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Fruit gardens enhance mammal diversity and biomass in a Southeast Asian rainforest

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Protected areas are frequently inhabited by people and conservation must be integrated with traditional management systems. Cultivation of fruit gardens is a low-impact agroforestry technique which alters the structure and composition of forest stands and has the potential to thereby influence animal communities. This is of particular interest in the rainforests of Southeast Asia, where limited fruit availability between intermittent mast fruiting events results in low mammal densities. We assessed how agroforestry practises of an indigenous community affect terrestrial mammal abundance, diversity and assemblage composition within Krau Wildlife Reserve, Pahang, Malaysia. We used baited camera traps to compare mammal abundance and diversity between seven fruit gardens and eight control sites. Fruit gardens contained similar species richness and abundance levels but higher diversity and almost threefold higher mammal biomass. Fruit gardens contained five times as many fruit-producing trees and a positive correlation was found between the number of fruit trees and total mammal biomass. Mammal community composition differed between the two habitats, with fruit gardens attracting nine species of conservation concern. These results suggest that traditional agroforestry systems may provide additional resources for mammals and therefore their net effects should be considered in conservation policy.

1. Introduction

Rainforests throughout the world have a long history of human occupation (Kareiva et al., 2007). This is often associated with shifting agriculture, which favours particular plant species during both cultivation and the subsequent regeneration (van Vliet et al., 2012). Agroforestry promotes favoured species such as fruiting trees, often with a higher nutrient content than the surrounding vegetation (Miller and Nair, 2006). Similar agricultural practises are widespread among indigenous communities throughout South America (Miller and Nair, 2006) and Southeast Asia (Nyhus and Tilson, 2004). Indigenous peoples have occupied and cultivated Southeast Asian forests for over 11,000 years (Hunt and Rabett, 2013). Conflicts frequently arise between the objectives of reserve managers and these communities, with a lack of understanding of the net effects of traditional practises acting as a barrier to their effective integration into conservation management (Aziz et al., 2013).

The rainforests of Southeast Asia are often described as food deserts due to the relatively low abundance of fruits between infrequent mast fruiting events (Corlett and Primack, 2011). Mast fruiting behaviour is displayed by several hundred tree species throughout the region, and in particular by the dominant Dipterocarp tree family (Curran and Leighton, 2000). Events occur at irregular intervals 2–7 years apart and result in synchronous production of large fruit crops over hundreds of kilometres (Numata et al., 2003). Rainforests elsewhere in the world commonly display annual fruit production (Stevenson et al., 2008) alongside a greater abundance of shrubs and small trees which fruit intermittently in the understory (LaFrankie et al., 2006).

Frugivorous animals therefore occur at relatively lower densities in mast fruiting forests where populations are likely to be highly sensitive to the abundance of fruits between mastings (Ghazoul and Sheil, 2010). This relationship has been well documented in primates whose density is reduced in those forests of Gabon which are dominated by masting trees in the Caesalpinaceae, in South America dominated by Lecythidacaeae, and in Southeast Asia dominated by Dipterocarpaceae (Brugiere et al., 2002). The characteristics of this type of forest therefore present a unique set of challenges for conservation as limited food availability leads to low frugivore densities, making populations intrinsically vulnerable to habitat loss. These challenges are further complicated when conservation management also has to consider the effects of traditional practises by indigenous populations within protected areas.

Krau Wildlife Reserve was gazetted in 1923. The Chewong are an indigenous group native to central peninsular Malaysia who have been present in the reserve since establishment. They have a small population of approximately 400 individuals, around half of whom still live

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within the reserve boundaries. The Chewong continue to practise traditional cultivation, hunting, fishing and gathering of wild fruits, herbs and plants for medicines (Howell, 1984). Their cultivation techniques include clearings for planted crops alongside fruit gardens which are enhanced with favoured fruiting trees. Fruit garden cultivation involves the selection of suitable patches of forest, removal of certain tree species within these areas (used for building materials or otherwise unwanted), then the planting of fruiting tree species such as durian *Durio* spp., kepayang *Pangium edule* and rambutan *Nephelium lappaceum*. Fruit gardens are lightly tended and fruit is collected annually during the months of June, July and August for up to 50 years. Fruit gardens are contiguous with old growth forest and involve limited forest clearance, maintaining much of the original vegetation composition and structure (Wiersum, 2004). Since favoured species of fruiting trees are planted among the existing vegetation, it is likely that the long-term effect will be to increase fruit resources through higher densities and seasonal availability of annually fruiting tree species.

