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Conservation in a changing landscape: habitat occupancy of the critically endangered Tennent's leaf-nosed lizard (*Ceratophora tennentii*) in Sri Lanka

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Landscape modification is a key driver of global species extinction. Thus, understanding how species react to changes is essential for effective conservation management in modified landscapes. We examined the impact of selected land use patterns on the critically endangered *Ceratophora tennentii* in the Knuckles mountain range of Sri Lanka where lizards occupy patches of both natural undisturbed forests and modified plantations – evidently, those with a forest canopy. We tested three potential explanations for non-random habitat selection: availability of suitable microhabitat pockets, availability of prey and direct threats from humans. The microhabitat pockets occupied by the lizards were characterised by shade, humidity and the density of perches. Most lizards were found in mixed cardamom forests followed by natural forests and cardamom plantations, but none were observed in the pine plantations. Food availability showed similar patterns among habitats. Direct mortality by humans did not influence the distribution of this species. Our work indicates that habitat modifications that retain the structural complexity of the vegetation would still permit the existence of the species in densities equal to or greater than that of undisturbed forest patches. It adds to a growing body of literature that signifies the importance of disturbed habitats (intermediate disturbance hypothesis) in protecting threatened species of fauna. It is highly unlikely that some disturbed habitats will be ever be returned to their former pristine state in time frames that are important for species' conservation. Hence, attention is needed in developing suitable approaches to manage and conserve species across disturbed habitats.

Keywords: cardamom; disturbed habitats; *Elettaria cardamomum*; Knuckle range; montane forests; mixed forests; *Pinus*

Introduction

Rapid alteration of natural habitats, driven by the ever-increasing demand for agricultural land, adds a significant component of habitat variability to tropical environments. Human population-driven habitat alteration is a trend particularly evident in developing countries, where more humans are dependent on the environment for basic survival and where land management practices are relatively poor (Smart et al. 2005; Scherr and McNeely 2008). The loss, degradation and fragmentation of natural habitats through

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these anthropogenic activities have caused most of the contemporary species extinctions and population declines (Pimm and Askins 1995; Brooks et al. 2002; Brook et al. 2003; Franco et al. 2006). Against this backdrop, a sound understanding of the determinants of the distribution of organisms through space and time is essential for the conservation management of modified landscapes. Furthermore, given the low availability of resources for conservation, improved understanding of the processes of threat also enables wildlife managers to prioritise expenditure more effectively (Ujvari et al. 2011).

Sri Lanka is well known for its high endemism (Meegaskumbura et al. 2002; Bossuyt et al. 2004; Pyron et al. 2013) as well as the alarming rate at which its natural habitats are being degraded (Gunatilleke et al. 2008). Among the most biologically diverse but also highly disturbed habitats within the island are the montane forests (Wikramanayake and Gunatilleke 2002; Pethiyagoda and Nanayakkara 2011) that once occupied almost the entire area above 1500 m elevation. By the end of the nineteenth century, expansive forest cover in these regions began to give way to the 'colonial landscape'. When the British administration titled most land on the island as 'crown land' in 1840, the rate of deforestation rapidly accelerated. Large areas of forests were cleared for plantations of cinchona and then coffee and tea up to 'few hundred feet of the crest' (Cooray 1961; Meyer 1998). During this era, the swidden (*chena* or slash and burn) cultivation also came to be more widely practised with devastating results on the forest cover (Chokkalingam and Vanniarachchy 2011). Afforestation with monocultures of exotic timber trees (e.g. *Eucalyptus*, *Cupressus*, *Acacia* and later *Pinus*) that commenced in 1890 (Werner 2001) added more landscape-level homogeneity and also negative environmental effects to the montane region. The remaining ~3000 ha of montane forests were restricted to isolated patches in the central massif and the isolated Knuckles hills (Wijesundara 2012). The burden on the Knuckles hills increased in the 1960s with the commencement of commercial-scale under-planting of the forest with cardamom (*Elettaria cardamomum*) (Badenoch 2008). Hence, over several decades, the post-colonial natural montane forests were degraded as a result of planting exotic timber trees and cardamom, and by vegetable and potato cultivation (Kariyawasam 1991). While the effects of these changes on the forest structure and the economy are relatively well studied, only a few long-term studies have been done to determine the effects of such changes on animals.

With the ever-increasing human-induced habitat alteration being the norm, conservation focusing only on pristine protected areas needs to be revisited. In this study, we examine the impact of different land-use patterns on a critically endangered lizard endemic to the montane and sub-montane regions of the Knuckles hill range. We tested the following predictions: (1) the abundance of lizards differs among structurally different habitat types with different levels of disturbance; (2) lizards occupy specific climatic and structural components of the microhabitat pockets; (3) the availability of food is different within the different habitats; and (4) farmers cause direct disturbances to the lizards.

