern region of Madagascar and *D. melanostictus*' native range in Asia (Kolby 2014). Generally, Madagascar's carnivores show dependence on intact forest and appear to be highly sensitive to forest degradation and fragmentation (Gerber et al. 2012c; Goodman 2012; Farris et al. 2015b). Therefore, our finding that *D. melanostictus* may converge with five of the carnivores on the vegetation cover niche axis (a non-climate variable) is also of major concern; this suggests that the toad is capable of expanding beyond its current distribution in Madagascar, which for the moment remains within the urban area of Toamasina and nearby disturbed forests (Moore et al. 2015). Model results indicating that *D. melanostictus* and *S. concolor* overlap on three of the four environmental axes (except precipitation) were unexpected given the restrictive elevation range of *S. concolor* within a portion of the eastern Madagascar rainforest (Farris et al. 2012; Goodman 2012). Similarly surprising was the lack of observed niche overlap between *D. melanostictus* and *C. ferox* along NDVI and elevation axes, since the latter is one of Madagascar's most wide-ranging carnivores and is known to move through primary, degraded, and non-forest habitats (Hawkins 2003; Gerber et al. 2012c). It is unclear whether this result is an artefact of the modeling technique (i.e., background test) or due to exclusion of relevant climate and environmental variables (see below). The niche breadth results for *G. fasciata* and *S. concolor* run contrary to our expectations, as they were predicted to have narrow ranges and restricted environmental niches. The best explanation for this is that although these species are widespread, they are locally rare and ENMs on

which the niche breadth measurement is based are unable to capture the complexity of their habitat selection. Given the high niche overlap with *D. melanostictus*, such species nonetheless may be more likely to encounter the toad and potentially consume it. These two rare carnivores consistently have the lowest probabilities of occurrence across eastern rainforest habitats (Farris et al. 2015b; Gerber et al. 2012c) and the potential for additive mortality resulting from the consumption of *D. melanostictus* poses even greater risk for these little known species.

This study offers valuable information about potential interactions between an incipient invader and native species across trophic levels; however, we advocate a degree of caution when using background tests to infer local-scale processes from large-scale spatial analyses as presented here. Although the background test can assess the differential use of habitats within larger ranges (McCormack et al. 2010), it may be difficult to ascertain potential niche overlap at small spatial scales, which may further complicate conservation approaches for species with narrow ranges and restricted environmental niches. For instance, environmental niche axes showed conflicting patterns of overlap for each species (e.g., overlap, divergence, and no difference from null) and none of the carnivores was predicted to overlap with *D. melanostictus* on all axes. This suggests that niche overlap is likely to be driven by multiple environmental determinants. It would therefore be informative to investigate whether local-scale trophic interactions between *D. melanostictus* and these carnivores are likely to be driven by all or a suite of environmental variables used in this study to elucidate potential patterns of overlap and areas of direct interaction. Of equal importance to appropriate spatial scales is the selection of relevant climate and environmental variables when developing the background test (Elith and Leathwick 2009; Warren 2012). We note that although it is possible for divergence to occur along niche dimensions not included in our study, the PCA axes used for this analysis, as well as elevation and vegetation cover, accounted for variables likely to be biologically relevant to both *D. melanostictus* and these carnivores. They are also the most common environmental variables in niche modeling, suggesting that these results are robust or at least comparable.

Management and conservation implications

One of the conservation priorities vis-à-vis the introduction of *D. melanostictus* should be monitoring the carnivore fauna in Madagascar and developing management actions tailored for these animals. Specifically, we recommend tracking toad incursions across relatively large areas and multiple, distinct habitat types within their range using walking transects, drift fences and pit-fall traps. Additionally, surveys of *D. melanostictus* and carnivores should be conducted in forest fragments near the invasion area and repeat surveys within protected areas near Toamasina (e.g., Corridor Ankeniheny Zahamena (CAZ), Mangerivola Reserve and Betampona Reserve). Our results suggest that particular attention should be given to *E. goudotii* and *S. concolor* due to a combination of high predicted niche similarity with *D. melanostictus*, biodiversity benefit (i.e., localized rarity), and scarcity of information concerning their natural history, behavior, and ecology. We should also note that the point source for the introduction of *D. melanostictus* (Toamasina) is in close proximity to the range of *S. concolor* and may warrant the closest monitoring. The results for *G. fasciata* were equivocal. Indeed, despite being locally rare, both *G. fasciata* and *S. concolor* exhibited high niche breadth values. *Fossa fossana* and *G. elegans* appear to be widespread, generalist carnivores with a highly variable diet and ability to occupy a wide range of habitat types (Goodman 2012). The expansive occurrence and broad diet of these carnivores may increase encounter rates with—and consumption rates

