



Patterns of spatiotemporal change in large mammal distribution and abundance in the southern Western Ghats, India

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ABSTRACT

Large mammals face high risks of anthropogenic extinction owing to their larger body mass and associated life history traits. Recent worldwide mammal declines have highlighted the conservation importance of effective assessments of trends in distribution and abundance of species. Yet reliable data depicting the nature and extent of changes in population parameters is sparse, primarily due to logistical problems in covering large areas and difficulties in obtaining reliable information at large spatial scales, particularly over time. We used key informant surveys to generate detection histories for 18 species of large mammals (body mass > 2 kg) at two points in time (present and 30 years ago) in the Southern sub-region of the Western Ghats global biodiversity hotspot. Multiple-season occupancy models were used to assess temporal trends in occupancy, detectability and vital rates of extinction and colonization for each species. Our results show significant declines in distribution for large carnivores, the Asian elephant and endemic ungulates and primates. There is a significant decline in detectability for 16 species, which suggests a decline in their abundance. These patterns of change in distribution and abundance repeat in our assessments of spatial variation in occupancy dynamics between the three contiguous forest complexes and two human-dominated landscapes into which the southern Western Ghats has been fragmented. Extinction rates are highest in the human-dominated landscapes. Declines in abundance for several species suggest the presence of extinction debts, which may soon be repaid with imminent range contractions and subsequent species extinctions unless immediate remedial conservation measures are taken. Detection/non-detection surveys of key informants used in an occupancy modeling framework provide potential for rapid conservation status assessments of multiple species across large spatial scales over time.

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1. Introduction

The risk of extinction for a given species is a measure governed by interactions between its intrinsic evolutionary and ecological traits (Maynard Smith, 1989; Pimm et al., 1988), and a suite of environmental and anthropogenic factors (Brashares, 2003; Brashares et al., 2001; Cardillo et al., 2004; Diamond et al., 1989). Although the drivers of extinction may be varied and their interactions complex, the process invariably involves temporal declines in the abundance of a species within its range, with or without accompanying declines in its geographic distribution (Ceballos and Ehrlich, 2002; Channell and Lomolino, 2000a,b; Rodriguez,

2002; Royle and Dorazio, 2008). Thus, monitoring extinction risk for a species in a given region requires that both its distribution and abundance be tracked reliably over time. Yet, for many species that may be elusive, cryptic or rare, monitoring changes in distribution and abundance over large spatiotemporal scales remains a serious challenge (Thompson, 2004).

Large mammals are particularly prone to extinction (Cardillo et al., 2004) due to their greater body mass and associated life history traits. Recent work has underlined that extinction risk for mammals increases sharply above a body mass threshold of 3 kg (Cardillo et al., 2005). Furthermore, the same evolutionary and life history characteristics that render large mammals intrinsically more susceptible to extinction (Cardillo et al., 2005) also make them vulnerable to a wide range of anthropogenic threats (Madhusudan and Mishra, 2003; Morrison et al., 2007). Consequently, the status of large mammals occurring in regions of high demographic pressures is critical (Schipper et al., 2008). Hunting, habitat loss, fragmentation and degradation, the foremost threats

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to large mammals (IUCN, 2010) have continued to impact the world's tropics (Acharid et al., 2002; Ceballos and Ehrlich, 2002), and led to population declines and range contractions of several species in tropical Asia (Morrison et al., 2007; Schipper et al., 2008). The southern Western Ghats (Fig. 1), an ecologically distinct region of India's Western Ghats biodiversity hotspot (Myers et al., 2000), combines high species richness and endemism with high anthropogenic pressure (Cincotta et al., 2000; Menon and Bawa, 1997; Nair, 1991) and has among the highest concentrations of threatened terrestrial mammals in the world (Schipper et al., 2008).

In this paper, we address the challenge of monitoring large-scale spatiotemporal changes in distribution and abundance, and

estimating extinction rates, focusing on 18 species of large mammals of body mass > 2 kg (Table 1) from the southern Western Ghats. We combined occupancy modeling (MacKenzie et al., 2003, 2006) with field interview data which recorded sightings and indirect detections of each of these species at two points in time: during 2008–2009 (present) and from 30 years earlier (past). We describe patterns of change in occupancy and detectability over these two periods of time and extinction rates in the intervening period across the southern Western Ghats. We also assess variation in these patterns in relation to characteristics of the five landscapes which comprise the southern Western Ghats, three contiguous forest complexes and two human-dominated

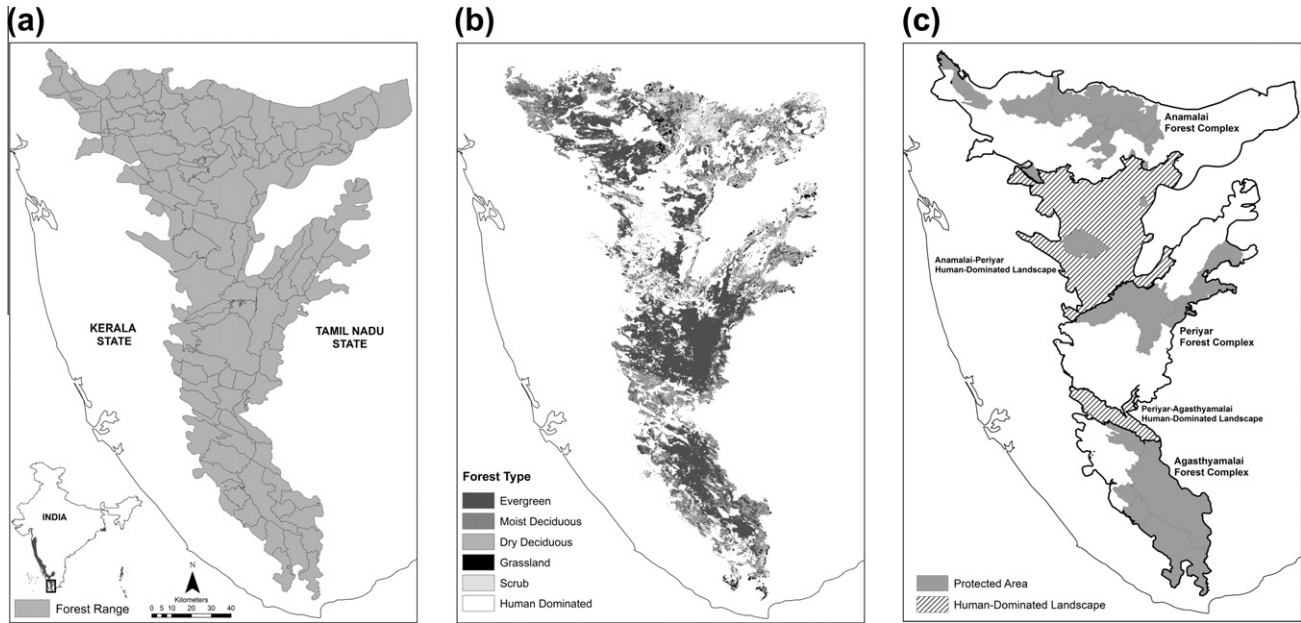


Fig. 1. The southern Western Ghats. (a) Location of study region and boundaries of forest ranges, which served as our sampling units. *Note:* While the southern Western Ghats is to scale, the forest range boundaries shown were aggregated from discrete, smaller scale maps and therefore, are not to scale. (b) Forest cover and broad habitat types. (c) The contiguous forest complexes and human-dominated landscapes.

