Short communication

Distributional shifts in a biodiversity hotspot

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ABSTRACT

Identifying ongoing changes in the distributions of species is critical for understanding and conserving biological diversity. Distributional shifts have been demonstrated in many ecosystems and taxa, yet the extent and nature of these changes remain largely undocumented for tropical forest mammals. Shifts over short time periods can be particularly alarming in areas of the world where mammals are already under threat as a result of human activities. This is the case for Madagascar, an island where deforestation, hunting, invasive species, and other human threats have resulted in the extinction of several endemic species. Here, we ask, are the distributions of Malagasy mammals changing? We test this by modeling local colonization and extinction dynamics, which are the biological processes that produce distributional shifts. We use camera trap data from the TEAM Network for four species along a 570 m elevational gradient in Ranomafana National Park, Madagascar. The endemic Eastern red forest rat (*Nesomys rufus*) declined in overall occupancy while the non-native bushpig (*Potamochoerus larvatus*) increased in occupancy overall. The two endemic carnivore species shifted their elevational use: the Malagasy ring-tailed mongoose (*Galidia elegans*) retracted from higher elevations and the Malagasy civet (*Fossa fossana*) moved to higher elevations, likely in response to anthropogenic pressures. These results show that shifts are occurring and we can detect them with just six years of data. These results appear near unique in documenting rapid changes in the spatial distributions of tropical forest mammals and provide important information for conservation.

1. Introduction

Multiple anthropogenic factors simultaneously threaten biological diversity worldwide (Pimm et al., 2014). This is particularly true in biodiversity hotspots where diversity, levels of endemism, and human threats are high (Myers et al., 2000). Land use change has caused extensive habitat loss globally (Haddad et al., 2015) and is considered a primary cause of species loss (Schipper et al., 2008). Anthropogenic greenhouse gas emissions have driven global climate change, which is

predicted to become a major cause of species loss over the next century (Pimm et al., 2014). Changes in climate are associated with changes in the distributions of many taxa in diverse ecosystems (Parmesan, 2006), notably rapid shifts towards higher latitudes and elevations in response to warming temperatures (Chen et al., 2011). Furthermore, invasive alien species threaten the persistence of many species (Bellard et al., 2016). These threats can interact to result in rapid retractions that are particularly concerning because rapid retractions can lead to extinction (Wiens, 2016). Given the multiplicity of anthropogenic threats,