of—*D. melanostictus*; however, their adaptability, including an ability to persist despite numerous anthropogenic pressures may not warrant the same conservation management response as required for the other native carnivores. As mentioned, we lack much information on the natural history and ecology of these carnivores, as well as *D. melanostictus*, and increasing our knowledge of these species will allow us to more accurately identify and mitigate threats posed by their emergent interactions in Madagascar.

Effective control or eradication of *D. melanostictus* will likely require multi-faceted approaches. The most cost effective post-introduction strategy is a swift and targeted eradication program while population sizes remain small (Kolby 2014) and it should be undertaken within the urban, agricultural, and *Eucalyptus* forest areas highlighted by Moore et al. (2015) and McClelland et al. (2015). Both Pearson (2015) and our results (Online Resource 2, 3) suggest that targeted conservation action should focus within this region since the invasion path of *D. melanostictus* will most likely extend from Toamasina along the eastern escarpment. However, Mecke (2014) warns that eradication may have unintended consequences to co-occurring native species and the ecosystems they occupy, while Andreone (2014) argues swift action is likely to be vital for diminishing the initial widespread invasion of *D. melanostictus*. Other studies highlight the importance of understanding the ecology and behavior of IAS, particularly within their novel environment, prior to developing a management strategy (Ward-Fear et al. 2010). Particular attention should also be given to documenting whether the range of *D. melanostictus* becomes coincident with any of these carnivores, as well as other predators not included in our analyses (e.g., *Acrantophis madagascariensis*, Madagascar ground boa). Early and continued monitoring of *D. melanostictus*—as is occurring with the Amphibian Specialist Group in Madagascar—will enable researchers to detect possible niche shifts that may allow it to spread to the interior and more semi-arid regions of the island (e.g., dry deciduous forest).

Finally, recent photographic sampling and population modeling for Madagascar's carnivore community occupying eastern rainforest habitat has pointed to the precipitous increase in exotic carnivore species (small Indian civet *Viverricula indica*, domestic dog *Canis familiaris*, and feral cat *Felis species*) occupying primarily degraded forest and non-forest areas (Gerber et al. 2012c; Farris et al. 2015b). The spatial and temporal overlap among native carnivores and a burgeoning exotic carnivore population suggests increased interactions across the landscape (Farris et al. 2015c; Farris et al. In press). In addition, these exotic carnivores are a nuisance and threat to Malagasy people as they consume domestic poultry and spread disease to native wildlife, domestic pets, livestock, and potentially humans (Brockman et al. 2008; Gerber et al. 2012b; Goodman 2012; Kotschwar et al. 2014; Farris et al. 2015a). It is possible that the toxic *D. melanostictus* may help control exotic carnivore populations occupying degraded and non-forested areas across the Toamasina region (S. Goodman, pers. comm.) given that these species have been observed and/or are believed to consume frogs across their range. Additional research is needed on the diet and behavior of these exotic carnivores to determine if they will consume the toad and what impact this interaction may have on the distributions of both predators and prey.

The underlying assumption here is that overlap between a carnivore and *D. melanostictus* along one or more niche dimensions will lead to consumption or other direct interaction. We also assume that carnivores that eat *D. melanostictus* will be susceptible to its toxins and are therefore at risk since their populations may not be robust enough to adapt quickly to this emergent threat. The likelihood of these scenarios occurring is difficult to estimate. We know that mammals are behaviorally adept at switching prey and can have high tolerance for toad toxins (Beckmann and Shine 2009). Despite that observation,

populations of snakes, crocodiles, and carnivorous mammals declined dramatically during *Rhinella marina* (formerly *Bufo marinus*; cane toad) invasion of Australia (Shine 2010). Rather than diminish our results, these caveats suggest that the Asian common toad invasion should be closely monitored to determine whether Madagascar's carnivore fauna does consume this novel prey item and, if so, the extent to which their populations are negatively affected.