Table 1

The study species, their red list status (IUCN, 2010) and body mass (Macdonald, 2001; Menon, 2003).

Common name	Scientific name	Species code	Red list status	Adult body mass (kg)
<i>Order Carnivora</i>				
Tiger	<i>Panthera tigris</i> (Linnaeus, 1758)	TGR	EN	100–258
Sloth bear	<i>Melursus ursinus</i> (Shaw, 1791)	SLB	VU	55–145
Leopard	<i>Panthera pardus</i> (Linnaeus, 1758)	LPD	NT	30–70
Dhole	<i>Cuon alpinus</i> (Pallas, 1811)	DHL	EN	17–20
Golden jackal	<i>Canis aureus</i> (Linnaeus, 1758)	JKL	LC	7–15
<i>Order Proboscidea</i>				
Asian elephant	<i>Elephas maximus</i> (Linnaeus, 1758)	ELP	EN	2700–5400
<i>Order Artiodactyla</i>				
Gaur	<i>Bos gaurus</i> (C.H. Smith, 1827)	GAR	VU	700–1225
Sambar	<i>Rusa unicolor</i> (Kerr, 1792)	SAM	VU	227–272
Nilgiri tahr	<i>Nilgiritragus hylocrius</i> (Ogilby, 1838)	NTR	EN	60–100
Wild pig	<i>Sus scrofa</i> (Linnaeus, 1758)	WPG	LC	50–100
Chital	<i>Axis axis</i> (Erxleben, 1777)	CHT	LC	50–86
Indian muntjac	<i>Muntiacus vaginalis</i> (Boddaert, 1785)	MJK	LC	18–20
Indian chevrotain	<i>Moschiola indica</i> (Gray, 1852)	MDR	LC	3–4
<i>Order Primates</i>				
Nilgiri langur	<i>Trachypithecus johnii</i> (J. Fischer, 1829)	NLG	VU	10–14
Tufted gray langur	<i>Semnopithecus priam</i> (Blyth, 1844)	TLG	NT	6–14
Lion-tailed macaque	<i>Macaca silenus</i> (Linnaeus, 1758)	LTM	EN	6–9
Bonnet macaque	<i>Macaca radiata</i> (E. Geoffroy, 1812)	BNT	LC	4–7
<i>Order Rodentia</i>				
Indian giant squirrel	<i>Ratufa indica</i> (Erxleben, 1777)	IGS	LC	1–3

EN = endangered; VU = vulnerable; NT = near threatened; LC = least concern.

landscapes. Finally, we discuss the promise and potential pitfalls of extending this approach for the monitoring of extinction risk for threatened species at large spatiotemporal scales.

2. Materials and methods

2.1. Study area

The 13,314 km² southern Western Ghats is dominated by moist forests and harbours greater levels of biodiversity and endemism than the rest of the Western Ghats (Das et al., 2006). Located south of the Palghat Gap, a 40 km break in the Western Ghats mountain range (Fig. 1a, inset), this region's greater diversity is a consequence of the wide variation in rainfall and complex geography that produces varied vegetation types (Fig. 1b). Tropical dry deciduous and thorn forests occur in the low-lying rain shadow of the eastern slopes, while tropical moist deciduous and wet evergreen forests dominate the windward side of this landscape up to an elevation of 1500 m, beyond which the vegetation mainly comprises montane grasslands and *shola* forests (Champion and Seth, 1968).

Anthropogenic impacts have fragmented this once contiguous forested stretch into three forest complexes, Anamalai (5127 km², CF1), Periyar (3678 km², CF2) and Agasthyamalai (2112 km², CF3) (Fig. 1c), which comprise large, relatively contiguous stretches of legally protected habitat although anthropogenic threats remain. The Anamalai–Periyar (2050 km², HL1) and Periyar–Agasthyamalai (346 km², HL2) landscapes are the two intervening human-dominated landscapes (Fig. 1c), which have witnessed extensive habitat loss and fragmentation over time (Fig. 1b).

2.2. Occupancy estimation and field surveys

Occupancy modeling makes it possible to reliably estimate the proportion of area occupied by a species, explicitly accounting for the possibility that a survey may fail to detect a species that is, in fact, present in a sampling unit. Such false absences are corrected by conducting replicated surveys within a sampling unit, which enables estimation of the probability of detecting at least one individual of a species during a survey, given its presence in the sampling unit (MacKenzie et al., 2002).

We chose Forest Ranges (hereinafter called sites), standard administrative units in forest and wildlife management throughout India, as sampling units. The 119 sites [mean area (\pm SE) = 111.89 km² (\pm 7.52)] across the southern Western Ghats (Fig. 1a) are located both within and outside protected areas. We visited each of these sites between April 2008 and May 2009 and conducted structured interviews in the local language with knowledgeable middle-aged key informants comprising Forest Department field personnel (341), people from forest-dwelling communities (341) and experts (14). Structured interviews with people possessing detailed local knowledge of wildlife have previously been combined with formal sampling designs and modeling frameworks to enable robust inferences about the status of wildlife populations (Gros et al., 1996; Karanth et al., 2009). Our choice of sampling units of variable area was inevitable as we were carrying out a large-scale spatiotemporal survey in which it was essential that our key informants recognized the boundaries of the sampling unit. Constant area sampling units, comprising a set of grids drawn on a map, are difficult to describe to key informants.

Since our method relied on encounters of key informants with species of interest, we took particular care to ensure reliability and quality of data. First, we chose species that are prominent, easily recognized, and have unambiguous local names. Thus we did not survey the lesser felids, viverrids, herpestids and mustelids, even though many qualified the body mass category of >2 kg, in

order to avoid reporting errors arising from confusion between two or more cryptic species of similar appearance especially with overlapping local names existing for many. Although some species surveyed are cryptic and nocturnal, we included them because they leave prominent signs such as tracks and droppings, or have diagnostic vocalizations. Second, we took particular care to recognize and include only an informant's actual detection of a species or its sign rather than record their subjective impressions about the occurrence of a species at a given site. This approach of asking informants to provide closed binary responses in the form of their own detections of species may have resulted in less uncertainty and more resilience to recall bias than if we had asked informants to provide estimates of their encounter rates of species, a continuous variable that may be more sensitive to misinterpretation and recall bias (White et al., 2005). Third, we strived to eliminate erroneous reporting and false presences in direct sightings by asking key informants to describe the morphological, ecological and behavioral traits of each species, and provide a description of the sighting location/s. In case of indirect evidence, we asked key informants to describe (scat), draw (pugmarks/tracks) or mimic (vocalization) the sign encountered. Lastly, we ensured that each informant could identify each species from photographs in Menon (2003). Our final dataset comprised 430 oral interviews with 696 key informants. Of these, 175 interviews involved multiple informants and 255 involved single informants. We were careful to collect data only from people who were active at either one or both time periods to prevent temporal variation in sampling effort biasing detection probabilities due to the reduced mobility of older respondents decreasing their contact with wildlife over time. Therefore, if questioning revealed that older key informants had been inactive recently, they were interviewed in the presence of a younger active informant such that the former reported past detections while the latter reported present detections.