Methods and materials

Study area

The Knuckles Forest Reserve (KFR; 7°21′–7°24′N, 80°45′–80°48′E) spreads across an altitudinal gradient ranging from 200–1900 m above sea level (a.s.l.) over a 20-km expanse in the central highlands of Sri Lanka (Bambaradeniya and Ekanayake 2003). This steep elevational gradient has resulted in a wide range of micro-climates and edaphic conditions that support several forest and grassland vegetation types (Balasubramaniam 1988; Bambaradeniya and Ekanayake 2003). The KFR harbours one of the most diverse vertebrate assemblages of any Sri Lankan forest reserve, and 10 of the island's 18 agamid lizard species occur here (Goonewardene et al. 2006; Rajapaksha et al. 2006; Somaweera and Somaweera 2009; Samarawickrama et al. 2012). The biological and hydrological value of the Knuckles forest region was recognised in 1873 when the area above 1500 m was declared a Climatic Reserve (Jayasuriya 2008). Since then, the region has received legal conservation status under the Forest Ordinance, administered by the Forest Department. It was declared a Proposed Conservation Area in 1998, as the Knuckles Conservation Area (175 km^2) in April 2000 and then a National Man and Biosphere (MAB) Reserve. More recently, a 313-km^2 section of the range was declared part of United Nations Educational, Scientific and Cultural Organization's (UNESCO's) Central Highlands World Heritage Site (UNESCO 2014).

Commencing in 1890, monocultures of the Caribbean pine (*Pinus caribaea* var. *hondurensis*) were established in 25,091 ha of the KFR, with a view to turning patches of degraded scrubland to productive forests (Ambagahaduwa et al. 2009). Some of these plantations are now naturally regenerating and expanding in extent (Medawatte et al. 2011). The resin produced from these pines is one of the most valuable non-wood forest products in the country (Forestry Department 2010), making these plantations economically important.

More than 55% of the cardamom (*Elettaria cardamomum*) crop in Sri Lanka – the herb's berries being widely used as a spice and a confectionary, and thus an important revenue earner – is located in the Knuckles region. Over 30 km^2 of forest in the KFR has been under-planted with cardamom, especially within the lower-montane and montane forests (Dhakal et al. 2012). Due to its environmental damage, in 1994, the Forest Department stipulated that cardamom cultivation above 1067 m should be terminated in Knuckles. Cultivation of cardamom is today prohibited within the protected area, causing a direct conflict with the local communities' 'traditional' way of life (Lindström et al. 2012), but collection of pods from abandoned plantations is allowed (IUCN 1994). Nonetheless, large-scale plantations continue to be managed and maintained within the conservation area (Jayasuriya 2008).

Study species

Among the reptiles endemic to the Knuckles range is the Tennent's leaf-nosed lizard, *Ceratophora tennentii*. This species is restricted to a ~130-km^2 extent between 700–1700 m elevation in the Knuckles range (Bahir and Surasinghe 2005), but this could be an overestimate as the species is patchily distributed within its range. It was among the first Sri Lankan reptilian species to be assessed for the International Union for Conservation of Nature (IUCN) Red List (IUCN 1996). From the onset, it has been nationally evaluated as 'critically endangered' (MoE 2012) based on its very limited extent of occurrence (under criteria B2ab[iii]). Despite this status, much of its range does not have protected status and is not subjected to conservation management (Bahir and Surasinghe 2005). Within its known range, large areas of the natural forest have been replaced by monocultures including tea and pine, and in most remaining areas the understory has been cleared for planting cardamom.

Site selection

In June 2011, we established four study sites in three regions: Riverston (two sites), Hunasgiriya and Deanston (Figure 1). Sites were selected based on distribution of the species (localised patches of forests where the species occurs), availability of all habitat types required, accessibility and clarity of land ownership. We were restricted by the dearth of natural forests without cardamom. At each of the four sites, we marked a 100 m transect across each of the four broad habitat types given below (resulting in 16 transects in total). In the absence of a broadly applicable definition of disturbed and undisturbed forests, whether in terms of age or vegetation characterisation, we classified the four habitats as follows:

(1) Natural forests: montane-forest fragments composed of *Calophyllum*, *Syzygium, Myristica*, *Garcinia, Neolitsea* and *Fahrenheitia* and without introduced plant species (e.g., *Clidemia hirta*, *Pinus caribaea*, *Acacia* sp. and *Alstonia macrophylla*), with a rich epiphytic community of mosses, filmy ferns and an understory dominated by shrubs of the genus *Strobilanthes* and dense stands of the dwarf bamboo *Arundinaria debilis.* In all sites, a very low density of naturally regenerating cardamom was sporadically present.
(2) Mixed cardamom forests: montane forest patches with an intact canopy for the most part and a mixed understory of cardamom and native flora. The abandoned cardamom plantations are not maintained apart from the harvesting of cardamom pods.