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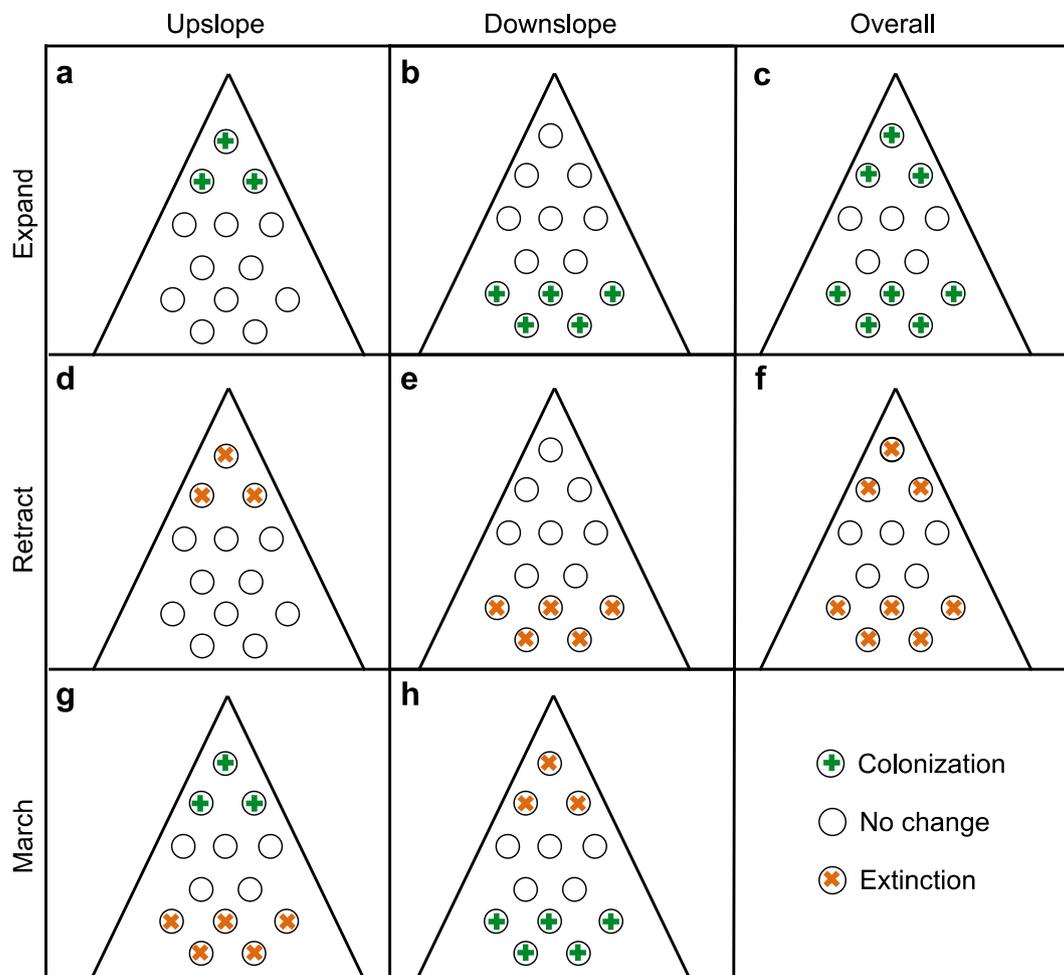
Fig. 1. Framework for modeling elevation shifts from dynamic occupancy models. Triangles depict elevation gradients and circles represent camera trap sampling locations. Green symbols (+) illustrate the net increase in occupancy from local colonization and extinction, orange symbols (×) illustrate the net decrease in occupancy from local colonization and extinction, and white circles illustrate no change in occupancy. The diagram depicts three types of elevation shifts: "expand" (a) upslope, (b) downslope or (c) overall, "retract" from (d) higher elevations (e) lower elevations or (f) overall, "march" (g) upslope or (h) downslope. Figure operationalizes aspects of a conceptual diagram from Lenoir and Svenning (2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

modeling changes in species distributions as they occur is essential for effective conservation planning.

Identifying ongoing changes in distribution requires reliable, up to date data on species occurrences. Field observations of animal occurrences are often incomplete because quantifying all individuals in a given area is unfeasible. Such "imperfect detection" can bias results if not accounted for because non-occurrence and non-detection are confounded. A number of statistical approaches have been developed to address this by simultaneously estimating the probabilities of detection and occurrence (i.e., occupancy) (MacKenzie et al., 2006). Dynamic occupancy models that account for imperfect detection offer a robust framework for modeling species distributions by estimating the processes that underlie range shifts - local colonization and extinction (Kery et al., 2013). The requisite data are typically collected through systematic field observations, such as point counts (Weir et al., 2009), and passive automatic sensors, such as camera traps or audio recorders (Acevedo and Villanueva-Rivera, 2006; Campos-Cerqueira and Aide, 2016). Pairing dynamic occupancy models with camera trap data permits the evaluation of changes in the distributions of elusive and difficult to study species, including many tropical forest mammals.

Tropical forests, and in particular those occurring on mountains, contain much of the world's biodiversity (Quintero and Jetz, 2018), including a large proportion of endemic species, which face elevated

extinction risk (Fjeldsa et al., 2012). Despite the fact that mammal diversity is concentrated in the tropics, the availability of time-series data for evaluating changes in tropical species' distributions is sparse (Collen et al., 2008; Dornelas et al., 2014). Consequently, our ability to gauge and understand how tropical species are responding to anthropogenic threats remains poor (Feeley and Silman, 2011). In 2002, the Tropical Ecology Assessment and Monitoring Network (TEAM) was established to fill this void. TEAM uses large-scale arrays of camera traps to monitor ground-dwelling mammals in protected forests throughout the tropics, including on Madagascar (Jansen et al., 2014).