Our sampling design for occupancy surveys was based on Pollock's robust design (Pollock, 1982) used in mark-recapture studies. Within each primary sampling season corresponding to the past (30 years ago) and present (2008–2009), we conducted three to nine interviews in each site [mean interviews/site (\pm SE) = 4.54 (\pm 0.14)], each interview corresponding to a secondary sampling occasion. We then summarized the data as past and present detection histories for each species. We acknowledge the possibility that informants may have been unable to pinpoint detections of a species from precisely 30 years ago. This, in effect, may have extended the window of time over which the data for past detections were obtained. However, our method of cross-examining key informants may have allowed the time window for the past primary sampling season to largely conform to the time window for the present primary sampling season. We therefore make a reasonable assumption that the occupancy state for a given species could change between the two primary sampling occasions, separated by a 30 year time period, but was closed to such changes across secondary sampling occasions, even though their durations may be unequal.

In addition to obtaining species detections, we also used the same interview surveys to obtain data on the current presence of anthropogenic threats in each site.

2.3. Data analyses

For each species, we used the extent of change in occupancy over time as a surrogate for distributional change. Similarly, we used the change in detection probability over time to index change in abundance. We emphasize that we make only temporal, and not spatial, comparisons in detection probability, as an index of abundance, within a given spatial region. Thus, although our sampling units are themselves of variable area, the area of each sampling

unit did not change between the two time periods covered in our study. Hence, we argue that an observed temporal change in detection probability, after having controlled for or measured other possible sources of variation, is a strong index of a change in abundance.

Variation in local abundance among sampling units is thought to be the principal source of heterogeneity in detection probabilities (Royle and Nichols, 2003), and such abundance-induced heterogeneity in detection probability may be ruled out only if the abundance of a species is constant across sites, unlikely in biological populations (MacKenzie et al., 2006). This functional dependence between abundance and detection probability has been formalized to estimate abundance from detection/non-detection data (Royle and Nichols, 2003), where variation in site-specific detectability is the basis for abundance estimation. Our interview-based method of recording detections over periods extending up to a year from a variety of key informants led to many more detections of a given species at a given site than other methods may have recorded. Therefore, our high estimates of site-specific detectability for many species provide little variation with which to estimate abundance with the Royle and Nichols (2003) model. Consequently, we decided to use variation in detection probability over time to index changes in abundance.

This goes with the caveat that detection probabilities within a site could vary with seasonal differences in species behavior, varying habitat and environmental conditions, variation in effort over time by observers, and differences in detection capability across multiple observers. We strived to keep these sources of variation in detection probability to a minimum by trying to control some while measuring those which could not be controlled. First, in our key informant surveys, detections were aggregated over primary sampling periods extending up to a year, which meant that environmental factors and seasonal behavioral differences in species were less likely to influence detectability across time periods than actual changes in species abundance. Second, we believe that our use of multiple modalities of detection (e.g., direct sightings, scats, pugmarks/tracks, carcasses and vocalizations) make our detection data more resilient to the effects of habitat changes and consequent changes to species encounter rates over time. Third, we tried to control for variation in effort over time by making sure that key informants were active during periods for which they reported detections.

However, variation in the capability of different key informant groups, forest watchers/guards, local communities, and experts, to detect a given species was a potential source of bias in estimating detection probability. To test for this possible bias, we selected all sites where two or more members from each of the three key informant groups were interviewed, and computed detection probabilities for each group by species over the two time periods, past and present. We used a two-way analysis of variance (ANOVA) with species as matching subjects, to examine if key informant group and time period independently and interactively explained observed variation in detection probabilities.

We used multiple-season occupancy models (MacKenzie et al., 2003) with the software PRESENCE 2 (Hines, 2006) to estimate the proportion of area occupied by each species in the past and present. Multiple-season models explicitly incorporate the processes of local extinction and colonization (MacKenzie et al., 2003) and avoid the otherwise de facto assumption that changes in occupancy of sites occurred at random between seasons. Additionally, they allow the explicit modeling of variation in detection probability between primary seasons, approximating biological reality (MacKenzie, 2005; MacKenzie et al., 2006). The analyses were carried out in two stages. In the first stage, we assessed temporal changes in occupancy and detectability, and estimated extinction and colonization rates for each species across the entire

southern Western Ghats. In the second stage, we modeled spatio-temporal variation in occupancy and detectability, and extinction and colonization rates across the three contiguous forest complexes and two human-dominated landscapes comprising the southern Western Ghats. For each species, we fit multiple models, each representing different hypotheses about the spatial variations, which had generated the data Appendix A. We ranked models in order of increasing Akaike's Information Criterion (AIC) values (Burnham and Anderson, 1998). Since multiple models were supported by the data for many species, we used model averaging on the basis of AIC model weights to obtain parameter estimates (Burnham and Anderson, 1998; MacKenzie et al., 2006).

Finally, we compared compositional similarity and turnover in large mammal species composition between the contiguous forest complexes and human-dominated landscapes. This was done by constructing a Bray–Curtis similarity matrix with fourth root transformed estimates of occupancy in each of the landscapes. Patterns of compositional similarity and turnover were visualized with non-metric multidimensional scaling (NMDS). The effect of landscape type (contiguous forest vs. human-dominated landscape) and time (past vs. present) on species composition was determined using a two-way nested analysis of similarity (ANOSIM). These analyses were carried out using the software PRIMER 6 (Primer-E, 2007).

3. Results

Detection probabilities for species did not vary by key informant groups (Two-way ANOVA, $F(2, 51) = 2.6$, $p = 0.087$) and neither were interactions observed between key informant group and time period ($F(2, 51) = 1.7$, $p = 0.197$). Time period, however, had a significant effect on detection probability ($F(1, 51) = 14$, $p < 0.01$). This, together with our efforts to control for other sources of variation in detection probability, strengthens our case that actual changes in abundance underlie the observed temporal changes in species detection probability.

3.1. Changes in large mammal distribution and abundance across the southern Western Ghats

The top ranked model for each species was the one parameterized as constant occupancy $\psi(\cdot)$, colonization $\gamma(\cdot)$, extinction $\epsilon(\cdot)$ and variation in detectability over the two primary seasons $p(\text{time})$. We did not select the model $\psi(\cdot) \gamma(\cdot) \epsilon(\cdot) p(\cdot)$ since it was always more than 10 AIC points of the top model for all species.

Thirteen out of the eighteen large mammal species in the southern Western Ghats have undergone declines in occupancy (Table 2). Foremost among these is the tiger, which has lost more than a quarter of its geographic range over the last 30 years. Among the other species that have lost over 10% of their historical range are the leopard, sloth bear, golden jackal, Asian elephant, the Nilgiri tahr and the lion-tailed macaque. However, widespread species such as the sambar, muntjac, wild pig, tufted gray langur, bonnet macaque and the Indian giant squirrel show negligible changes in occupancy, while the sloth bear and chital even managed to colonize new areas during this period.