Conclusions

Madagascar's ecosystems contain some of the highest levels of biodiversity in the world, but are highly susceptible to—and already suffer from—alien invasive species. Our study highlights a nascent threat to the poorly-studied endemic carnivore community already threatened by a wide range of anthropogenic pressures. It provides evidence from niche models suggesting that eastern rainforest carnivores will likely overlap with this potential prey species. These results should be used to inform a strategy for tracking the spread of the Asian common toad through a pre-invasion risk assessment that determines the ecological niche dimensions that predators and prey may share. More targeted conservation actions can then concentrate on areas with environmental conditions that fall within limits known to drive niche similarity between the toad and carnivores. For example, conservation authorities might focus on marsh or stream locations within forest habitats where *D. melanostictus* and *E. goudotii* are likely to have the greatest number of interactions. We advocate closely monitoring carnivores that are likely to overlap with *D. melanostictus* on multiple niche dimensions, particularly *E. goudotii* and *S. concolor*. Moreover, given the potential overlap with all endemic carnivores, we advocate preemptive strategies and action plans of McClelland et al. (2015) to slow toad incursions and to eradicate or reduce their populations. In particular, we point to the need for the establishment of biosecurity measures to prevent the spread of toads to new areas, density estimation of toads within and bordering the invasion area, implementation and testing of a wide-range of detection and removal techniques, and establishment of a local governance and leadership body to oversee these efforts. We suggest these management actions, when combined with repeat, wide-ranging photographic surveys of carnivore populations, will provide robust population and range assessments and allow managers to monitor the impact of *D. melanostictus* on Madagascar's threatened carnivore community.

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References

- Albignac R (1972) The carnivora of Madagascar. In: Biogeography and ecology in Madagascar. Springer, pp 667–682
- Albignac R, Jolly A, Oberle P, Albignac R (1984) The carnivores. In: Jolly A, Oberle P, Albignac R (eds) Key environments: Madagascar. Pergamon Press, Oxford, pp 167–182
- Anderson RP, Peterson AT, Gomez-Laverde M (2002) Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos* 98:3–16
- Andreone F (2014) Risk review is under way for invasive toad. *Nature* 512:253
- Beckmann C, Shine R (2009) Impact of invasive cane toads on Australian birds. *Conserv Biol* 23:1544–1549. doi:[10.1111/J.1523-1739.2009.01261.X](https://doi.org/10.1111/J.1523-1739.2009.01261.X)
- Britt A, Virkaitis V (2003) Brown-tailed Mongoose *Salanoia concolor* in the Betampona Reserve, eastern Madagascar: photographs and an ecological comparison with ring-tailed Mongoose *Galidia elegans*. *Small Carniv Conserv* 28:1–3
- Britt A, Welch C, Katz A (2001) The impact of *Cryptoprocta ferox* on the *Varecia v. variegata* reinforcement project at Betampona. *Lemur News* 6:35–37