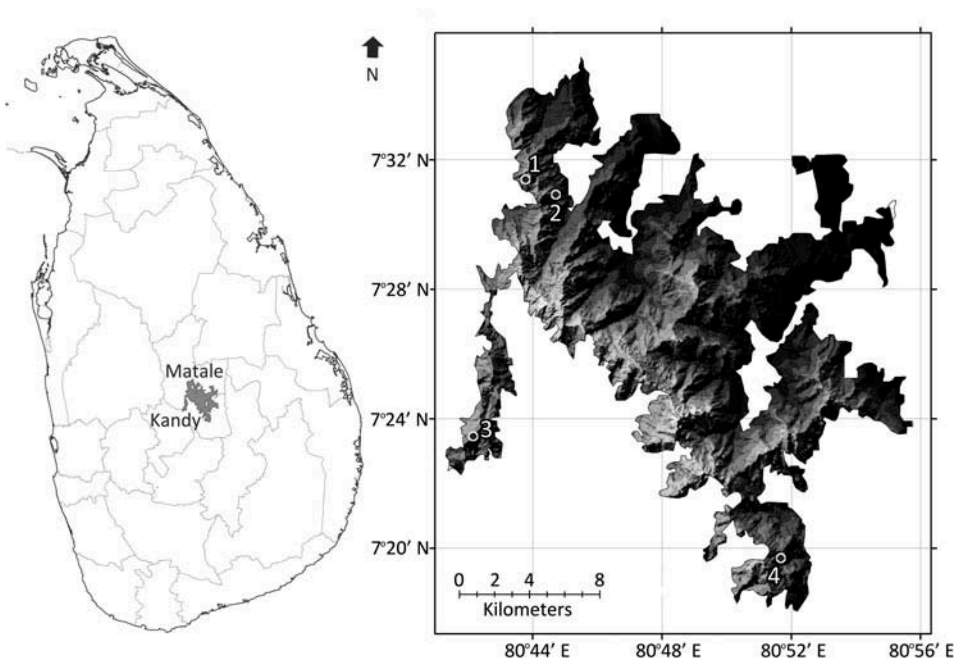


Figure 1. Location of Knuckles forest reserve within Kandy and Matale Districts (left) and the four study sites [two at Riverston (1 and 2), Hunasgiriya (3) and Deanston (4)] within the reserve (right).

(3) Managed cardamom plantations: actively maintained plantations that are mechanically weeded to remove competing vegetation, thus preventing natural regeneration of the forest. In some areas, the land is more intensively managed and the natural undergrowth is pruned. These plantations are mostly located below ~1200 m a.s.l.
(4) Pine plantations: monocultures of Caribbean pine with little or no undergrowth.

The number and location of transects was strongly influenced by the limited options available with regard to the localised distribution of the species and the uneven spatial distribution of different land-use types. Nonetheless, transects were selected as centrally as possible within the respective habitat type patch, in an attempt to reduce potential edge effects. All transects were located within ~950–1385 m a.s.l., well within the known elevational distribution of *C. tennentii* (700–1700 m: Bahir and Surasinghe 2005; de Silva et al. 2005). The elevation and general aspect of each transect was recorded with a global positioning system (GPS) and the slope (mean of the beginning, centre and end of each transect) was measured with a clinometer. Transects were located so as to avoid evidently unfavourable habitat patches such as open grasslands, tea plantations, paths, roads and streams. However, we conducted random searches for lizards in these habitats. Studying the variation of abundance across land-use patterns allows an understanding of species' responses to disturbances (Louzada et al. 2010; Peres et al. 2010), and ecological characteristics that make them adaptable or vulnerable (Kawecki 2008; Moller 2009).

Habitat use by lizards

We surveyed each transect four times: 21–28 June 2011 (during the southwest monsoon rains), 18–24 October 2011 (dry inter-monsoonal season), 7–13 February 2012 (relatively dry during the northeast monsoon rains as these areas are in a wind shadow) and 16–23 June 2012 (southwest monsoon rains). All microhabitats up to 3 m in height 2 m on either side of transects (thus resulting in a maximum search space of $100 \times 4 \times 3$ m at each transect) were investigated at a slow pace by the same group of experienced field workers. Trees were searched all around including the side facing away from the transect as the lizards tend to move to the opposite side of a tree trunk when approached or disturbed, a behaviour common to many arboreal agamids (Greer 1989), which may influence the probability of sighting and thus enumeration. Data were collected between 0830 and 1200, coinciding with the basking activity of lizards. All lizards observed were hand captured, measured (data not provided in this manuscript) and sexed but not marked. The search time at each transect was constrained to 1.5–2 h, with a similar sampling effort at all sites.

Attributes of each habitat type

To characterise the microhabitats occupied by the lizards, we measured a set of three climatic and three structural environmental variables within a 2×2 m plot surrounding the location of each lizard recorded. The microhabitat variables we measured that could potentially influence the spatial distribution and habitat selection of the lizards included:

(1) Air temperature: in °C, using a digital thermometer.
(2) Relative humidity (RH): using a digital hygrometer.
(3) Incident solar radiation: we calculated the canopy openness and then estimated the incident solar radiation using hemispherical photography and Gap Light Analyser software (Frazer et al. 1999, 2001). Photographs were taken with a super-wide fisheye lens attached to a single-lens reflex digital camera, placed on the ground facing directly upwards at each location. We set the time period for analysis as 365 days, the duration of the study.
(4) Number of perches: we counted the number of woody living and dead plants < 50 cm in height in a 2 × 2 m area surrounding the lizard. Tillers of cardamom plants were considered as individual perches.
(5) Presence of ground vegetation: presence and absence of grass, herbs and terrestrial vines.
(6) Presence of leaf litter: presence and absence of leaf litter.

To understand the heterogeneity of microhabitat conditions, we chose one random location for each location occupied by a lizard by throwing a six-sided pencil (marked with a single number from 5 to 30 in increments of 5 on each side) straight up into the air. The direction the pencil pointed when it landed determined the direction of the random location, and the number determined the distance (in metres) from the lizard location. If lizards were found at the location or if no trees were found, we repeated the process. At each of these selected random sites, we measured the same variables as determined for occupied locations (see above). In the event that no lizards were encountered within a habitat, we chose random locations along each transect.