Our study aimed to investigate how fruit gardens influence the abundance, diversity and composition of terrestrial mammalian frugivore assemblages at this site. We anticipated that (a) fruit gardens would leave a legacy of greater abundance of fruiting trees than natural forest areas, and (b) this would act as a resource drawing in greater abundance and diversity of frugivores.

2. Methods

2.1. Study area

Krau Wildlife Reserve, Pahang, (3°33′ N 102°30′ E; Fig. 1) is approximately 600 km^2 in size, with a range in altitude from 45 to 2108 m above sea level. Vegetation within the reserve predominantly consists of lowland dipterocarp forest (61%), hill dipterocarp forest (22.5%) and upper dipterocarp forest (9%) with minor components of secondary forest (1.1%) and cultivated/cleared land (0.6%) (Chou and Saw, 2006). Contiguous forests in the mountainous North and lowland South-West combine to a total area of 1100 km^2; however forests outside the reserve are highly fragmented by rubber tree and oil palm plantations. Over the past 50 years defaunation of many large-bodied mammal species has occurred in this reserve, with the total loss of the Asian elephant *Elephas maximus*, gaur *Bos gaurus*, Sumatran rhino *Dicerorhinus sumatrensis* and Javan rhino *Rhinoceros sondaicus*, alongside a reduction in numbers of Malayan Tiger *Panthera tigris jacksoni*, Malayan tapir *Tapirus indicus*, sambar deer *Rusa unicolor* and barking deer *Muntiacus muntjak*.

2.2. Sampling strategy

We surveyed two types of plots: fruit gardens and controls (natural forest). Fruit gardens were identified by local guides as areas currently or previously cultivated for growing fruiting tree species for local consumption. Time since establishment varied from 6 to 55 years according to estimates from local elders (30 ± 8, mean ± SE). Fruit gardens are often situated in close proximity to current or abandoned villages within the forest; those selected for study were 1015 ± 446 m from the nearest active village (mean ± SE). Control plots were chosen based on local knowledge as being natural unmodified forest (no known previous management) with potential for conversion into a fruit garden based on Chewong impressions of suitability. This depends upon existing plant species (trees and understory) along with the suitability of the site for growing fruiting species and accessibility (882 ± 202 m from nearest active village).

A minimum distance of 0.5 km between fruit garden and control plots was used to ensure independent sampling of locations. While a distance of 1–2 km is preferred for terrestrial mammal species (Brodie and Giordano, 2013), we were constrained by the positions of fruit gardens, and aimed to maximise survey effort in line with recommendations by Tobler et al. (2008).

The boundaries of fruit gardens were marked out by local guides and measured in straight line segments. The distance from a central point to each corner was measured and Heron's formula used to calculate area (Colakoglu et al., 2013). A circular plot was placed randomly within each site. Diameter at breast height (dbh, measured at 1.3 m) was measured for all saplings (1–10 cm dbh) within a 9 m radius and trees (>10 cm dbh) within an 18 m radius (~1000 m^2). Specimens were collected for fruit tree identification as determined by local guidance.

2.3. Camera trapping

Seven fruit garden and eight control plots were surveyed over a two-month period using 24 HD Bushnell camera traps. Our aim was to obtain