- Brockman DK, Godfrey LR, Dollar LJ, Ratsirarson J (2008) Evidence of invasive *Felis silvestris* predation on *Propithecus verreauxi* at Beza Mahafaly Special Reserve, Madagascar. *Int J Primatol* 29:135–152
- Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. *Biol Lett* 4:585–589. doi:[10.1098/Rsbl.2008.0254](https://doi.org/10.1098/Rsbl.2008.0254)
- Broennimann O, Treier UA, Muller-Scharer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. *Ecol Lett* 10:701–709. doi:[10.1111/J.1461-0248.2007.01060.X](https://doi.org/10.1111/J.1461-0248.2007.01060.X)
- Brown KA, Spector S, Wu W (2008) Multi-scale analysis of species introductions: combining landscape and demographic models to improve management decisions about non-native species. *J Appl Ecol* 45:1639–1648. doi:[10.1111/J.1365-2664.2008.01550.X](https://doi.org/10.1111/J.1365-2664.2008.01550.X)
- Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM (2004) Human population density and extinction risk in the world's carnivores. *PLoS Biol* 2:909–914. ARTN e197. doi: [10.1371/journal.pbio.0020197](https://doi.org/10.1371/journal.pbio.0020197)
- Cassey P, Hogg CJ (2015) Escaping captivity: the biological invasion risk from vertebrate species in zoos. *Biol Conserv* 181:18–26. doi:[10.1016/J.Biocon.2014.10.023](https://doi.org/10.1016/J.Biocon.2014.10.023)
- Chen KK, Kovarikova A (1967) Pharmacology and toxicology of toad venom. *J Pharm Sci* 56:1535–1541
- Costa GC, Wolfe C, Shepard DB, Caldwell JP, Vitt LJ (2008) Detecting the influence of climatic variables on species distributions: a test using GIS niche-based models along a steep longitudinal environmental gradient. *J Biogeogr* 35:637–646
- Crawford AJ, Lips KR, Bermingham E (2010) Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of central Panama. *Proc Natl Acad Sci USA* 107:13777–13782. doi:[10.1073/Pnas.0914115107](https://doi.org/10.1073/Pnas.0914115107)
- Crottini A, Madsen O, Poux C, Strauß A, Vieites DR, Vences M (2012) Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K-T boundary in Madagascar. *Proc Nat Acad Sci* 109:5358–5363
- Dollar L (1999) Preliminary report on the status, activity cycle, and ranging of *Cryptoprocta ferox* in the Malagasy rainforest, with implications for conservation. *Small Carniv Conserv* 20:7–10
- Dunham AE (1998) Notes on the behavior of the Ring-tailed mongoose, *Galidia elegans*, at Ranomafana National Park, Madagascar. *Small Carniv Conserv* 19:21–24
- Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annu Rev Ecol Evol Syst* 41:59–80
- Elith J et al (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151
- Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Evol Syst* 40(1):677
- ESRI (2012) ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, Redlands
- Farris ZJ (2014) Response of Madagascar's endemic carnivores to fragmentation, hunting, and exotic carnivores across Masoala-Makira landscape. Dissertation, Virginia Tech, Blacksburg
- Farris ZJ, Kelly MJ, Karpanty SM, Ratelolahy F, Andrianjakarivelo V, Holmes C (2012) Brown-tailed *Vontsira Salanoia concolor* (Eupleridae) documented in Makira Natural Park, Madagascar: new insights on distribution and camera-trap success. *Small Carniv Conserv* 47:82–86