Madagascar's forests are the focus of considerable conservation concern because of their rich endemic fauna and their rapid rate of loss (Myers et al., 2000; Harper et al., 2007). Seventy million years of relative isolation has resulted in high levels of species endemism (e.g., 90% of mammals are endemic (Garbutt, 1999)). Over the past century, Madagascar suffered extensive deforestation and forest fragmentation (Harper et al., 2007) threatening many species with extinction from habitat loss (Schwitzer et al., 2014). Hunting is an unsustainable threat on the island in part because the most commonly hunted mammals are long-lived and slowly-reproducing primates and carnivores (Golden, 2009). Many studies emphasize the urgency of addressing knowledge gaps to clarify how conservation can be effective within Madagascar's increasingly modified landscapes (Irwin et al., 2010).

The biodiversity of Madagascar is more susceptible to disturbances than mainland areas because insular populations are more vulnerable to extinction (Foufopolous et al., 2011). Invasive alien species, for example, threaten more species on Madagascar than mainland Africa (Bellard et al., 2016). Like other islands, Madagascar's endemic species may have evolved in the absence of strong natural enemies making them more vulnerable to predation, competition and disease from invasive species (Shea and Chesson, 2002), particularly alien invasive mammals (Courchamp et al., 2003). On Madagascar, invasive carnivores, such as domestic cats and dogs, have caused rapid declines in endemic carnivores (Farris et al., 2017a). Madagascar has nine species of carnivore all of which are endemic and belong to the family Eupleridae. Eupleridae has been argued to be the World's least studied and most threatened family of the order Carnivora (Brooke et al., 2014).

Here, we test for changes in the distribution of four tropical mammals along a 570 m elevation gradient in Ranomafana National Park, Madagascar. We assessed the four species with sufficient data for analysis: the Eastern red forest rat (*Nesomys rufus*), an endemic small-bodied nocturnal omnivore; the bushpig (*Potamochoerus larvatus*), a large-bodied nocturnal omnivore native to mainland Africa; the Malagasy civet (*Fossa fossana*), an endemic medium-sized nocturnal carnivore; and the Malagasy ring-tailed mongoose (*Galidia elegans*), an endemic small-bodied diurnal carnivore. We use six years of data collected by TEAM from 60 camera traps and apply dynamic occupancy modeling to test for spatially structured elevation shifts (Fig. 1).

2. Methods

2.1. Study site

TEAM camera trap sampling occurred within mid-altitude montane rainforest in Ranomafana National Park (47° 18′–47° 37′ E and 21° 02′–21° 25′ S). Elevation ranges from 500 to 1500 m asl and climate is variable, with rainfall ranging between 2300 and 4000 mm a year and temperatures ranging from 3 to 30 °C (Lehtonen et al., 2001).

2.2. Data collection

We used data collected by TEAM from 2010 to 2015. TEAM surveyed terrestrial (i.e., ground-dwelling) tropical mammal populations on an annual basis, using a published standardized protocol and permanent camera-trap points (Jansen et al., 2014). Sixty camera traps were deployed in systematic arrays arranged in a grid and covering an area of 142 km². Each camera trap was active for 30 consecutive days during the dry season. Camera trap images were identified following the standard IUCN Red List (IUCN, 2014). These camera traps detect predominately ground-dwelling mammal species > 100 g in body mass. For a complete list of species, see (Beaudrot et al., 2016).

Elevation data were extracted for the coordinates of each camera trap from the Shuttle Radar Topography Mission (SRTM) digital elevation model (90 m resolution with vertical accuracy of 4–7 m) (Gorokhovich and Voustianiouk, 2006) from the Consortium for Spatial Information (CGIAR-CSI) (Jarvis et al., 2008). Elevation of the camera traps in the sampling area ranged from 689 m to 1258 m asl.