Prey availability

We used sweep net surveys to assess the abundance of potential prey near the beginning, middle and end of each of the four transects at each site (16 transects altogether). Sweep-netting was done after the transect searches for lizards and was only conducted during one sampling session (June 2012). At each location, a sweep net (430 × 410 × 560 mm net with a mesh size of 2 × 2 mm) was scooped 10 times on vegetation (leaves, branches, stems, above-ground roots, grass, etc.) and 10 times immediately above the ground (to include the space where lizards usually feed: authors' pers. obs.). Thus, we collected 240 sweeps in each habitat type. Sweep-netting was conducted at 1000–1400 h, the time most of the lizards were active, but after the transect had been surveyed for lizards. Captures at each transect were counted, sized and categorised to taxonomic orders. However, we restricted the analysis to animals over a 'target size' of 4 mm, according to the palette presented by Webb et al. (1982) for categorising prey items by size. This selection was based on the minimum size of ingested prey items recorded during anecdotal field observations.

Vulnerability to direct mortality

Previous work suggests that some farmers kill *C. tennentii* under the misapprehension that they damage cardamom pods and flowers (de Silva et al. 2005). We conducted a questionnaire-based survey to assess the perception of cardamom and swidden farmers of lizards inhabiting their plantations. Interviewees were asked to identify four species of lizards (of which two do not occur in the region) and answer a set of questions regarding encounter rates, location of encounter, benefits for farming, effect on farming and reaction upon encounter. We were constrained by the small number of farmers operating in the area; thus, the interview sample comprised only 18 interviewees.

Data analysis

Analyses were performed in R version 3.0.1 (R core_team 2013) and JMP version 11.1.1 (SAS Institute Inc 2013). We calculated the rate of encounter, the number of sightings detected per 100 m of transect, as an index of abundance. Prior to analysis, data on lizard encounters during surveys were *ln*-transformed, after adding a small arbitrary value (0.05), to maintain variance homogeneity. All percentage values were arcsine transformed before analysis. To be more biologically meaningful, we pooled data from June surveys as 'wet season' and those from February and October as 'dry season'.

We used one-way analysis of variance (ANOVA) tests followed by Fisher's protected least significant difference (PLSD) post-hoc tests to compare the number of sightings among habitats with lizards, and generalised linear mixed effects models with Poisson errors to detect the spatial and temporal fluctuations of lizard abundance within the habitats. Linear regressions were used to analyse the co-relationships among different climatic variables.

To compare habitat parameters among habitat types, we used general linear mixed-effects models for parameters with a normal distribution, and generalised linear mixed effects models for those with a binomial distribution. Mixed effects models were built with the functions 'lmer' (from the package 'lme4': Bates et al. 2014) and 'lme' (from the package 'nlme': Pinheiro et al. 2015). For the generalised models (binomial distributions), we compared a model with and a model without 'habitat' through a likelihood ratio test. We considered 'season' as a fixed effect and the 'year' as a random effect in all models.

To find out how locations occupied by lizards are different to random locations without lizards, we built a generalised linear mixed-effects model, in which the presence of lizards (lizard or random) was the response variable, the 'year' was a random effect and 'habitat' and 'season' were fixed effects. Then we compared three models: one with the habitat parameter of interest and its interaction with habitat type, one with the habitat parameter but no interaction, and one with only covariates (habitat and season), but no habitat parameter. Comparisons were conducted through likelihood ratio tests.

Results

Habitat use by lizards

We made 362 sightings of individuals (152 sightings of males, 112 females and 98 juveniles) of *C. tennentii* from the four sites over the four surveys. The greatest number of observations was made in mixed cardamom forests (n = 169, 46.7% of the total) followed by natural forests (n = 127, 35.1%) and cardamom plantations (n = 66, 18.2) (Figure 2). No lizards were recorded within the pine plantations. When

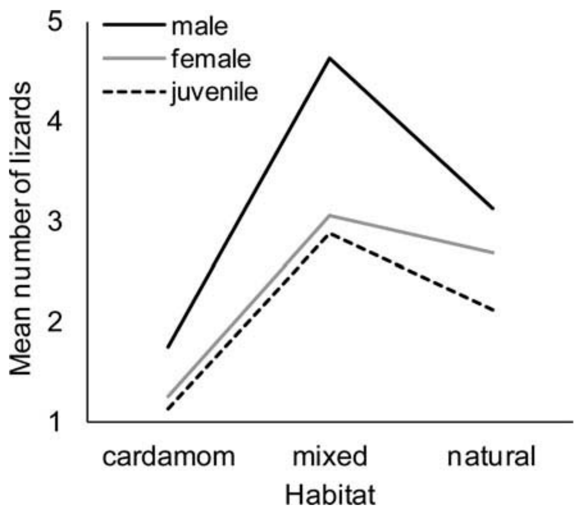


Figure 2. Mean number of sightings of *Ceratophora tennentii* within three habitat types at Knuckles Range, Sri Lanka.

the three habitat types with lizards present are considered, the total number of lizard sightings differed among habitats (likelihood ratio = 47.21, df = 2, $p < 0.0001$) with significantly more lizards sighted at mixed cardamom forests. Our sites with lizards spanned from 1110–1384 m a.s.l. in elevation and, within this range, the number of sightings did not differ with elevation ($F_{1,10} = 0.13$, $R^2 = 0.01$, $p = 0.73$), slope ($F_{1,10} = 0.003$, $R^2 = 0.0003$, $p = 0.96$) or aspect ($F_{6,5} = 0.49$, $p = 0.79$).