Sixteen out of the eighteen species show declines in detectability (Table 2), suggesting reductions in their population over the last three decades. Large predators such as the tiger and leopard, endemics like the Nilgiri tahr and lion-tailed macaque, which show large declines in occupancy, also show major declines in detectability. The golden jackal, whose range has declined by 13%, shows a 50% reduction in detectability, signaling a potentially catastrophic population decline. Also importantly, many common species that barely show changes in occupancy, show major declines in detectability. Prominent among these are the Indian chevrotain,

Table 2

Past and present estimates of occupancy, detectability and extinction rates (± 1 SE) over the last 30 years for 18 species of large mammals across the southern Western Ghats. Parameter estimates calculated on the basis of Pollock's robust design (Pollock, 1982).

Species	Occupancy (ψ)		Extinction rate (ϵ) over 30 years (± 1 SE)	Detectability (p)		Proportion change in p over 30 years
	Past (± 1 SE)	Present (± 1 SE)		Past (± 1 SE)	Present (± 1 SE)	
TGR ^{a,b}	0.91 (0.03)	0.66 (0.05)	0.27 (0.05)	0.84 (0.02)	0.65 (0.03)	0.23
SLB ^{a,b}	0.90 (0.03)	0.79 (0.04)	0.14 (0.04)	0.88 (0.01)	0.73 (0.02)	0.17
LPD ^{a,b}	0.97 (0.02)	0.86 (0.03)	0.11 (0.03)	0.94 (0.01)	0.79 (0.02)	0.16
DHL ^{a,b}	0.98 (0.01)	0.95 (0.02)	0.03 (0.02)	0.97 (0.01)	0.86 (0.02)	0.11
JKL ^{a,b}	0.93 (0.02)	0.81 (0.05)	0.12 (0.04)	0.84 (0.02)	0.43 (0.03)	0.49
ELP ^{a,b}	0.98 (0.01)	0.87 (0.03)	0.11 (0.03)	0.96 (0.01)	0.91 (0.01)	0.05
GAR ^{a,b}	0.95 (0.02)	0.89 (0.03)	0.06 (0.02)	0.96 (0.01)	0.86 (0.02)	0.1
SAM ^{a,b}	0.99 (0.01)	0.98 (0.01)	0.01 (0.01)	0.99 (0)	0.91 (0.01)	0.08
NTR ^{a,b}	0.58 (0.05)	0.51 (0.05)	0.13 (0.04)	0.84 (0.02)	0.68 (0.03)	0.19
WPG	1 (0)	1 (0)	0 (0)	1 (0)	1 (0)	0
CHT ^b	0.58 (0.05)	0.59 (0.05)	0.03 (0.03)	0.73 (0.03)	0.69 (0.03)	0.05
MJK ^b	0.97 (0.02)	0.97 (0.02)	0 (0)	0.98 (0.01)	0.83 (0.02)	0.15
MDR ^{a,b}	1 (0)	0.96 (0.02)	0.04 (0.02)	0.95 (0.01)	0.74 (0.02)	0.22
NLC ^{a,b}	0.92 (0.02)	0.84 (0.03)	0.09 (0.03)	0.92 (0.01)	0.77 (0.02)	0.16
TLG ^b	0.38 (0.05)	0.39 (0.04)	0 (0)	0.77 (0.03)	0.69 (0.03)	0.1
LTM ^{a,b}	0.57 (0.05)	0.51 (0.05)	0.12 (0.04)	0.75 (0.02)	0.62 (0.03)	0.17
BNT	1 (0)	1 (0)	0 (0)	1 (0)	1 (0)	0
IGS ^{a,b}	1 (0)	0.98 (0.01)	0.02 (0.01)	0.98 (0.01)	0.89 (0.01)	0.09

Local colonization (γ) was observed for the sloth bear 0.17 (0.11), chital 0.07 (0.04) and tufted gray langur 0.01 (0.01).

^a Decline in occupancy over the last 30 years.

^b Decline in detectability over the last 30 years.

munjtjac, dhole, and sambar (Table 2). In contrast, the Asian elephant shows lesser changes in its detectability than in its occupancy, while species like wild pig and bonnet macaque show no changes in either occupancy or detectability.

3.2. Contiguous forest complexes versus human-dominated landscapes: anthropogenic threats and spatial variation in large mammal distribution and abundance over time

A wide range of anthropogenic activities were in evidence both in the contiguous forest complexes as well as in the human-dominated landscapes (Table 3). However, the relative incidence of threats, particularly logging, livestock grazing and road and rail networks are higher in the human-dominated landscapes. Among the contiguous forest complexes, CF1 shows higher levels of human disturbance, particularly human settlements, shifting cultivation, poaching and extraction of non-timber forest produce.

Fig. 2 shows patterns of change in occupancy and detectability of the 18 large mammal species across the forest complexes and human-dominated landscapes. Appendix A shows best models and model selection procedure for estimating probabilities of occupancy, extinction, colonization and detectability across the forest complexes and human-dominated landscapes. The tiger and leopard have registered declines in both occupancy and detectability in both human-dominated landscapes as well as in all three forest complexes. Occupancy of tigers has declined by more than 50% in the human-dominated landscapes, by 26% in CF1 but to a smaller degree in CF2 and CF3. Leopards have lost around 20% of their range in the human-dominated landscapes. The golden jackal has declined by 12% in occupancy and 54% in detectability in CF1. The Asian elephant has undergone declines in occupancy in all landscapes while the gaur has declined in occupancy in all landscapes except CF3. Endemic species such as the Nilgiri tahr and lion-tailed macaque, and widely distributed species such as the sloth bear, dhole, sambar, Indian muntjac, Indian chevrotain, tufted gray langur and Indian giant squirrel have registered declines in detectability while occupancy has declined in a few landscapes, in most cases either the highly disturbed HL1 or CF1. The chital, wild pig and bonnet macaque have not shown changes in either occupancy or detectability in any of the forest complexes or human-dominated landscapes. In general, HL1 has seen the highest

Table 3

Management activities, land-use patterns and anthropogenic threats in the three contiguous forest complexes (CF) and human-dominated landscapes (HL) of the southern Western Ghats.

Characteristic	CF1	CF2	CF3	HL1	HL2
No. of forest ranges	53	26	19	17	4
Area (km ²)	5127	3678	2112	2050	346
Human population density (no./km ²)	35.4	16.5	26.3	41.1	36.3
Field staff (no./km ²)	0.28	0.15	0.24	0.44	0.25
Staff vacancies (no./km ²)	0.07	0.03	0.01	0.05	0.04
Threat category/threat	Proportion of sites in which present				
	CF1	CF2	CF3	HL1	HL2
<i>Agriculture</i>					
Settlements	79	54	63	53	75
Encroachments	26	19	21	47	50
Plantations	42	69	47	59	100
Shifting cultivation	15	0	0	0	0
Marijuana cultivation	23	46	32	29	75
Median agriculture	26	46	32	47	75
<i>Biomass extraction</i>					
Livestock grazing	79	73	63	94	75
Poaching	72	65	53	65	50
Non-timber forest produce	91	92	68	71	100
Firewood	91	92	74	94	100
Fodder	51	42	47	65	75
Other plants	40	23	21	41	50
Official logging	38	31	32	59	50
Illegal logging	47	38	53	82	75
Median biomass extraction	62	54	53	68	75
<i>Other land-use</i>					
Mines and quarries	72	85	89	88	100
Windfarms	6	8	0	24	0
Dams and reservoirs	0	4	5	12	0
Roads and railroads	57	27	89	41	75
Infrastructure networks	85	65	58	88	100
Mass tourism	57	58	79	71	100
Median other land-use	57	43	69	56	88
Fire	30	31	47	41	25

rates of extinction over the last 30 years for 13 species (Table 4), followed by CF1 and HL2.