2.3. Occupancy modeling

Occupancy – the estimated probability of a species occurrence at a site (MacKenzie et al., 2006) – can be used as a measure of the use of space as well as an indicator of abundance (MacKenzie et al., 2005). The relationship between abundance and occupancy is not linear (Thompson et al., 1998; Royle and Dorazio, 2008), but empirical studies have documented a positive correlation in field settings (MacKenzie and Nichols, 2004). Occupancy provides a useful and practical metric for assessing infrequently detected tropical vertebrates because it requires fewer detections than do metrics of abundance

(O'Brien et al., 2010).

Changes in distributions are the result of occupancy changes over time from local colonization and extinction. We modeled population-specific local colonization and extinction using a maximum-likelihood parameterization of a dynamic (multi-season) occupancy model that considers changes in occupancy as a first-order Markov process (i.e., the estimated probability of a site being occupied depends on its occupancy in the previous time period) (MacKenzie et al., 2003). This model is an appropriate and robust tool for evaluating changes in occupancy based on local colonization and extinction dynamics while accounting for imperfect detection (Royle and Dorazio, 2008) and making few assumptions about equilibrium (Clement et al., 2016). We parameterized all models using the "colext" function in R (Fiske and Chandler, 2011).

In this approach, the ecological processes that influence occupancy (i.e., local colonization and extinction) are modeled separately from the observation process (i.e., detection), which is considered imperfect. In the ecological process model, the incidence of a species i in the first year of observation is an unobserved latent variable Z_{i1}, resulting from a Bernoulli process with expected probability ψ_{i1}:$Z_{ij1} \sim \text{Bernoulli}(\psi_{i1})$. For subsequent years, the site remains occupied by the species with probability ϕ_i, or goes locally extinct from that site with probability $(1 - \phi_i)$, where ϕ_i is the apparent survival of the species from one year to the next and $(1 - \phi_i)$ is the local extinction probability. If the species did not occupy the site in year t ($Z_{it} = 0$), it can colonize this site the following year $(t + 1)$ with probability γ_i. The dynamics of a species i can be described recursively for any two contiguous years as:

$$\psi_{i(t+1)} = P(Z_{i(t+1)} = 1) = Z_{it}\phi_i + [1 - Z_{it}]\gamma_i \tag{1}$$

The observation process of the model assumes the observations for each species i at each sampling point j, year t, and observation period k, y_{ijtk}, as realizations of a Bernoulli process with mean $Z_{it} p_i$, where p_i is the detection probability of species i at year t:$y_{ijtk} \sim \text{Bernoulli}(Z_{it} p_i)$. This formulation takes into account imperfect detection at the sampling point (i.e., false negatives) and provides an unbiased estimate of occupancy.

This modeling approach assumes that a population is open to colonization and extinction between primary periods, but closed to emigration and immigration during the secondary sampling periods. Violation of the closure assumption can affect estimates, but conducting sampling surveys close to each other decreases the chances of violating this assumption (Kendall, 1999; Rota and Fletcher, 2009). Our primary period consisted of years, thus colonization and extinction occur on an annual basis. Secondary periods consisted of 24-hour intervals within the annual 30-day camera-trap sampling period, which we further collapsed into six days of sampling to reduce the number of secondary periods without detections and aid model convergence. Secondary periods are necessary for detection probability to be modeled because the likelihood is constructed using the product of the detection probabilities at each sampling occasion. For more detailed explanation of how detection probability is estimated, see (MacKenzie et al., 2002; MacKenzie, 2006).

We used Aikake Information Criteria adjusted for small sample sizes (AICc) to test for the most parsimonious combination of covariates that best predicted changes in occupancy over the six-year study period for each species, (Burnham and Anderson, 2002). We used an intercept-only model (no covariates) as a null dynamic occupancy model. In the absence of covariates, the probabilities of initial occupancy, colonization, extinction and detection are equal across sampling sites. The null model without any covariates can produce estimates of overall occupancy increases or overall declines, but variation in occupancy change as a function of elevation requires a model with elevation as a covariate. When elevation is included as a covariate of initial occupancy, colonization, extinction and/or detection, then these probabilities can vary between sites (i.e., camera trap locations). We conducted model selection with and without elevation as a covariate for initial occupancy

Table 1

Model set. We used a published dynamic occupancy model that accounts for imperfect detection (MacKenzie et al., 2003) and conducted AIC$_c$ model selection to identify the model with the most parsimonious combination of covariates for predicting occupancy change over time. Our model set included a null model without elevation (~1 ~1 ~1 ~1) as well as models with elevation as a covariate of colonization and/or extinction and detection. We conducted model selection on the entire model set for each of the 4 species.