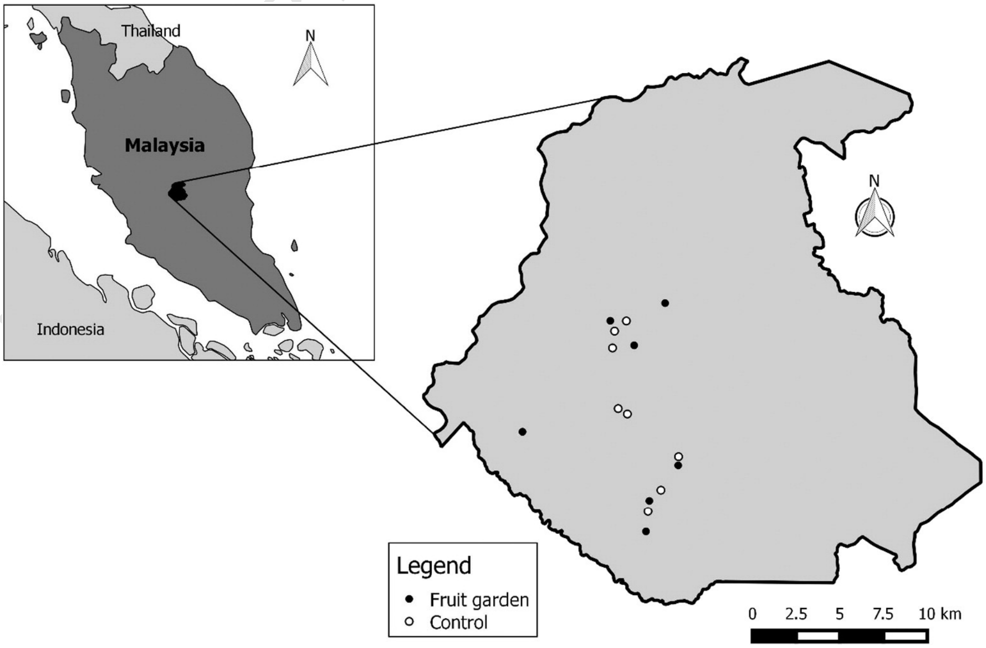

Fig. 1. Map showing locations of fruit garden and control study plots within Krau Wildlife Reserve, Pahang, Malaysia.

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the equivalent of eight weeks of camera trapping per plot (56 days). Each survey consisted of two camera trapping phases per plot with a duration of 7–10 days per phase and four camera traps deployed per phase. Cameras were placed along active animal trails to maximise chance of detecting species and locations changed for the second phase to increase coverage. LED sensitivity was low, one minute video duration, one second trigger delay, highest resolution and date-time stamp enabled. Cameras were 40 cm above the ground with a slight downward angle to ensure consistent capture rates of both small and large mammal species.

Fruit baits were deployed to increase capture rates and designed to emulate small-scale fruiting events. Bait was placed 220 cm from the camera to reduce glare from infrared detection and for consistent identification. Some fruits were split to increase scent and attract more frugivores. The type and individual weights of fruit bait were dependent on local market availability. Baits included a combination of langsat (*Lansium domesticum*), mango (*Mangifera* spp.), cempedak (*Artocarpus integer*) and kepayang. 1.5 kg of fruit bait was used per camera trap per phase, totalling 31 kg of fruit bait for 20 cameras over each 7–10 day period. Longer durations could not be achieved due to degradation and consumption of fruit. The fruits were chosen for their varied characteristics to appeal to a wide range of frugivore species, though may not have attracted all species present.

Mammals were identified using Francis (2008). Due to limitations of camera trap images, reliable identification to species level was not possible for smaller mammals. Two mouse deer species (*Tragulus kanchil* and *Tragulus napu*), three squirrel species (*Callosciurus notatus*, *Lariscus insignis* and *Rhinosciurus laticaudatus*) and four rat species (*Leopoldamys sabanus*, *Maxomys surifer*, *Rattus tiomanicus* and *Maxomys whiteheadi*) were grouped into three functional taxa for diversity analysis. Foraging guilds of animal species were determined based on recommendations from Pineda-Munoz and Alroy (2014) and obtained from a range of sources (Appendix A).

2.4. Data analysis

Numbers of individuals were based upon independent captures. All triggers of the same species were considered to be the same individual until a period greater than one hour had elapsed between triggers after which a new individual was counted (Silveira et al., 2003). Average body mass for mammal species was taken from Francis (2008) apart from sambar deer from Dahlan and Dawend (2013). These were multiplied by the number of individuals to estimate total mammal biomass. To ensure that inconsistent detection did not confound assessments of community structure we calculated per-species detectability using PRESENCE and compared values obtained from gardens and control plots (Hines, 2006).

Coverage was calculated to assess completeness of sampling, defined as the proportion of the total number of individuals in a community that belong to the species represented in the sample (Chao and Jost, 2012). Hill's numbers (Hill, 1973) were calculated in line with current consensus on quantifying species diversity (Tuomisto, 2010). Hill's numbers are defined to the order q (^{q}D), with estimated species richness (^{0}D) weighted towards rare species due to its insensitivity to relative frequencies, exponential of Shannon's entropy (^{1}D) weighted towards common species, and inverse of Simpson's diversity (^{2}D) weighted towards highly abundant species. These therefore provide complementary information on the richness and evenness of assemblages.