- Farris ZJ, Karpanty SM, Ratelolahy F, Kelly MJ (2014) Predator–primate distribution, activity, and co-occurrence in relation to habitat and human activity across fragmented and contiguous forests in northeastern Madagascar. *Int J Primatol* 35:859–880
- Farris ZJ, Gerber B, Karpanty SM, Murphy A, Ratelolahy F, Kelly MJ (2015a) When carnivores roam: temporal patterns and partitioning among Madagascar's native and exotic carnivores. *J Zool* 296:45–57. doi:[10.1111/jzo.12216](https://doi.org/10.1111/jzo.12216)
- Farris ZJ et al (2015b) Hunting, exotic carnivores, and habitat loss: anthropogenic effects on a native carnivore community, Madagascar. *PLoS One* 10:e0136456
- Farris ZJ, Kelly MJ, Karpanty SM, Ratelolahy F (2015c) Patterns of spatial co-occurrence among native and exotic carnivores in NE Madagascar. *Anim Conserv*. doi:[10.1111/acv.12233](https://doi.org/10.1111/acv.12233)
- Farris ZJ, Gerber B, Kelly MJ, Karpanty SM, Ratelolahy F, Andrianjakarivelo V (In press) Spatio-temporal overlap between a native and exotic carnivore in Madagascar: evidence of spatial exclusion. In: Do Linh San E, Sato JJ, Belant JL, Somers MJ (eds) *Small carnivores: evolution, ecology, behaviour and conservation*. Wiley, Chichester
- Faulkner KT, Robertson MP, Rouget M, Wilson JR (2014) A simple, rapid methodology for developing invasive species watch lists. *Biol Conserv* 179:25–32. doi:[10.1016/j.biocon.2014.08.014](https://doi.org/10.1016/j.biocon.2014.08.014)
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ Conserv* 21:38–49
- Fisher DO, Blomberg SP, Owens IPF (2003) Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proc R Soc B* 270:1801–1808. doi:[10.1098/Rspb.2003.2447](https://doi.org/10.1098/Rspb.2003.2447)
- Garbutt N (2007) *Mammals of Madagascar: a complete guide*. Yale University Press, New Haven
- Gerber BD (2011) Comparing density analyses and carnivore ecology in Madagascar's southeastern rainforest. Masters Thesis, Virginia Tech, Blacksburg
- Gerber BD, Karpanty SM, Kelly MJ (2012a) Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. *Popul Ecol* 54:43–54
- Gerber BD, Karpanty SM, Randrianantenaina J (2012b) Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. *J Mammal* 93:667–676
- Gerber BD, Karpanty SM, Randrianantenaina J (2012c) The impact of forest logging and fragmentation on carnivore species composition, density and occupancy in Madagascar's rainforests. *Oryx* 46:414–422
- Glaw F, Vences M (2007) *A field guide to the amphibians and reptiles of Madagascar*, 3rd edn. Vences and Glaw Verlag, Köln
- Gobron N, Pinty B, Verstraete MM, Widlowski JL (2000) Advanced vegetation indices optimized for upcoming sensors: design, performance, and applications. *IEEE Trans Geosci Remote Sens* 38:2489–2505
- Godsoe W, Case BS (2015) Accounting for shifts in the frequency of suitable environments when testing for niche overlap. *Methods Ecol Evol* 6:59–66. doi:[10.1111/2041-210x.12307](https://doi.org/10.1111/2041-210x.12307)
- Goodman S (2003a) Carnivora: *Galidia elegans*, ring-tailed Mongoose, Vontsira mena. In: Goodman S, Benstead JP (eds) *The natural history of Madagascar*. The University of Chicago Press, Chicago, pp 1351–1354
- Goodman S (2003b) Carnivora: *Galidictis fasciata*, Broad-striped Mongoose, Vontsira fotsy. In: Goodman S, Benstead JP (eds) *The natural history of Madagascar*. The University of Chicago Press, Chicago, pp 1354–1357
- Goodman S (2003c) Predation on lemurs. In: Goodman S, Benstead JP (eds) *The natural history of Madagascar*. The University of Chicago Press, Chicago, pp 1159–1186
- Goodman SM (2012) *Les Carnivora de Madagascar*. Association Vahatra, Antananarivo
- Goodman SM, Benstead JP (2005) Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* 39:73–77. doi:[10.1017/S0030605305000128](https://doi.org/10.1017/S0030605305000128)
- Goodman SM, Pidgeon M (1999) Carnivora of the reserve naturelle integrale d'Andohahela Madagascar. *Fieldiana Zool* 94:259–268
- Goodman S, Langrand O, Rasolonandrasana B (1997) The food habits of *Cryptoprocta ferox* in the high mountain zone of the Andringitra Massif, Madagascar (Carnivora, Viverridae). *Mammalia* 61:185–192
- Hawkins CE (1998) Behaviour and ecology of the fossa, *Cryptoprocta ferox* (Carnivora: Viverridae) in a dry deciduous forest, western Madagascar. University of Aberdeen, Scotland
- Hawkins C (2003) *Cryptoprocta ferox*, fossa, fosa. In: Goodman SM, Benstead JP (eds) *The natural history of Madagascar*. University of Chicago Press, Chicago, pp 1360–1363
- Hawkins CE, Racey PA (2005) Low population density of a tropical forest carnivore, *Cryptoprocta ferox*: implications for protected area management. *Oryx* 39:35–43
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978. doi:[10.1002/Joc.1276](https://doi.org/10.1002/Joc.1276)