~Occupancy	~Colonization	~Extinction	~Detection
~1	~1	~1	~1
~1	~Elevation	~Elevation	~Elevation
~1	~Elevation	~1	~Elevation
~1	~1	~Elevation	~Elevation
~Elevation	~Elevation	~Elevation	~Elevation
~Elevation	~Elevation	~1	~Elevation
~Elevation	~1	~Elevation	~Elevation
~Elevation^2	~Elevation^2	~Elevation^2	~Elevation^2
~Elevation^2	~Elevation^2	~1	~Elevation^2
~Elevation^2	~1	~Elevation^2	~Elevation^2

because initial occupancy may vary with elevation for some species but not others; some species may be more likely to occur at certain elevations whereas other species may be equally likely occurring at all elevations. We also conducted model selection with elevation as a covariate of local colonization and/or extinction. We consistently included elevation as a covariate of detection because variation in abundance can be a chief determinant of detection probability (Royle and Nichols, 2003). We modeled both linear and quadratic terms for elevation because a range of ideal conditions for a species could result in non-monotonic relationships (e.g. initial occupancy or colonization is highest at intermediate elevations). The 10 models in the model set are listed in Table 1.

Colonization and extinction were modeled as single parameters rather than year-specific parameters therefore the parameters do not change by year. We explored year effects on colonization and extinction in an attempt to explore non-stationarity (i.e. that occupancy is not approaching equilibrium). However, models with year effects did not converge.

We used a combination of condition numbers, evaluation of standard errors and likelihood ratio tests to ensure that the most parsimonious model fit the data appropriately. Condition numbers provide information on how much information is lost when a problem is solved numerically rather than analytically. Models with a condition number $> 10^4$ are indicative of parameters that are unidentifiable or models with optimization problems (Cheney and Kincaid, 2008). Therefore, we chose the combination of a condition number < 5000 and standard errors smaller than or near the value of the estimate as a conservative way of selecting models for this study. This ensured that the model selected through AICc model selection had an appropriate fit to the data. Species were included in the results if the null model and at least one non-null model had a condition number < 5000. Finally, we conducted likelihood ratio tests to compare the fit of the top model with the fit of the null model. All modeling was conducted in R using the library "unmarked" (Fiske and Chandler, 2011; R Development Core Team, 2016).

2.4. Elevation shifts

Local colonization and extinction result in changes in occupancy. To determine whether an elevation shift occurred (i.e., if there were changes in occupancy over time with elevation), we used the best model for each species from the AIC model selection to plot predicted occupancy at low to medium elevations and at high elevations (Ferraz et al., 2007). Specifically, we plotted the mean occupancy of camera traps in the first two quartiles of elevation sampled, which we lumped for sample size (689–1008 m asl; N = 10 camera traps sampling points),

and the fourth quartile of elevation sampled (1125–1258 m asl; N = 38 camera trap sampling points).

We operationalized conceptual representations of range shifts based on changes in occupancy resulting from local colonization and extinction (Fig. 1). Specifically, we assessed the three spatially structured (rather than birth-death) shifts described and labeled by (Lenoir and Svenning, 2015): "march", "expand" and "retract". Expand: a population expanded upwards when the best-fit model predicted an increase in occupancy at higher elevations over time (Fig. 1a). A population expanded downwards when the best-fit model predicted an increase in occupancy at lower elevations over time (Fig. 1b). A population expanded both overall when the best-fit model predicted an increase in occupancy at both lower and higher elevations (Fig. 1c). Retract: a population retracted from high elevations when the best-fit model predicted a decrease in occupancy at higher elevations (Fig. 1d); a population retracted from low elevations when the best-fit model predicted a decreased in occupancy at low elevations over time (Fig. 1e). A population retracted overall when the best-fit model predicted a decrease in occupancy at higher and lower elevations (Fig. 1f). March: a population marched upslope when the best-fit model predicted higher occupancy over time at higher elevation and lower occupancy at lower elevation (Fig. 1g). A population marched downslope when the best-fit model predicted an increase in occupancy at lower elevations over time and decrease in occupancy at higher elevations (Fig. 1h).