Additional covariates were analysed to evaluate potential biases in the data. Spatial autocorrelation of abundance and diversity indices was assessed using Moran's I. No evidence of spatial autocorrelation was found (see Appendix B) and subsequent analyses therefore omitted spatial covariates. Further potential confounding effects of age of fruit garden and distance to closest active village on the abundance and diversity of mammals were assessed; no significant relationships were found (Appendix B).

An analysis of similarity (ANOSIM) assessed whether species composition varied between samples. This grouped samples according to the a priori hypothesis that they would differ among habitat types (fruit garden or control). Significance was assessed by comparison of the observed value of R (ANOSIM statistic) against 1000 values generated via random permutations of the group assignment. All statistics were calculated using `R` version 3.0.2 and package `vegan` 2.0-10 (Oksanen et al., 2013; R Development Core Team, 2014). Sørensen's Index of dissimilarity was calculated for every pair of sites then averaged to determine levels of turnover among assemblages (fruit garden and control).

3. Results

3.1. Vegetation

A total of 15 plots were sampled; seven fruit gardens and eight control plots. The average area of a fruit garden was 3200 ± 759 m^2. Sampling plots within fruit gardens did not differ significantly from controls in number of saplings (fruit gardens: 52.7 ± 41.8, controls: 79.6 ± 29.1, mean ± SE; $t = 1.349$, df = 8.5, $P = 0.212$) or basal area (m^2/ha) (fruit gardens: 3.03 ± 0.71, controls: 3.66 ± 0.40; $t = 0.840$, df = 12, $P = 0.420$) but they contained half as many trees per 1000 m^2 (fruit gardens: 28.8 ± 3.9, controls: 60.4 ± 1.9; $t = 8.214$, df = 6.4, $P = 0.001$) of which there were approximately five times more fruiting trees than control plots (fruit garden: 12.80 ± 3.13, control: 2.63 ± 0.65; $t = 3.620$, df = 12, $P = 0.004$). 45% of tree stems within fruit gardens were fruit-bearing compared with 4% in control forest plots.

3.2. Frugivore diversity

3.2.1. Vertebrate community

We recorded 1678 individuals of 21 vertebrate species (16 mammal, four bird and one reptile) (Table 1) from 1024 camera trap nights. Of the 21 species nine were of notable IUCN status with one endangered (Malayan tapir *Tapirus indicus*), six vulnerable (large spotted civet *Viverra megaspila*, Asian small-clawed otter *Aonyx cinerea*, southern pig-tailed macaque *Macaca nemestrina*, sun bear *Helarctos malayanus*, sambar deer, Malayan Peacock Pheasant *Polyplectron malacense*), and two near threatened (Crested Fireback *Lophura ignita* and the Great Argus *Argusianus argus*). Birds (52 individuals) were excluded from subsequent analyses.

All species were recorded within fruit gardens, though five were not found in control plots (Asian small-clawed otter, small-toothed-palm civet *Arctogalidia trivirgata*, masked-palm civet *Paguma larvata*, long-tailed macaque *Macaca fascicularis* and the Malayan tapir). Of all individuals detected within fruit gardens 44% were omnivorous, 38% herbivorous, 16.5% exclusively frugivorous and 0.5% carnivorous compared to controls with 74% omnivorous, 21% herbivorous and 5% frugivorous. There was therefore a higher proportion of frugivores in fruit gardens, contributed predominantly by southern pig-tailed macaques.

Coverage was 0.996 and 0.999 for fruit garden and control plots respectively, indicating that sampling was close to completion and estimates of diversity within habitats are reasonable. No significant difference in per-species detectability was found between areas ($t = -0.1746$, $P = 0.864$).

3.2.2. Mammal community

Fruit gardens did not differ significantly from control plots in mean abundance of mammal individuals (fruit gardens: 101 ± 22, controls: 114 ± 16, $t = 0.53$, df = 13, $P = 0.606$). When total body mass (kg) of mammal species was taken into account, however, fruit gardens were found to have significantly higher body mass of mammals than control areas ($t = 3.60$, df = 12, $P = 0.004$). Fruit gardens contained almost three times the total biomass of mammals with an average of

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Table 1
Species list, total abundance (TA), body mass (BM), foraging guild and IUCN status (least concern (LC), near threatened (NT), vulnerable (VU) and endangered (EN)) of animals detected fruit gardens (F) and control (C) plots.