- Inderjit (2005) Plant invasions: habitat invasibility and dominance of invasive plant species. *Plant Soil* 277:1–5. doi:[10.1007/S11104-004-6638-2](https://doi.org/10.1007/S11104-004-6638-2)
- IUCN (2016) The IUCN red list of threatened species Version 2016.1. www.iucnredlist.org. Accessed June 2016
- Jansen P, Ahumada J, Fegraus E, O'Brian T (2014) TEAM: a standardised camera trap survey to monitor terrestrial vertebrate communities in tropical forests. In: Camera trapping: wildlife management and research. CSIRO Publishing, Melbourne, pp 263–270
- Julliard R, Clavel J, Devictor V, Jiguet F, Couvet D (2006) Spatial segregation of specialists and generalists in bird communities. *Ecol Lett* 9:1237–1244. doi:[10.1111/J.1461-0248.2006.00977.X](https://doi.org/10.1111/J.1461-0248.2006.00977.X)
- Kerridge F, Ralisoamalala R, Goodman S, Pasnick S (2003) *Fossa fossana*, Malagasy striped civet, Fanaloka. In: Benstead SGJ (ed) The natural history of Madagascar. The University of Chicago Press, Chicago, pp 1363–1365
- Kolby JE (2014) Stop Madagascar's toad invasion now. *Nature* 509:563
- Kotschwar M, Gerber B, Karpanty SM, Justin S, Rabenahy F (2014) Assessing carnivore distribution from local knowledge across a human-dominated landscape in central-southeastern Madagascar. *Anim Conserv* 18:82–91. doi:[10.1111/acv.12137](https://doi.org/10.1111/acv.12137)
- Kull CA, Tassin J, Carriere SM (2014) Approaching invasive species in Madagascar. *Madag Conserv Dev* 9:60–70
- Levins R (1968) Evolution in changing environments. Monographs in population biology, vol 2. Princeton University Press, New Jersey
- Lührs ML, Kappeler PM (2013) Simultaneous GPS tracking reveals male associations in a solitary carnivore. *Behav Ecol Sociobiol* 67:1731–1743
- McClelland P, Reardon J, Kraus F, Raxworthy C, Randrianantoandro C (2015) Asian toad eradication feasibility report for Madagascar. Te Anau, New Zealand
- McCormack JE, Zellmer AJ, Knowles LL (2010) Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation?: insights from tests with niche models. *Evolution* 64:1231–1244. doi:[10.1111/J.1558-5646.2009.00900.X](https://doi.org/10.1111/J.1558-5646.2009.00900.X)
- Mecke S (2014) Review risks before eradicating toads. *Nature* 511:534
- Meyer JY, Pouteau R, Spotswood E, Taputuarai R, Fourdrigniez M (2015) The importance of novel and hybrid habitats for plant conservation on islands: a case study from Moorea (South Pacific). *Biodivers Conserv* 24:83–101. doi:[10.1007/S10531-014-0791-6](https://doi.org/10.1007/S10531-014-0791-6)
- Moore M, Fidy JF, Edmonds D (2015) The new toad in town: distribution of the Asian toad, *Duttaphrynus melanostictus*, in the Toamasina area of eastern Madagascar. *Trop Conserv Sci* 8:440–455
- Nakazato T, Warren DL, Moyle LC (2010) Ecological and geographic modes of species divergence in wild tomatoes. *Am J Bot* 97:680–693. doi:[10.3732/Ajb.0900216](https://doi.org/10.3732/Ajb.0900216)
- Ordóñez A (2014) Global meta-analysis of trait consistency of non-native plants between their native and introduced areas. *Global Ecol Biogeogr* 23:264–273. doi:[10.1111/Geb.12123](https://doi.org/10.1111/Geb.12123)
- Pearson RG (2015) Asian common toads in Madagascar: an urgent effort to inform surveys and eradication efforts. *Global Change Biol* 21:9. doi:[10.1111/Gcb.12693](https://doi.org/10.1111/Gcb.12693)
- Perl RB, Nagy ZT, Sonet G, Glaw F, Wollenberg KC, Vences M (2014) DNA barcoding Madagascar's amphibian fauna. *Amphib-Reptil* 35:197–206
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Model* 190:231–259
- Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol Appl* 19:181–197
- Pittman SJ, Brown KA (2011) Multi-scale approach for predicting fish species distributions across coral reef seascapes. *PLoS One* 6:e20583. doi:[10.1371/journal.pone.0020583](https://doi.org/10.1371/journal.pone.0020583)
- R Development Core Team (2012) R: A language and environment for statistical computing. Vienna, Austria
- Radosavljevic A, Anderson RP (2014) Making better MAXENT models of species distributions: complexity, overfitting and evaluation. *J Biogeogr* 41:629–643. doi:[10.1111/Jbi.12227](https://doi.org/10.1111/Jbi.12227)
- Rasoloarison R, Rasolonandrasana B, Ganzhorn J, Goodman S (1995) Predation on vertebrates in the Kirindy Forest, western Madagascar. *Ecotropica* 1:59–65
- Reaser JK, Meyerson LA, Von Holle B (2008) Saving camels from straws: how propagule pressure-based prevention policies can reduce the risk of biological invasion. *Biol Invasions* 10:1085–1098. doi:[10.1007/S10530-007-9186-X](https://doi.org/10.1007/S10530-007-9186-X)
- Rebollar EA, Hughey MC, Harris RN, Domangue RJ, Medina D, Ibanez R, Belden LK (2014) The lethal fungus *Batrachochytrium dendrobatidis* is present in lowland tropical forests of far eastern Panama. *PLoS One* 9:e95484. doi:[10.1371/journal.pone.0095484](https://doi.org/10.1371/journal.pone.0095484)