3. Results

We made inferences about the four species with successful model convergence based on the condition number of the models (see Methods): Eastern red forest rat (*Nesomys rufus*), bushpig (*Potamochoerus larvatus*), Malagasy ring-tailed mongoose (*Galidia elegans*) and Malagasy civet (*Fossa fossana*). The species had 274, 66, 77, and 366 observations, respectively.

The null model was the best model for two species – Eastern red forest rat and bushpig (Table 2) – suggesting that the probabilities of local colonization and extinction did not change with elevation for these two species. However, the overall occupancy of both the Eastern red forest rat and bushpig changed during the six-year study period. The Eastern red forest rat declined in occupancy overall, suggesting that this species retracted its overall distribution (Fig. 2a). Bushpig increased in overall occupancy, suggesting that this species expanded its overall distribution (Fig. 2b).

Our best models for the Malagasy ring-tailed mongoose and Malagasy civet included elevation (Table 2). Specifically, the best model for the Malagasy ring-tailed mongoose included elevation as a covariate for local colonization, extinction and detection. Parameter estimates and likelihood ratio test results are specified in Table 2. A plot of occupancy estimates over time at high and low-medium elevations illustrates that the Malagasy ring-tailed mongoose retracted from high elevations. Its occupancy declined from 0.55 ± 0.05 SE to 0.20 ± 0.04 SE at high elevations while remaining relatively stable at low-medium elevations (0.53 ± 0.11 SE to 0.50 ± 0.08 SE; Fig. 2c). The best model for the Malagasy civet included elevation as a covariate of initial occupancy, local extinction and detection. Parameter estimates are provided in Table 2. A plot of occupancy estimates from the best model at high and low-medium elevations indicate that the Malagasy civet marched upslope during the six-year study (Fig. 2d). Estimated occupancy for Malagasy civet steadily increased at high elevations from 0.55 ± 0.06 SE to 0.91 ± 0.01 SE while simultaneously declining from 0.996 ± 0.002 SE to 0.49 ± 0.09 SE at low-medium elevations (Fig. 2c). Thus, these two species exhibited marked shifts in elevation during the short time period examined.

4. Discussion

We analyzed the occupancy dynamics of four mammal species and

Table 2

Best-fit models. The covariates for initial occupancy, colonization, extinction and detection are listed for each species. A null model (i.e., dynamic occupancy model without covariates) is indicated as ~1 ~1 ~1 ~1. The condition number, the number of parameters, the AIC value, the change in AIC$_c$ between the best-fit model and the null model, the weight of each best-fit model, likelihood ratio test results, and parameter estimates and standard errors are listed.

Species	Covariates in best model				Model information			Likelihood ratio tests		
	Initial occupancy	Colonization	Extinction	Detection	Condition number	N parameters	AICwt	Chi-sq	df	p-Value
Fossa fossana	~Elevation	~1	~Elevation	~Elevation	112.76	7	0.27	15.53	3	0.001
Galidia elegans	~1	~Elevation	~Elevation	~Elevation	132.69	7	0.31	10.64	3.00	0.014
Nesomys rufus	~1	~1	~1	~1	20.41	4	0.15	–	–	–
Potamochoerus larvatus	~1	~1	~1	~1	402.73	4	1.00	–	–	–