Order	Family	Genus	Species	Common name	BM (kg)	TA (F)	TA (C)	Foraging guild	IUCN
Artiodactyla	Cervidae	*Muntiacus*	*muntjak*	Barking deer	21	6	3	Herbivore	LC
Artiodactyla	Cervidae	*Rusa*	*unicolor*	Sambar deer	134	14	12	Herbivore	VU
Artiodactyla	Suidae	*Sus*	*scrofa*	Eurasian wild pig	32	16	7	Omnivore	LC
Artiodactyla	Tragulidae	*Tragulus*	*spp*	Mouse deer	4	12	20	Herbivore	LC
Carnivora	Mustelidae	*Aonyx*	*cinerea*	Asian small-clawed otter	3.5	5	0	Carnivore	VU
Carnivora	Ursidae	*Helarctos*	*malayanus*	Sun bear	45	7	3	Omnivore	VU
Carnivora	Viverridae	*Viverra*	*megaspila*	Large spotted civet	8	56	57	Omnivore	VU
Carnivora	Viverridae	*Paguma*	*larvata*	Masked-palm civet	4	6	0	Omnivore	LC
Carnivora	Viverridae	*Arctogalidia*	*trivirgata*	Small-toothed-palm civet	2	9	0	Omnivore	LC
Columbiformes	Columbidae	*Chalcophaps*	*indica*	Emerald dove	–	6	3	Frugivore	LC
Galliformes	Phasianidae	*Argusianus*	*argus*	Great argus	–	4	8	Frugivore	NT
Galliformes	Phasianidae	*Lophura*	*ignita*	Crested fireback	–	1	5	Omnivore	NT
Galliformes	Phasianidae	*Polyplectron*	*malacense*	Malayan peacock pheasant	–	3	9	Omnivore	VU
Perissodactyla	Tapiridae	*Tapirus*	*indicus*	Malayan tapir	300	4	0	Herbivore	EN
Primates	Cercopithecidae	*Macaca*	*fascicularis*	Long-tailed macaque	5	1	0	Omnivore	LC
Primates	Cercopithecidae	*Macaca*	*nemestrina*	Southern pig-tailed macaque	6	111	40	Frugivore	VU
Rodentia	Hystricidae	*Atherurus*	*macrourus*	Brush-tailed porcupine	2	124	61	Herbivore	LC
Rodentia	Hystricidae	*Hystrix*	*brachyura*	Malayan porcupine	8	115	112	Herbivore	LC
Rodentia	Muridae	N/A	N/A	Rat species	0.5	130	498	Omnivore	N/A
Rodentia	Sciuridae	N/A	N/A	Squirrel species	0.25	91	116	Omnivore	N/A
Squamata	Varanidae	*Varanus*	*salvator*	Water monitor lizard	–	1	2	Insectivore	LC

930 ± 138 kg per fruit garden compared to controls with 345 ± 72 kg. Fig. 2 shows control plots contained a higher abundance of small-bodied mammals, while fruit gardens contained relatively more medium to large-bodied mammals. A significant positive correlation was found between number of fruit trees and overall mammal biomass ($r^2 = 0.311$, $P = 0.048$; Fig. 3).

Both observed and estimated species richness of mammalian frugivores was marginally higher in fruit gardens, though not significantly so (Table 2). Diversity indices, however, revealed significantly greater mammal diversity in fruit gardens for both exponential of Shannon's entropy (${}^1D$) and inverse of Simpson's diversity indices (${}^2D$). This signifies that fruit gardens contain a greater effective number of mammal species with moderate to high abundance than control areas, demonstrating greater evenness in abundance (Table 2). A Hill series plot shows higher effective species richness for fruit gardens at all orders of q above 0 (Fig. 4). This uneven abundance of mammals is clearly demonstrated in control plots where three taxa accounted for 74% of individuals: rats (52%), squirrels (12%) and Malayan porcupines *Hystrix brachyura* (12%). In fruit garden plots five taxa accounted for 70% of individuals: rats (18%), brush-tailed porcupines *Atherurus macrourus* (17%), southern pig-tailed macaque (15%), squirrels (12%) and large spotted civet (8%). All diversity analysis was repeated including birds and excluding squirrel and rat groups, with no qualitative difference in results (see Appendix C).