The total number of lizards sighted differed significantly among sampling rounds ($F_{3,44} = 2.77$, $p = 0.05$), with more lizards observed in round 1 and 4 (June 2011 and June 2012). This trend was shared by all three habitat types (habitat × round $F_{6,36} = 0.19$, $p = 0.97$). Using generalised linear mixed-effects models, where the sex of the animal was the response variable, we found that the populations were female-dominant ($F_{2,141} = 12.70$, $p = 0.0018$), a trend common to all habitat types (habitat × sex $F_{4,135} = 0.91$, $p = 0.92$). Though not statistically significant, more juveniles were observed in round 2 (October 2011).

While *C. tennentii* were not observed in the adjoining tea plantations and grasslands, several individuals were observed at the edges of these habitats. However, several individuals were observed in bamboo ('*bata*') thickets adjoining mixed cardamom forests and cardamom plantations, especially in the Riverston sites. The species was syntopic with *Calotes pethiyagodai*, *Calotes manamendrai, Cophotis dumbara*, *Lyriocephalus scutatus* and *Otocryptis weigmanni* in natural forests and mixed cardamom forests, and with *C. pethiyagodai*, *C. calotes*, *Cophotis dumbara* and *Otocryptis weigmanni* in cardamom plantations. Only *C. calotes* was observed within pine plantations.

Comparison of habitat types

The four habitat types differed from one another in all climatic features (Table 1; Figure 3). Post-hoc analysis shows that pine plantations had higher average temperatures, and that pine and cardamom plantations had lower RH, the four habitats differing significantly in the intensity of insolation (Fisher's PLSD test $p < 0.05$ for all comparisons). Structurally, cardamom plantations and mixed cardamom forests had higher perch densities ($p < 0.05$ for all interactions). Pine plantations had the least cover of ground vegetation but the greatest cover of leaf litter.

Comparison of occupied and random locations

The microhabitat occupancy by lizards within a habitat type were predominantly in shaded and moist areas with a higher density of perches (trees and shrubs; Table 2). The presence of terrestrial vegetation and leaf litter did not have a significant effect on the probability of lizard occurrence in a site, but all other variables did. However, only RH and solar radiation showed this pattern consistently over all three habitat types compared (Table 2).

Comparison of occupied locations among habitats

The occupied sites within the three habitats varied significantly in all variables (Figure 4). Occupied locations within cardamom plantations were within relatively warmer ($F_{2,348} = 6.32$, $p = 0.002$) and drier ($F_{2,348} = 6.02$, $p = 0.002$) microclimates. However, the perch density was highest within this habitat ($F_{2,348} = 290.78$, $p < 0.001$) as a result of counting individual trillers.

In general, both temperature ($F_{1,10} = 28.57$, $p = 0.003$) and humidity ($F_{1,10} = 16.32$, $p = 0.002$) had a significant effect on the probability of lizard occurrence at a site. Juveniles showed a significant preference for locations with leaf litter ($\chi^2 = 30.52$, $p < 0.0001$) with 42.3% of the sites with juveniles being covered with leaf litter. None of the other variables showed any correlation with the number or sex of the lizards.

Prey availability

Sweep-netting revealed that natural and mixed cardamom forests had a high number of potential prey items; cardamom plantations had fewer prey items, while pine plantations had a significantly lower number of potential prey items ($F_{3,44} = 4.56$, $p = 0.007$; post hoc > 0.05 for comparisons; Figure 4), a trend common to all sites (prey density vs habitat × site $F_{9,32} = 0.74$, $p = 0.67$). Lepidopterans (especially moths and caterpillars) and orthopterans were the most abundant food items, followed by homopterans.

Farmers' perceptions of lizards

All 18 interviewees correctly identified *C. tennentii* as occurring in the region, although the identification ability regarding the other lizards varied (e.g. three individuals identified *Ceratophora stoddartii* as occurring in their plantations whereas it does not; Table 3). More farmers had seen *Cophotis dumbara* more frequently within cardamom plantations than in the natural forests. Fifteen respondents (83%) encountered lizards more early in the morning than at any other time of the day, and most commonly observed them close to flowers of the cardamom plants followed by

Table 1. Comparison of microhabitat variables in the four habitat types studied at four regions of the Knuckles range, central Sri Lanka. The season is considered a fixed effect and the year a random effect in all linear and generalised models. Data from both locations with lizards and random locations are considered in combination. Boldface p value denotes statistically significant differences ($p < 0.05$) between occupied sites and random sites. Standard deviations are given.

Variable	Natural forests	Mixed cardamom forests	Managed cardamom plantations	Pine plantations	Statistic
Climatic features					
Temperature (C)	18.43 ± 1.60	18.15 ± 2.27	18.50 ± 2.16	21.90 ± 2.11	$F_{3,795} = 180.9$, $\boldsymbol{p < 0.0001}$
RH (%)	81.73 ± 8.07	81.69 ± 8.87	76.02 ± 10.59	69.55 ± 8.43	$F_{3,795} = 57.6$, $\boldsymbol{p < 0.0001}$
Solar radiation (Mj/m^2)	6.19 ± 2.78	11.06 ± 3.89	22.29 ± 6.63	24.66 ± 3.87	$F_{3,795} = 695.18$, $\boldsymbol{p < 0.0001}$
Structural features					
Perch density (m^{-2})	8.04 ± 2.98	16.45 ± 9.50	36.07 ± 18.15	3.55 ± 1.86	$F_{3,797} = 337.73$, $\boldsymbol{p < 0.0001}$
Ground vegetation	Present at 23.08% of locations	Present at 29.46% of locations	Present at 31.06% of locations	Present at 23.23% of locations	LR = 4.72, df = 3, $p = 0.19$
Leaf litter	Present at 41.45% of locations	Present at 39.29% of locations	Present at 26.52% of locations	Present at 80.81% of locations	LR = 76.58, df = 3, $\boldsymbol{p < 0.0001}$

Note: LR = likelihood ratio; RH = relative humidity.