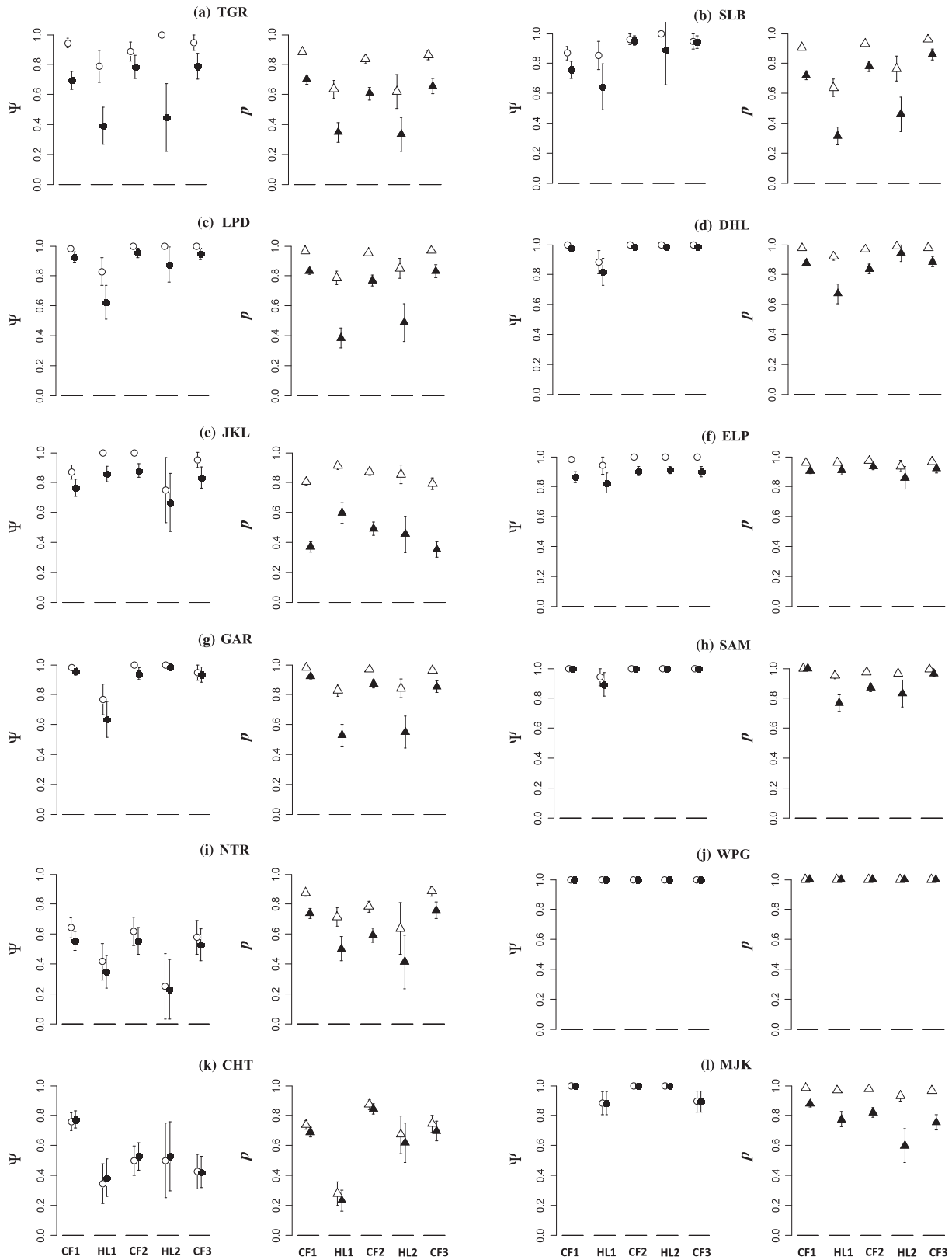


Fig. 2. Spatiotemporal changes in occupancy (ψ) and detectability (p) of 18 species of large mammals in the southern Western Ghats.

Two patterns stand out in the overall changes in large mammal community composition (Fig. 3) in the southern Western Ghats. First, both in the past and in the present, there is a difference in the mammal community composition between the contiguous

forests and the human-dominated landscapes which is significantly greater than can be expected by chance alone (ANOSIM, Global $R = 0.708$, $p = 0.01$). Second, the turnover in large mammal composition within contiguous forest complexes and human-dominated

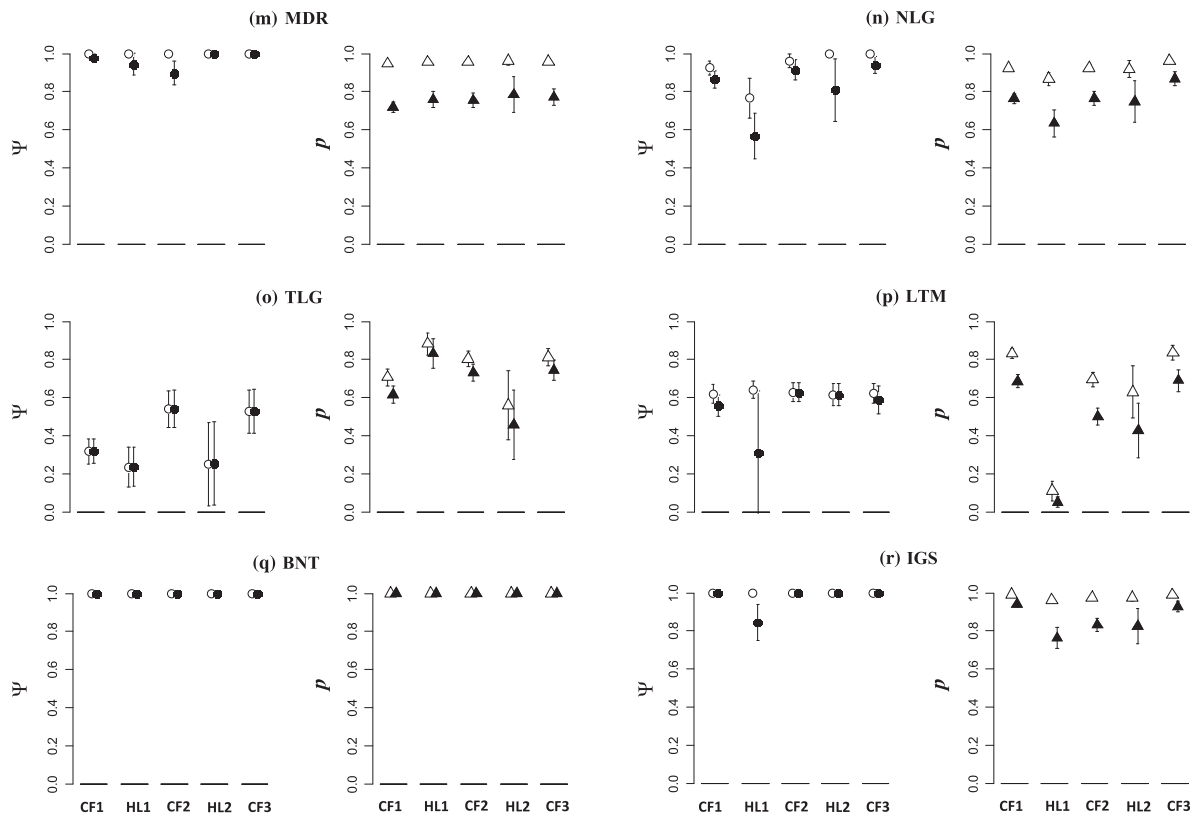


Fig. 2 (continued)

landscapes over time is not significantly greater than expected from chance alone (ANOSIM, Global $R = 0.5$, $p = 0.333$).