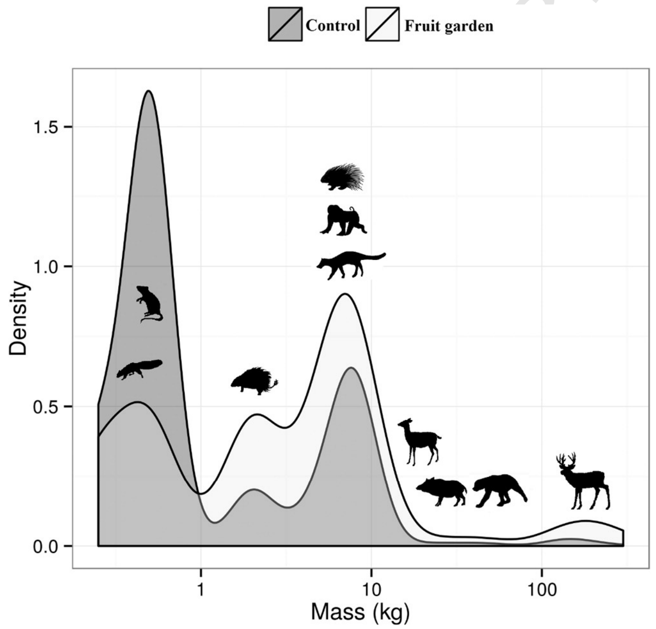

Fig. 2. Kernel density estimate of frugivore relative frequencies by body mass (kg) for both fruit garden and control plots with illustrative mammal species. Mammals depicted relative to body mass size (from left to right; squirrel sp., rat sp., brush-tailed porcupine, large spotted civet, southern pig-tailed macaque, Malayan porcupine, barking deer, Eurasian wild pig, sun bear and sambar deer).

ANOSIM demonstrated that the most similar samples are grouped by habitat type ($R = 0.41$, $P = 0.001$), confirming a strong difference in composition between fruit gardens and control plots. Sørensen's Index of dissimilarity calculates beta diversity at 0.40 between fruit garden and control areas. Beta diversity was slightly lower when fruit garden and control areas were compared among themselves (0.37 and 0.35 respectively), indicating that turnover is greatest between fruit gardens and controls.

4. Discussion

Fruit gardens within this rainforest reserve attracted a greater diversity and biomass of terrestrial frugivorous mammals compared to control plots. This can be attributed to a higher density of fruiting

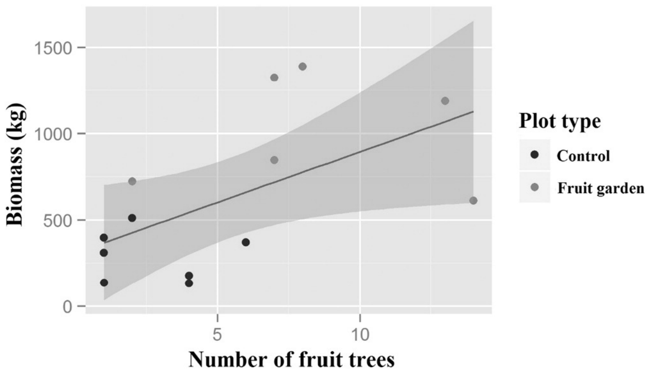

Fig. 3. Correlation between number of fruit trees and total mammal biomass (kg) within fruit garden and control plots.

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Table 2
Diversity indices of mammals for fruit garden and control plots with significance ($P > 0.05$). ($S_{Obs,}$ observed species richness; $S_{Chao,}$ estimated species richness; $e^{H'}$, exponential of Shannon's entropy H; $1/D$, inverse of Simpson's diversity index (±SE)).

^qD	Metric	Fruit garden	Control	$F_{1,13}$	P
	S_{Obs}	9 ± 0.9	7 ± 0.6	3.7	0.075
^0D	S_{Chao}	9.8 ± 1	8.7 ± 1.6	0.3	0.583
^1D	$e^{H'}$	5.4 ± 0.5	3.5 ± 0.4	8.9	0.011
^2D	$1/D$	4.4 ± 0.5	2.6 ± 0.3	9.4	0.009

trees; a positive correlation was found between number of fruiting trees and mammal biomass. Although mammal species richness and overall abundance did not differ between fruit gardens and control areas, the evenness of communities was greater in fruit gardens, average body size was larger, and a distinct species composition was present, including a number of species of conservation importance. This demonstrates that fruit gardens are playing an important role in attracting and supporting terrestrial mammals.