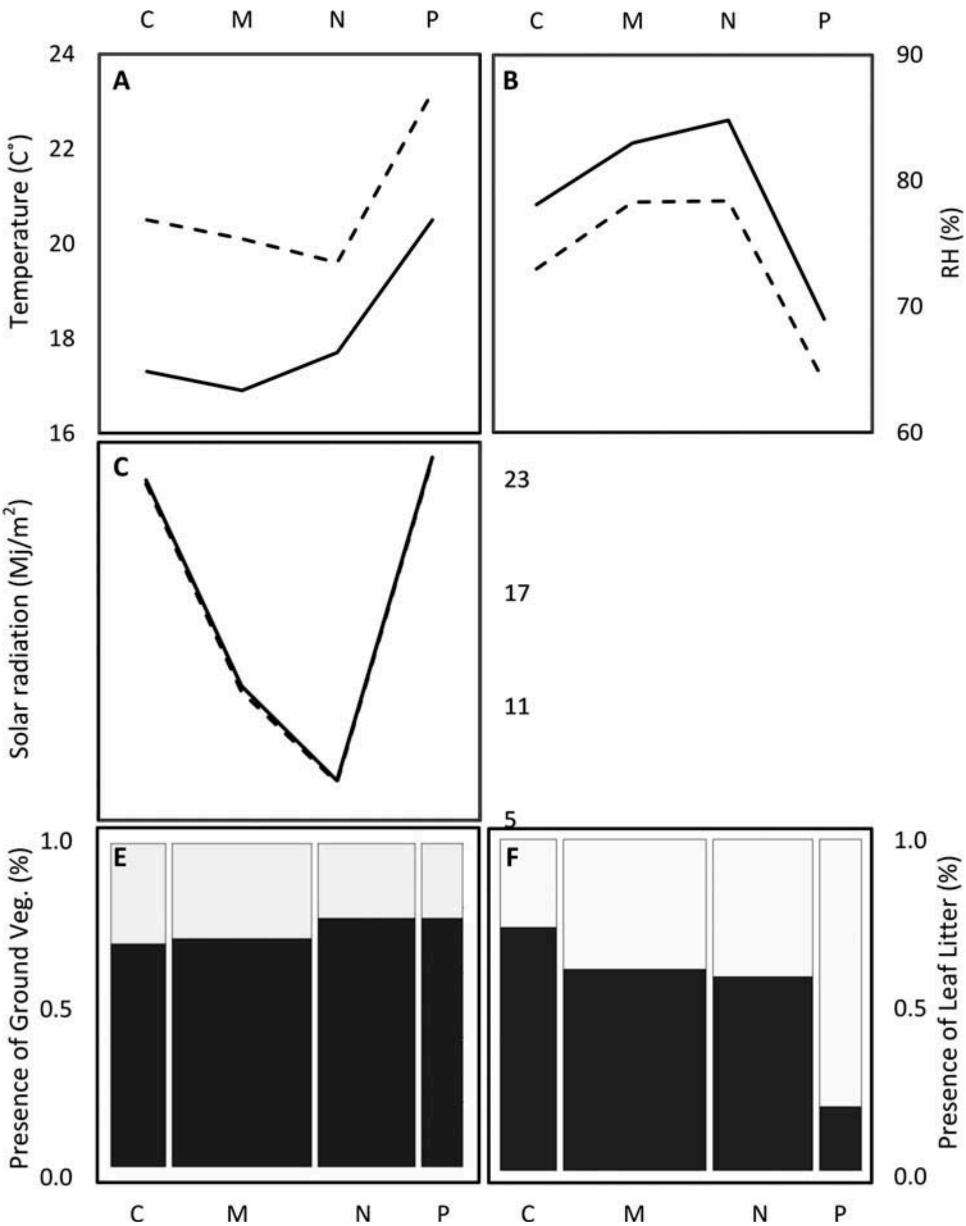


Figure 3. Comparison of climatic and structural parameters among the four habitat types during the dry (dashed line) and wet (solid line) seasons. Data from both locations with lizards and random locations are considered in combination. (C = Cardamom plantations, M = Mixed cardamom forests, N = Natural forests, P = Pine plantations.)

mid-trunk on larger trees. Almost half the farmers believed that the lizards benefit cardamom plantations by feeding on insect pests, a smaller number (3; ~17%) believing that they harm plantations by feeding on the flowers and pods. Two individuals admitted to having killed lizards for this reason, but the majority said

Table 2. Comparison of microhabitat variables in locations occupied by *Ceratophora tennentii* (Ct) and random locations in four regions of the Knuckles range, central Sri Lanka. Generalised linear mixed effects models have been used. Boldface p value denotes statistically significant differences ($p < 0.05$) between occupied sites and random sites. Standard deviations are given.