4. Discussion

Our results indicate a dire situation for the endangered tiger which has lost more than a quarter of its range in the southern Western Ghats over the last 30 years. Recent abundance estimates suggest that there may be less than 50 tigers in three flagship protected areas within the contiguous forest complexes (Jhala et al., 2008). That the leopard, hitherto considered a resilient species (Athreya et al., 2004), has also undergone range contraction is a matter of concern and underscores the high anthropogenic disturbance in the southern Western Ghats. Hitherto listed as Least Concern (IUCN, 2010), the golden jackal, which has seen catastrophic declines in population and range, may actually be in urgent need of a status reassessment and possibly even a focused recovery program. The situation for the endangered Asian elephant is also grim with an 11% decline in distribution. Declines in distribution and abundance in endemic mountain ungulates such as the Nilgiri tahr and rainforest primates such as the lion-tailed macaque and Nilgiri langur are serious concerns since habitat and diet specialization in the Nilgiri tahr and lion-tailed macaque greatly restrict their geographic distributions and consequently pose a much greater risk of anthropogenic extinction (Cardillo et al., 2004; Purvis et al., 2000). The Nilgiri langur is still widespread and may be relatively biologically robust against extinction but its rainforest habitat has dwindled and it has also been subjected to severe hunting pressure. Although species such as the sambar, muntjac, wild pig and the Indian giant squirrel are hunted, they are very widespread in the southern Western Ghats. Therefore, hunting pressures, while reducing local abundance, may not reflect in range declines until abundance goes below a certain threshold (Rodriguez, 2002; Royle

and Dorazio, 2008). On the other hand, the replacement of rainforest habitats by dry deciduous forests and the proliferation of degraded areas may not affect generalist species such as the wild pig and bonnet macaque which have adapted to thriving near human presence. As one of the commonest species, wild pigs may be resilient to prevailing levels of hunting. Religious beliefs have protected species such as the bonnet macaque from hunting. The chital, an ungulate preferring deciduous forests, is by nature patchily distributed in the rainforest-dominated southern Western Ghats. It has shown colonization due to managed introductions into some sites in the southern Western Ghats.

Declines in large mammal distribution and abundance are lower in the contiguous forest complexes compared to the human-dominated landscapes. In HL1 and the CF1, where anthropogenic pressures are highest, the tiger's range has contracted by more than 50%. This may be because of its intrinsic traits as a large-bodied carnivore, which make it particularly susceptible to anthropogenic extinction through depletion of its large-bodied prey (Carbone and Gittleman, 2002; Karanth et al., 2004) such as the gaur and sambar. These widespread prey species are themselves declining in abundance (Fig. 2) although such declines have not yet manifested as range contractions (Rodriguez, 2002; Royle and Dorazio, 2008) (Fig. 2). This may be exacerbated by the fact that the chital may not be a primary prey for the tiger in the southern Western Ghats given its patchy distribution and low densities (Johnsingh and Sankar, 1991; Ramakrishnan et al., 1999) while the wild pig largely prefers forest fringe habitats which tigers tend to avoid. Similarly, Asian elephant range has contracted by 9–12% in the human-dominated landscapes, again possibly the fallout of the large body size and wide ranging habits of this species, which bring it into frequent conflict with humans. Slow recruitment rates in the elephant (Sukumar, 2003) exacerbate extinction risk from anthropogenic causes.

Table 4
Extinction and colonization rates over 30 years (± 1 SE) for 18 large mammal species across three contiguous forest complexes (CF) and intervening human-dominated landscapes (HL) in the southern Western Ghats.

Species	CF1	CF2	CF3	HL1	HL2
<i>Extinction rate</i>					
TGR	0.26 (0.06)	0.11 (0.06)	0.17 (0.08)	0.50 (0.14)	0.55 (0.23)
SLB	0.16 (0.05)	0.02 (0.01)	0.02 (0.01)	0.28 (0.16)	0.11 (0.24)
LPD	0.06 (0.03)	0.04 (0.03)	0.05 (0.04)	0.25 (0.09)	0.12 (0.12)
DHL	0.02 (0.02)	0.02 (0.01)	0.02 (0.01)	0.07 (0.04)	0.02 (0.01)
JKL	0.12 (0.05)	0.12 (0.05)	0.12 (0.05)	0.14 (0.05)	0.11 (0.04)
ELP	0.12 (0.03)	0.10 (0.03)	0.10 (0.03)	0.12 (0.04)	0.09 (0.02)
GAR	0.03 (0.02)	0.06 (0.04)	0.01 (0.01)	0.17 (0.09)	0.01 (0.01)
SAM	0 (0)	0 (0)	0 (0)	0.05 (0.06)	0 (0)
NTR	0.14 (0.05)	0.10 (0.05)	0.09 (0.03)	0.17 (0.08)	0.09 (0.03)
WPG	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
CHT	0.01 (0.01)	0.01 (0.01)	0.14 (0.09)	0.01 (0.01)	0.01 (0.01)
MJK	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
MDR	0.02 (0.02)	0.10 (0.06)	0 (0)	0.06 (0.06)	0 (0)
NLG	0.07 (0.03)	0.05 (0.04)	0.06 (0.04)	0.26 (0.11)	0.19 (0.16)
TLG	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
LTM	0.10 (0.06)	0 (0)	0.06 (0.08)	0.52 (0.51)	0 (0)
BNT	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
IGS	0 (0)	0 (0)	0 (0)	0.15 (0.1)	0 (0)
<i>Colonization rate</i>					
SLB	0.19 (0.12)	0.19 (0.12)	0.19 (0.12)	0.19 (0.13)	0.19 (0.12)
CHT	0.09 (0.06)	0.07 (0.04)	0.10 (0.06)	0.07 (0.04)	0.07 (0.04)
TLG	0.003 (0.02)	0.002 (0.02)	0.002 (0.02)	0.002 (0.02)	0.002 (0.02)