Species	Estimates															
	Initial occupancy (psi)				Colonization				Extinction				Detection (p)			
	Elevation	SE	Intercept	SE	Elevation	SE	Intercept	SE	Elevation	SE	Intercept	SE	Elevation	SE	Intercept	SE
Fossa fossana	−1.70	0.93	1.35	0.74	–	–	−0.33	0.51	−0.88	0.45	−2.63	0.87	−0.28	0.11	−0.27	0.12
Galidia elegans	–	–	0.11	0.51	−2.58	1.40	−1.67	0.80	−2.83	1.74	0.75	1.28	0.05	0.19	−1.56	0.23
Nesomys rufus	–	–	1.17	0.57	–	–	−0.82	0.56	–	–	−0.41	0.44	–	–	−0.71	0.15
Potamochoerus larvatus	–	–	−2.53	1.11	–	–	−1.24	0.67	–	–	−2.81	5.04	–	–	−2.24	0.49

documented overall changes in occupancy for an endemic rodent and a non-native pig, and distinct changes in elevational use for two endemic carnivores. Systematic camera trap observations over multiple years allowed us to assess changes in the spatial distribution of these poorly known and enigmatic species. This appears to be the first evidence-based report of rapid (i.e. short-timescale) shifts in tropical mammal distributions (McCain and King, 2014; Lenoir and Svenning, 2015). Nevertheless, given the duration of the study and how little is known about the ranging behavior of Eupleridae, it is unclear to what extent these findings represent longer-term trends.

The Eastern red forest rat is an endemic species that occurs in humid forests from 750 m to 2300 m and thrives in selectively-logged forests above 900 m (Lehtonen et al., 2001). The species is currently listed by IUCN as a species of Least Concern (Kennerley, 2016). Nevertheless, our analysis identified a decline in occupancy in this island native. The species is susceptible to disease spillover from non-native rodents and

has been observed to suffer extreme mortality from the plague (Kennerley, 2016). The black rat (*Rattus rattus*), which is a host for the plague, occurs as an alien species in Ranomafana and increased in occupancy during the study period (Beaudrot et al., 2016). Further work would be needed to assess the extent to which disease may have impacted the Eastern red forest rat at this site. Irrespective of the cause, declining occupancy could affect local plant communities due to reduced seed dispersal for the plants whose fruits this rodent consumes.

Our finding that bushpigs have increased in occupancy and expanded their space use in Ranomafana National Park is consistent with their ecology. Bushpigs occur throughout much of mainland Africa where they occupy a range of relatively densely vegetated habitats including highlands over 3000 m. The species was likely introduced to Madagascar in pre-colonial times (Kingdon et al., 2013) and has been difficult to eliminate. The bushpig's omnivorous diet, nocturnal activity and high reproductive potential all contribute to its success (Kingdon
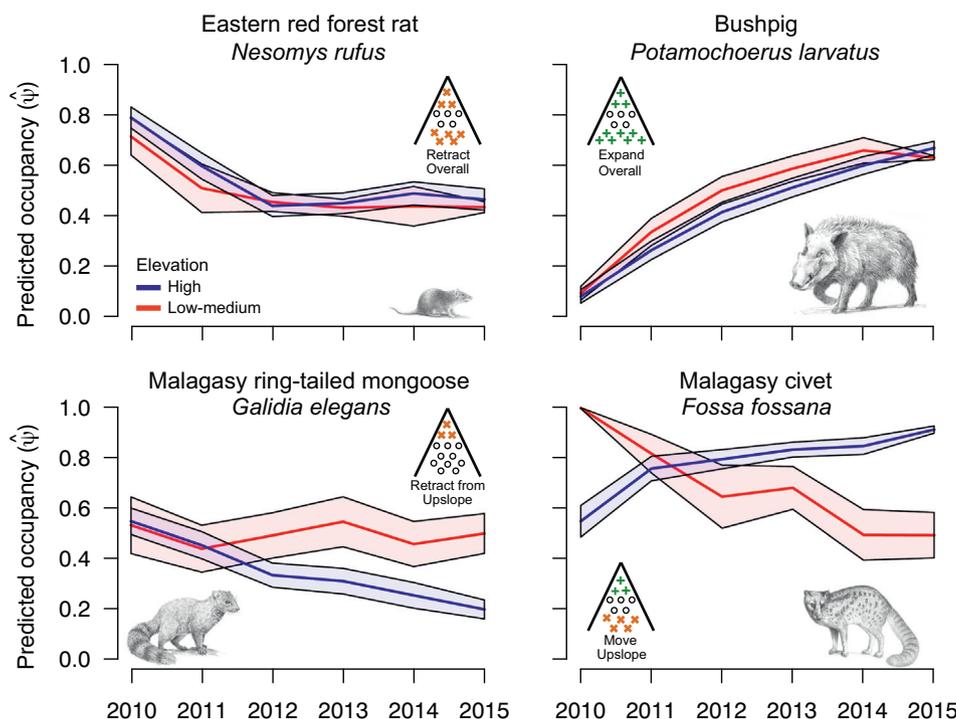