Variable	Locations with Ct	Locations without Ct	Statistical test	Trend among habitats (habitat × variable)
Temperature (C)	18.02 ± 1.86	19.31 ± 2.57	LR = 24.95, df = 1, $\boldsymbol{p < 0.001}$	LR = 17.20, df = 3, $\boldsymbol{p < 0.001}$
RH (%)	82.31 ± 8.14	76.89 ± 10.38	LR = 28.45, df = 1, $\boldsymbol{p < 0.001}$	LR = 2.69, df = 3, $p = 0.44$
Solar radiation (Mj/m^2)	8.93 ± 2.51	16.47 ± 8.23	LR = 346.55, df = 1, $\boldsymbol{p < 0.001}$	LR = 0.48, df = 3, $p = 0.92$
Perch density (m^{-2})	14.47 ± 15.34	15.11 ± 13.68	LR = 9.86, df = 1, $\boldsymbol{p = 0.02}$	LR = 72.51, df = 3, $\boldsymbol{p < 0.001}$
Ground vegetation	Present in 28.49%	Present in 26.78%	LR = 0.25, df = 1, $p = 0.61$	LR = 3.03, df = 3, $p = 0.39$
Leaf litter	Present in 40.46%	Present in 34.76%	LR = 2.46, df = 1, $p = 0.12$	LR = 7.22, df = 3, $p = 0.9$

Note: LR = likelihood ratio; RH = relative humidity.

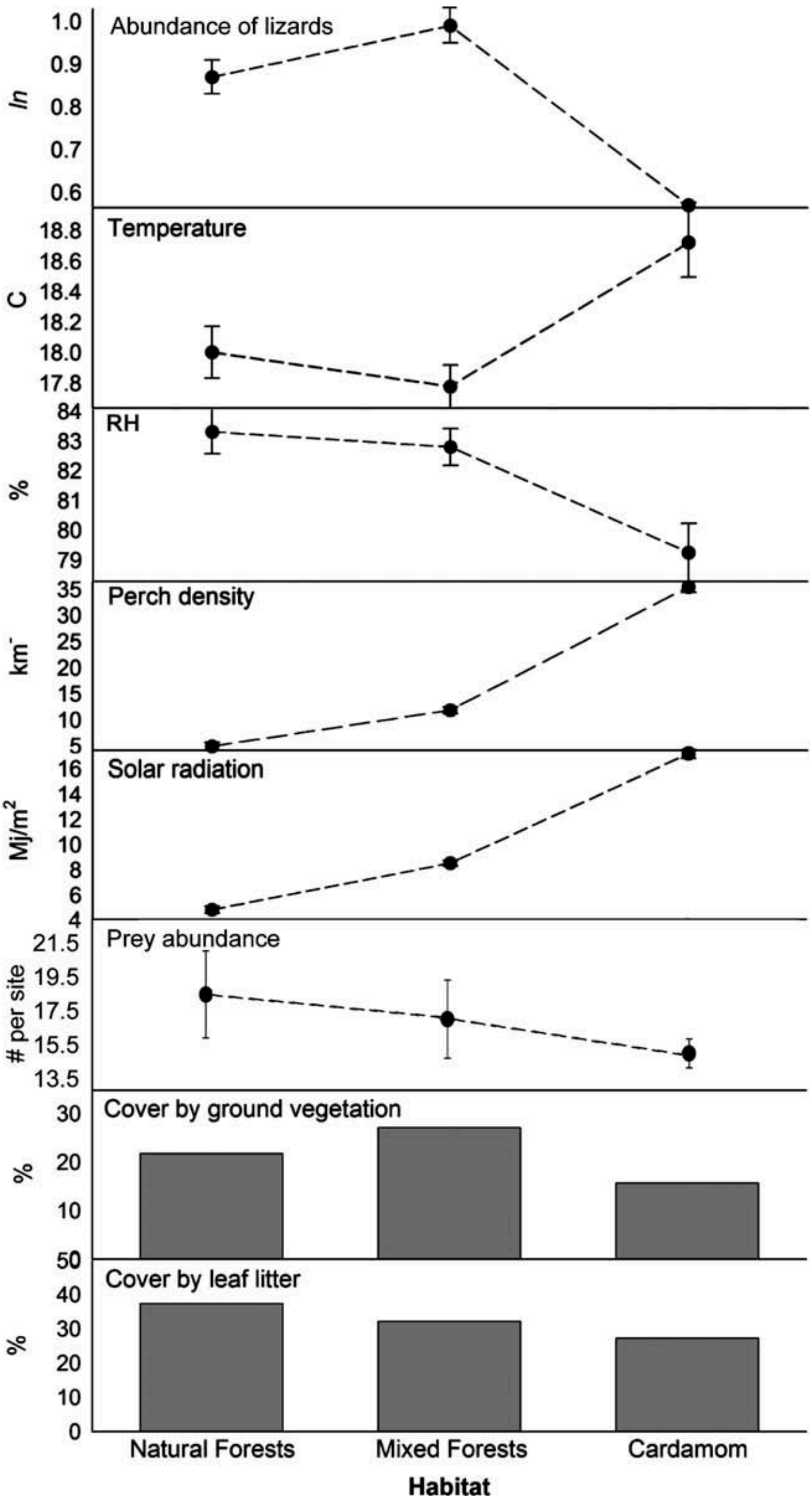
they ignored the presence of lizards in cardamom plantations. Half of the farmers believed that the populations of lizards had not changed over the past decade, whereas one third of them believed the lizards to be more common within the plantations than they were a decade previously (Table 3).