Fruit gardens contained an increased density of fleshy-fruit-producing tree species such as durian, mango, rambutan, cempedak and kepayang. These fruit annually over the months of June, July and August, when fruits are also collected by the Chewong. Mammal communities within fruit gardens contained a higher proportion of primarily frugivorous species, contributed mainly by southern pig-tailed macaques, which are known to favour areas with high fruit availability (Laska, 2001). Pyke et al. (1977) showed that many mammal species direct movement towards areas where encounter rates of desirable food types are increased. Many mammal species are known to shift their diets in relation to spatial and temporal fruit availability, including masked-palm civets, which switch their diet from rodents and birds in primary forests to a predominantly fruit-based diet during the fruiting season in logged forest and farmland (Zhou et al., 2008). Sun bears have been documented switching from a predominantly insectivorous diet during inter-mast periods to almost entirely fruit-based during mast fruiting events (Fredriksson et al., 2006). Densities of mouse deer have been found to correlate with the abundance of small fruits due to their requirements for a highly nutritious and readily digestible diet (Heydon and Bulloh, 1997).

Fruiting events in gardens occur annually, much higher frequency and distinct from the mast fruiting events exhibited by the dominant dipterocarp trees of Southeast Asian rainforests, which occur at intervals of up to 7 years with limited fruit availability in between (Corlett and Primack, 2011; Curran and Leighton, 2000; Numata et al., 2003).

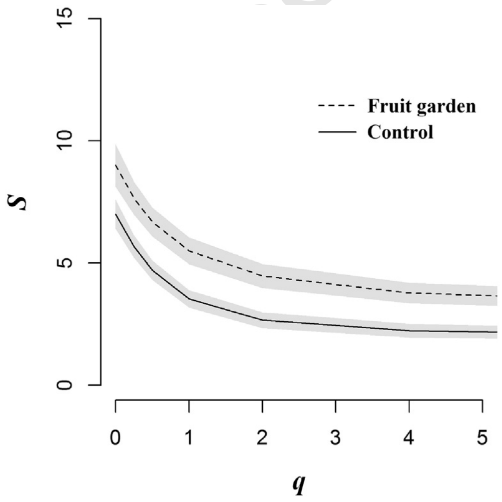

Fig. 4. Hill series plot (order ^qD) indicating diversity of terrestrial mammalian frugivores for fruit garden and control plots. Effective species S with shaded standard error.

The relative scarcity of fruit within Southeast Asian forests is more pronounced than is typical for rainforest regions, and therefore the effects of supplementary fruit are expected to be particularly strong in this region. Rainforests with comparable fruit scarcity exist in both Africa (Newbery et al., 2006) and South America (Norden et al., 2007) and we predict that similar phenomena will occur in these areas. There are also similar agricultural practises to the Chewong, with the potential to enhance mammal communities, which occur elsewhere in Southeast Asia, such as the fruit gardens of the Orang Rimba in Indonesia (Cairns, 2014), the Dusun of Saparua island, Central Maluku, Indonesia (Kaya et al., 2002) and the forest gardens of the Dayak people in East Kalimantan, Indonesia (Mulyoutami et al., 2009). Elsewhere analogous systems of forest gardens are found in the Uvan Uplands of Sri Lanka (Nuberg et al., 1994), the forest gardens of the Kayapo Indians of the Brazilian Amazon (Posey, 1985) and Maya forest gardens in Mexico (Gómez-Pompa Arturo, 1990). The phenomenon of terrestrial mammal enhancement resulting from anthropogenically enhanced fruit availability is therefore potentially widespread throughout the tropics.

Chewong gardens are located within an intact forest landscape, which is an important factor in interpreting these patterns. Duelli and Obrist (2003) found that agroforestry systems connected with natural forest remnants facilitated dispersal, increasing diversity of animal species. The Chewong gardens differ from the majority of tropical agroforestry systems studied to date which are typically located on the edge of forests (Bhagwat et al., 2008; Scales and Marsden, 2008). Bali et al. (2007) demonstrated that agroforests and plantations which are distant from natural forest have reduced mammal species richness.

Chewong fruit gardens have similar basal area to natural forest, are relatively small in scale and involve limited forest clearance, maintaining much of the original vegetation composition and canopy structure. This is crucial in sustaining greater diversity of faunal species both old growth forest specialists and generalists (Chazdon et al., 2009; Tscharntke et al., 2011; Wiersum, 2004). In particular, intensively managed agroforests with reduced canopy connectivity have negative influences on large mammal distributions (Cassano et al., 2014), especially for arboreal mammals which rely on canopy pathways for movement across landscapes (Estrada et al., 2012).