Fig. 2. Elevation shifts. Predicted annual occupancy estimates (solid lines) ± SE (shaded areas) from the best model for each species are shown for low-medium and high elevations in red and blue, respectively. Triangles correspond to Fig. 1. Overall, eastern red forest rat occupancy declined and bushpig occupancy increased over the six-year study. Malagasy ring-tailed mongoose occupancy only declined over time at high elevations, thus retracting from upslope. Malagasy civet occupancy declined at low-medium elevations over time while simultaneously increasing at high elevations, thus moving upslope. Animal illustrations by John Megahan. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2013). Accordingly, bushpigs have been classified as a species of Least Concern by IUCN (Seydack, 2016). Their overall increase in occupancy could have ramifications for plant communities within Ranomafana. For example, bushpigs are known to consume seeds dispersed by primates and other primary seed dispersers (Seufert et al., 2010). Increased seed predation or seed predation that disproportionately targets certain plant species could in turn differentially affect germination and recruitment rates thereby affecting plant community composition. Furthermore, bushpigs scrape and dig, which leads to disturbed soils and promotes invasive vegetation such as bracken fern (*Pteridium aquilinum*) that appear favored by these conditions (Ssali et al., 2017).

We found that two poorly studied carnivores of conservation concern exhibited distinct spatial shifts. The IUCN Red List has classified the Malagasy civet as Vulnerable (Hawkins, 2015b) and the Malagasy ring-tailed mongoose is close to being listed as Near Threatened (Hawkins, 2015a). The Malagasy ring-tailed mongoose is vulnerable to non-native carnivore species (Gerber et al., 2012; Farris et al., 2015) and is hunted for human consumption, often by dogs that accompany humans (Golden, 2009). Its diurnal activity overlaps with dogs (Farris et al., 2015) and this may have contributed to its persecution. The nocturnal Malagasy civet, on the other hand, is not active during the day when dogs are and may have suffered less predation as a result. In fact, the species alters its activity patterns when dogs are present (Farris et al., 2015). The Malagasy civet may have shifted to higher elevation because the species does not do well in degraded forest or near human settlements (Gerber et al., 2012). Lower elevation areas within Ranomafana National Park areas are more likely to have been logged than higher elevation areas (Brown and Gurevitch, 2004) and human activity within the park increased during the six-year study (Farris et al., 2017b) with natural resource extraction occurring at higher rates closer to villages (Brown et al., 2011). While the Malagasy civet is known to occur up to 1600 m, it is uncommon above 1000 m (Goodman, 2012). Anthropogenic pressures may have caused the Malagasy civet to shift into higher elevations. If the carnivores' observed distributional shifts are part of longer-term trends, then there may be subsequent ecological consequences. For example, density compensation could occur if their competitors increase in density due to reduced competition (Peres and Dolman, 2000) or their prey could increase as a result of reduced predation with the potential for cascading consequences (Terborgh et al., 2001).

Detecting ongoing changes in species distributions and determining their causes is essential information for effective land management and conservation planning. In this study, we show that dynamic occupancy models provide a robust approach for modeling changes in species distributions because they estimate the underlying colonization and extinction processes (see also Kery et al., 2013), and we demonstrate that some poorly studied tropical mammals have exhibited shifts in their elevation use over just six years. A critical next step is to identify causal mechanisms for these shifts so that management can be targeted accordingly.

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