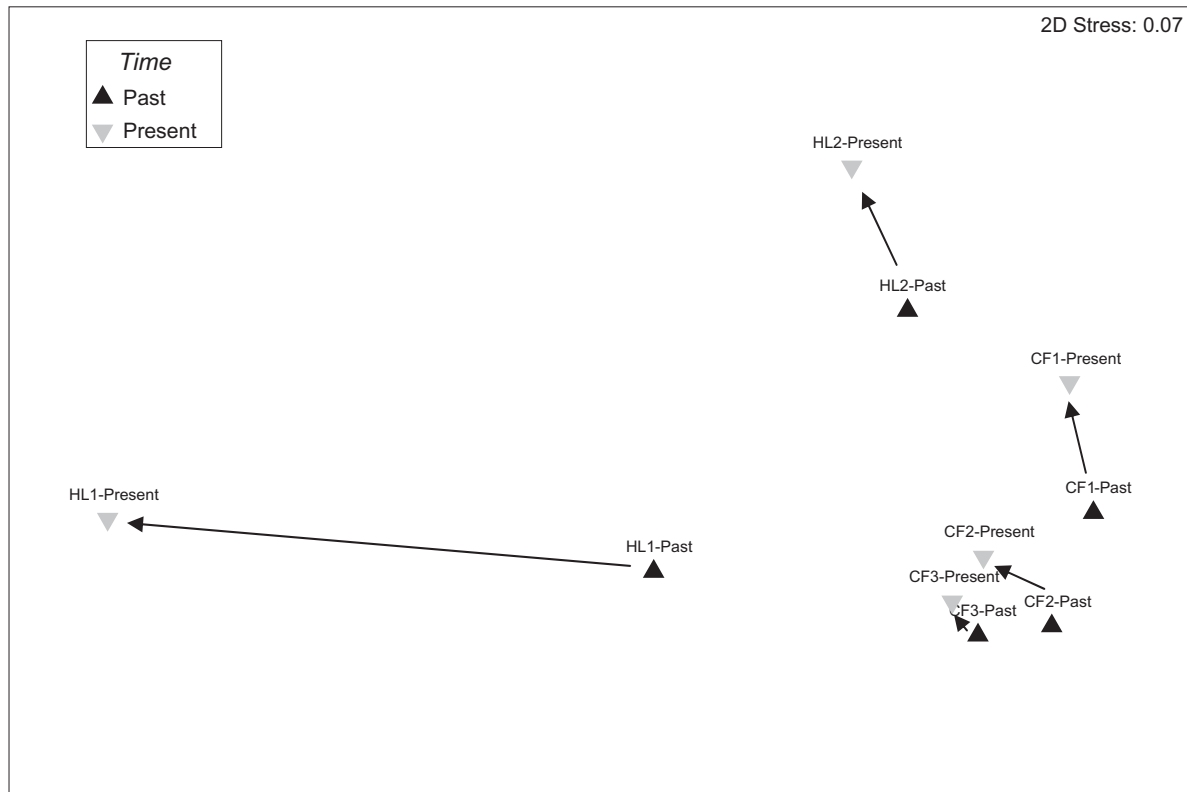


Fig. 3. Non-metric multidimensional scaling (NMSD) plot illustrating compositional similarity and turnover in terms of large mammal occupancy within and between contiguous forest complexes and human-dominated landscapes over time. CF1, CF2 and CF3 = Anamalai, Periyar and Agasthyamalai contiguous forest complexes respectively. HL1 and HL2 = Anamalai–Periyar and Periyar–Agasthyamalai human-dominated landscapes respectively.

Compositional similarity in terms of large mammal occupancy within the contiguous forest complexes and human-dominated landscapes has remained relatively unchanged over time but the differences between these two types of landscapes have increased over the same period (Fig. 3). The forest complexes constitute conservation landscapes where clusters of protected areas are

connected by reserved forests. It is therefore critical that these large contiguous conservation landscapes are integrated into conservation efforts, which have hitherto focused on protected areas, such that wildlife populations can be consolidated at larger regional scales (Johnsingh et al., 2009). Our surveys point to the possibility of connecting CF1 and CF2 conservation landscapes

through remnant forest patches along the main ridge of the Western Ghats. Although these forest patches cover steep terrain, are isolated and are subjected to immense biotic pressures; a scientific program of habitat restoration together with stringent protection against habitat encroachment and poaching may enable them to serve as stepping stones (Bennett, 2003) in the future so as to facilitate large mammal movement and gene flow (Johnsingh et al., 2009).

The proportion of area occupied by closely related, ecologically similar species is positively correlated with average abundance and this pattern is manifested across a range of spatial scales (Brown, 1984; Gaston, 1996). This positive relationship between abundance and distribution suggests that a decline in abundance of a species may lead to a decline in distribution due to local extinction of that species from parts of its geographic range. However, if declines in abundance occur in parts of the species geographic range where abundances are the highest or uniformly across the species range (Rodriguez, 2002), there may be a delay before such declines in abundance lead to range contraction and local extinction (Royle and Dorazio, 2008) following habitat loss, degradation or other anthropogenic and environmental perturbations (Kuussaari et al., 2009). Since such extinctions occur generations after the perturbation event, they are known as extinction debt (Tilman et al., 1994), a future ecological price of recent or current habitat perturbations. For species which have undergone range contractions, the repayment of extinction debts may have commenced. However, our results show declines in abundance but not in distribution for species such as the dhole, sambar, Indian muntjac, Indian chevrotain and Indian giant squirrel. These indicate the accrual of extinction debts, which will be repaid in the form of range contractions and subsequent species extinctions once abundance goes below a certain threshold.

Our reliance on the recall of multiple key informants at each site to generate past and present detection histories makes it possible that the temporal precision with which interviewees report past detections may be lower than for reports of present detections. This leads to the possibility that past detection histories come from a wider time window than the 1 year time window we used to develop detection histories for the present. However, we believe that our method of extensively cross-examining key informants may have allowed the time window for the past primary sampling season to largely conform to the time window for the present primary sampling season. Additionally, our use of multiple-season models which allow for different detection probabilities in the past and present primary sampling seasons may absorb some violations of the closure assumption possibly resulting from unequal time windows for the past and present primary sampling seasons (MacKenzie et al., 2006).

However, it would have been difficult to obtain past data and assess changes in large mammal distribution and abundance without this interview-based method. Our work demonstrates the potential of structured interview surveys of knowledgeable key informants in developing detection histories for a given species across multiple sites. When combined with occupancy modeling, these data can reliably depict large-scale spatiotemporal trends in species distributions. Although traditional field surveys for estimating abundance would continue to be preferred for population assessments, our method may be used to survey trends in the distribution and abundance of multiple species over large landscapes in relatively short time periods at a minimal cost. From a conservation perspective, our work supports previous studies (Brashares et al., 2001; Cardillo et al., 2004; Karanth et al., 2010; Schipper et al., 2008) which underline anthropogenic impacts as the primary drivers of mammal declines. Addressing this suite of demographic threats in the highly impacted tropical regions of the world is a complex task, but nonetheless one that must be effective and

enduring if large mammals are to thrive in these biodiverse regions of the world.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.01.026.