Nine species of conservation concern (43% of species recorded in this study), classified as endangered, vulnerable and near threatened (IUCN, 2014), were found actively foraging within fruit garden areas, compared with just seven species of conservation concern in control plots. This emphasises that the habitat provided by fruit gardens supports vulnerable populations. Most studies of tropical agroforestry have focused on trees, plants, insects or birds, and at sites with a single or limited mixture of fruiting tree species. These differ from the diverse Chewong fruit gardens. The complexity, composition and tree species type incorporated in agroforests, along with the surrounding forest mosaics, are all important factors determining how animal communities respond to them (Bali et al., 2007; Gallina et al., 1996; Harvey et al., 2006; Oliveira et al., 2011).

Estrada et al. (2012) reviewed the importance for primate conservation of tropical agro-ecosystems ranging from simplified pasturelands to more complex polycultures and agroforestry. Across four regions they found 49% of the 57 primate taxa recorded were classified as critically endangered, endangered, vulnerable or near threatened. While our camera trapping was restricted to terrestrial vertebrates, we anticipate that similar patterns might be found in Krau Wildlife Reserve for arboreal and volant frugivores. Agro-ecosystems can therefore play an important role in conservation.

Since many indigenous tribes inhabit what have now been designated as protected areas, balancing conservation while respecting indigenous peoples' rights and practises is difficult (Aziz et al., 2013). The Chewong are largely forest-dwelling and have limited integration into the wider society. They rely predominantly on forest resources. Activities include hunting of small to medium-sized mammals, birds and fish, which provide essential dietary protein. In addition, they gather

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forest products such as rattan for building, herbs for medicinal purposes, honey for consumption and plant poisons for hunting. Crops such as rice and cassava are grown in agricultural clearings to provide a sustained carbohydrate source. These practises all have potential impacts on the surrounding forest and animal communities. While fruit gardens were found in our study to enhance the diversity and biomass of terrestrial frugivores, these effects should be seen as part of a wider portfolio of activities within the forest. Decisions on the impacts of indigenous practises should be made on a case-by-case basis, taking into account the conservation objectives of a given protected area and considering the overall sustainability of the indigenous community (Robinson et al., 2011). Integration of conservation management schemes alongside indigenous peoples is essential, and certain aspects of traditional practises can have net benefits for conservation (Dressler et al., 2010).

High densities of small-bodied rats and squirrels were present in control plots (Fig. 2). Lower densities in fruit gardens may be attributed to a shift in habitat usage to avoid predators such as civets and other carnivorous species (Dickman, 1992). The abundance of small-bodied mammals is an indicator of a partially defaunated system. Many large-bodied frugivores such as elephants and rhino are absent from Krau or greatly reduced in number. Larger frugivores are capable of feeding on and consuming a greater size range of large-seeded plant species (Levey, 1987). A greater gut capacity with a longer seed retention time (Nathan et al., 2008), larger home ranges, and travelling at higher speeds means that large frugivores are capable of providing long-distance and high-quality seed dispersal (Harestad and Bunnell, 1979). Their loss has implications for future plant recruitment (Harrison et al., 2013). To some extent the Chewong, through creation of fruit gardens, may be providing a partial replacement for these ecological services.

5. Conclusion

Traditional fruit gardens within this forest reserve attracted a greater diversity and biomass of terrestrial mammalian frugivores than were found in control plots, including a number of species of conservation concern. Fruit gardens are likely to play an important role in maintaining vulnerable species through increased abundance of annual-fruiting tree species. The mast fruiting nature of dipterocarp forests is likely to enhance this effect, but similar patterns are expected in regions where agroforestry practises supplement available fruit, particularly during seasons of relative scarcity. Agroforestry practises vary widely between indigenous communities in terms of their clearance techniques, tree species incorporated, management and landscape context. Their potential role in conservation should therefore be assessed on a case-by-case basis. The maintenance of traditional land-use systems can in some cases have positive outcomes for conservation and should therefore be considered when developing management plans for inhabited reserves.

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Map. KML file containing the Google map of the most important areas described in this article.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi: http://dx.doi.org/10.1016/j.biocon.2015.12.015. These data include Google map of the most important areas described in this article.

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