- Reddy S, Dávalos LM (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *J Biogeogr* 30:1719–1727
- Rosa GM, Crottini A, Noel J, Rabibisoa N, Raxworthy CJ, Andreone F (2014) A new phytotelmic species of *Platypelis* (Microhylidae: cophylinae) from the Betampona Reserve, eastern Madagascar. *Salamandra* 50:201–214
- Searcy CA, Shaffer HB (2014) Field validation supports novel niche modeling strategies in a cryptic endangered amphibian. *Ecography* 37:983–992
- Shine R (2010) The ecological impact of invasive cane toads (*Bufo Marinus*) in Australia. *Quat Rev Biol* 85:253–291
- Srinivasulu C, Das I (2008) The herpetofauna of Nallamala Hills, Eastern Ghats, India: an annotated checklist, with remarks on nomenclature, taxonomy, habitat use, adaptive types and biogeography. *Asiat Herpetol Res* 11:110–131
- Thuiller W, Richardson DM, Pysek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biol* 11:2234–2250. doi:[10.1111/J.1365-2486.2005.01018.X](https://doi.org/10.1111/J.1365-2486.2005.01018.X)
- Thuiller W, Gasso N, Pino J, Vila M (2012) Ecological niche and species traits: key drivers of regional plant invader assemblages. *Biol Invasions* 14:1963–1980. doi:[10.1007/S10530-012-0206-0](https://doi.org/10.1007/S10530-012-0206-0)
- Van Dijk P et al (2004) *Duttaphrynus melanostictus*. In: The IUCN red list of threatened species 2004: e. T54707A11188511
- Ward-Fear G, Brown GP, Shine R (2010) Factors affecting the vulnerability of cane toads (*Bufo marinus*) to predation by ants. *Biol J Linn Soc* 99:738–751
- Warren DL (2012) In defense of ‘niche modeling’. *Trends ecol evol* 27(9):497–500
- Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62:2868–2883. doi:[10.1111/J.1558-5646.2008.00482.X](https://doi.org/10.1111/J.1558-5646.2008.00482.X)
- Warren DL, Glor RE, Turelli M (2010) ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33:607–611. doi:[10.1111/J.1600-0587.2009.06142.X](https://doi.org/10.1111/J.1600-0587.2009.06142.X)
- Wood JR, Dickie IA, Moeller HV, Peltzer DA, Bonner KI, Rattray G, Wilmshurst JM (2015) Novel interactions between non-native mammals and fungi facilitate establishment of invasive pines. *J Ecol* 103:121–129. doi:[10.1111/1365-2745.12345](https://doi.org/10.1111/1365-2745.12345)
- Wright P, Heckscher S, Dunham A (1997) Predation on Milne-Edward’s sifaka (*Propithecus diadema edwardsi*) by the fossa (*Cryptoprocta ferox*) in the rain forest of southeastern Madagascar. *Folia Primatol* 68:34–43
- Yin H, Udelhoven T, Fensholt R, Pflugmacher D, Hostert P (2012) How normalized difference vegetation index (NDVI) trends from advanced very high resolution radiometer (AVHRR) and système probatoire d’observation de la terre vegetation (spot vgt) time series differ in agricultural areas: an inner-mongolian case study. *Remote Sens* 4:3364–3389. doi:[10.3390/Rs4113364](https://doi.org/10.3390/Rs4113364)