References

- Achard, F., Eva, H.D., Stibig, H.J., Mayaux, P., Gallego, J., Richards, T., Malingreau, J.P., 2002. Determination of deforestation rates of the world's humid tropical forests. *Science* 297, 999–1002.
- Athreya, V.R., Thakur, S.S., Chaudhuri, S., Belsare, A.V., 2004. A study of the man-leopard conflict in Junnar Forest Division, Pune District, Maharashtra, Submitted to the Office of the Chief Wildlife Warden, Nagpur. Maharashtra Forest Department.
- Bennett, A.F., 2003. Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation. IUCN, Gland, Switzerland and Cambridge, UK.
- Brashares, J.S., 2003. Ecological, behavioral, and life-history correlates of mammal extinctions in West Africa. *Conservation Biology* 17, 733–743.
- Brashares, J.S., Arcese, P., Sam, M.K., 2001. Human demography and reserve size predict wildlife extinction in West Africa. *Proceedings of the Royal Society of London B, Biological Sciences* 268, 2473–2478.
- Brown, J.H., 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124, 255–279.
- Burnham, K.P., Anderson, D.R., 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Carbone, C., Gittleman, J.L., 2002. A common rule for the scaling of carnivore density. *Science* 295, 2273–2276.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309, 1239–1241.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J., Mace, G.M., 2004. Human population density and extinction risk in the world's carnivores. *PLoS Biology* 2, 909–914.
- Ceballos, G., Ehrlich, P.R., 2002. Mammal population losses and the extinction crisis. *Science* 296, 904–907.
- Champion, H.G., Seth, S.K., 1968. *A Revised Survey of the Forest Types of India*. Natraj Publishers, Dehradun, India.
- Channell, R., Lomolino, M.V., 2000a. Dynamic biogeography and conservation of endangered species. *Nature* 403, 84–86.
- Channell, R., Lomolino, M.V., 2000b. Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography* 27, 169–179.
- Cincotta, R.P., Wisniewski, J., Engelman, R., 2000. Human population in the biodiversity hotspots. *Nature* 404, 990–992.
- Das, A., Krishnaswamy, J., Bawa, K.S., Kiran, M.C., Srinivas, V., Kumar, N.S., Karanth, K.U., 2006. Prioritisation of conservation areas in the Western Ghats, India. *Biological Conservation* 133, 16–31.
- Diamond, J.M., Ashmole, N.P., Purves, P.E., 1989. The present, past and future of human-caused extinctions. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 325, 469–477.
- Gaston, K.J., 1996. The multiple forms of the interspecific abundance–distribution relationship. *Oikos* 76, 211–220.
- Gros, P.M., Kelly, M.J., Caro, T.M., 1996. Estimating carnivore densities for conservation purposes: indirect methods compared to baseline demographic data. *Oikos* 77, 197–206.
- Hines, J.E., 2006. PRESENCE 2. Software to Estimate Patch Occupancy and Related Parameters. USGS-PWRC. <<http://www.mbr-pwrc.usgs.gov/software/presence.html>>.
- IUCN, 2010. Summary Statistics for Globally Threatened Species, In 2010 IUCN Red List of Threatened Species. <<http://www.redlist.org>> (accessed 26.07.10).

- Jhala, Y.V., Gopal, R., Qureshi, Q., 2008. Status of Tigers, Co-predators and Prey in India. National Tiger Conservation Authority, Government of India, New Delhi and Wildlife Institute of India, Dehradun.
- Johnsingh, A.J.T., Pillay, R., Raghunath, R., Anand, M.O., Madhusudan, M.D., 2009. Opportunities and challenges for tiger (*Panthera tigris*) conservation in the southern Western Ghats, India. In: Shifting Trajectories of Ecology and Coexistence: Proceedings of the National Seminar on People and Tigers, Kerala Forest Department, Periyar Tiger Reserve, Thekkady, India, pp. 135–147.
- Johnsingh, A.J.T., Sankar, K., 1991. Food plants of chital, sambar and cattle on Mundanthurai plateau, Tamil Nadu, south India. *Mammalia* 55, 57–66.
- Karanth, K.K., Nichols, J.D., Hines, J.E., Karanth, K.U., Christensen, N.L., 2009. Patterns and determinants of mammal species occurrence in India. *Journal of Applied Ecology* 46, 1189–1200.
- Karanth, K.K., Nichols, J.D., Karanth, K.U., Hines, J.E., Christensen, N.L., 2010. The shrinking ark: patterns of large mammal extinctions in India. *Proceedings of the Royal Society B: Biological Sciences* 277, 1971–1979.
- Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., Hines, J.E., 2004. Tigers and their prey: predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences* 101, 4854–4858.
- Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution* 24, 564–571.
- Macdonald, D.W., 2001. *The New Encyclopaedia of Mammals*. Oxford University Press, Oxford.
- Mackenzie, D.I., 2005. What are the issues with presence–absence data for wildlife managers? *Journal of Wildlife Management* 69, 849–860.
- Mackenzie, D.I., Nichols, J.D., Gideon, B.L., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- Mackenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207.
- Mackenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, San Diego, California, USA.
- Madhusudan, M.D., Mishra, C., 2003. Why big, fierce animals are threatened: conserving large mammals in densely populated landscapes. In: Saberwal, V., Rangarajan, M. (Eds.), *Battles over Nature: Science and the Politics of Conservation*. Permanent Black, New Delhi, pp. 31–55.
- Maynard Smith, J., 1989. The causes of extinction. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 325, 241–252.
- Menon, S., Bawa, K.S., 1997. Applications of geographic information systems, remote-sensing, and a landscape ecology approach to biodiversity conservation in the Western Ghats. *Current Science* 73, 134–145.
- Menon, V., 2003. *A Field Guide to Indian Mammals*. Dorling Kindersley/Penguin, New Delhi, India.
- Morrison, J.C., Sechrest, W., Dinerstein, E., Wilcove, D.S., Lamoreux, J.F., 2007. Persistence of large mammal faunas as indicators of global human impacts. *Journal of Mammalogy* 88, 1363–1380.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Nair, S.C., 1991. *The Southern Western Ghats: A Biodiversity Conservation Plan*. Indian National Trust for Art and Cultural Heritage (INTACH), New Delhi, India.
- Pimm, S.L., Jones, H.L., Diamond, J.M., 1988. On the risk of extinction. *The American Naturalist* 132, 757–785.
- Pollock, K.H., 1982. A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46, 752–757.
- Primer-E, 2007. *PRIMER 6 for Windows*. Version 6.1.8. Primer-E Ltd., Ivybridge, UK.
- Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B, Biological Sciences* 267, 1947–1952.
- Ramakrishnan, U., Coss, R.G., Pelkey, N.W., 1999. Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. *Biological Conservation* 89, 113–120.
- Rodriguez, J.P., 2002. Range contraction in declining North American bird populations. *Ecological Applications* 12, 238–248.
- Royle, J.A., Dorazio, R.M., 2008. *Hierarchical Modeling and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities*. Academic Press, San Diego, CA.
- Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence–absence data or point counts. *Ecology* 84, 777–790.
- Schipper, J. et al., 2008. The status of the world's land and marine mammals: diversity, threat and knowledge. *Science* 322, 225–230.
- Sukumar, R., 2003. *The Living Elephants. Evolutionary Ecology, Behaviour and Conservation*. Oxford University Press, New York, USA.
- Thompson, W.L., 2004. *Sampling Rare or Elusive Species: Concepts, Designs and Techniques for Estimating Population Parameters*. Island Press, Washington, DC.
- Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. *Nature* 371, 65–66.
- White, P.C.L., Jennings, N.V., Renwick, A.R., Barker, N.H.L., 2005. Questionnaires in ecology: a review of past use and recommendations for best practice. *Journal of Applied Ecology* 42, 421–430.