Discussion

Human-induced habitat loss is the main threat to reptiles worldwide (Böhm et al. 2013), including Sri Lanka (Gunatilleke et al. 2008; Dela 2009). Thus, understanding the processes that shape the distribution and abundance patterns in altered habitats is fundamental for their effective conservation. While several recent studies in Sri Lanka have evaluated disturbed habitats as living spaces for amphibians (Kudavidanage et al. 2012; Pethiyagoda Jr. and Manamendra-Arachchi 2012; Weerawardhena and Russell 2012), little is known about the role of disturbed habitats in maintaining viable populations of threatened reptiles (Eedelen 2012), despite the island being an important hotspot for this group (Somaweera and Somaweera 2009; Pyron et al. 2013). In general, there is also a significant paucity of detailed ecological studies on the reptiles of Sri Lanka. Such knowledge is vital for the successful management and conservation of reptiles by identifying priority concerns and enabling better allocation of resources to those that are most threatened. Given that *C. tennentii* is listed as a critically endangered species (MoE 2012), threatened by habitat modification, we believe that the improved ecological understanding derived from this study could be helpful in refining research and conservation priorities for this threatened lizard.

The current land-use practices have substantially altered the vegetation structure of the Knuckles area, with under-planting of cardamom often flagged as a key threat to this species and the other sympatric agamids (Manamendra-Arachchi and Liyanage 1994; Bahir and Surasinghe 2005; Samarawickrama et al. 2012). Contrary to this belief, our work indicates that while full-scale clearings and plantations that disturb the canopy by removing shade trees would affect the distribution of this taxon (no individuals were recorded from monocultures during the study, but see de Silva et al. 2005), practices that involve retaining some structural complexity of the vegetation, as in the mixed cardamom forests, may facilitate the persistence of *C. tennentii* in densities comparable to that of undisturbed forest patches. Our findings complement those of de Silva et al. (2005), who found *C. tennentii* to reach higher densities within mixed forests with cardamom than in undisturbed forests. We observed similar trends in two other sympatric endemic agamids, *Calotes pethiyagodai* and *Cophotis dumbara* (also see Samarawickrama et al. 2006), where both species occurred in mixed cardamom forests (but numbers were too low to allow for meaningful statistical analysis). On the other hand, no individuals were observed in the pine plantations, scrublands or tea plantations.

The detection of some reptiles in their natural environment poses difficulties (Mazerolle et al. 2007), and the estimation of densities can be problematic due to the rarity or patchy distribution of many species (Noon et al. 2006). However, we believe such effects to have been insignificant in the case of the present study given that the surveys were conducted by highly experienced field workers, and that sampling for lizards were made along narrow stretches (with a well-demarcated sampling area) with little possibility of missing an individual, as these lizards are



Abundance of lizards
ln
1.0
0.9
0.8
0.7
0.6
Temperature
C
18.8
18.6
18.4
18.2
18.0
17.8
RH
%
84
83
82
81
80
79
Perch density
km
35
30
25
20
15
10
5
Solar radiation
Mj/m2
16
14
12
10
8
6
4
Prey abundance
per site
21.5
19.5
17.5
15.5
13.5
Cover by ground vegetation
%
30
20
10
Cover by leaf litter
%
50
40
30
20
10
0
Natural Forests
Mixed Forests
Cardamom
Habitat

Table 3. Percentage of respondents who agreed with each statement in the questionnaire.

Question and responses				
1. Presence of three species of lizards				
	Seen in cardamom plantations	Seen in natural forests	Seen in pine forests	Never seen
Ceratophora tennentii	100	100	0	0
Cophotis dumbara	67	17	1	11
Ceratophora stoddartii	17	0	0	83
2. Encounter rates of *C. tennentii*				
	Every visit	Frequently	Seldom	Never
	50	33	17	0
3. Location of encounter of *C. tennentii*				
	On cardamom	On tree trunks	On bushes	On floor
	83	67	33	22
4. Any benefits to farming from C. *tennentii*				
	Yes	No	Not known	
	78	11	11	
5. Any damage to farming by *C. tennentii*				
	Yes	No	Not known	
	17	83	0	
6. Reaction upon encountering a of *C. tennentii* in the plantation				
	Chase away	Kill	Leave alone	
	0	11	89	
7. Trend in the abundance of *C. tennentii* in the area (change over the past decade)				
	Increased	Decreased	No change	
	33	17	50	

easy to locate and move in response to the observer (thus enabling easy detection) but are slow to evade. Thus, our finite population sampling approach suits this system.

Cardamom vs pine

The impact of cardamom cultivation on the forest structure, tree species composition and soil properties of the KFR, though well studied (see Dhakal et al. 2012), remains poorly understood with regard to the impact on faunal species. Nevertheless, several workers have emphasised potentially negative impacts on different faunal components (e.g. Goonewardene et al. 2006 on fossorial reptiles; Pethiyagoda 2013 on amphibians; Ranawana and Priyadarshana 2012 on land snails; Van Der

Figure 4. Comparison of attributes of the micro-climatic pockets occupied by *Ceratophora tennentii* at the three habitat types studies at Knuckles range. Error bars indicate standard deviations.

Poorten 2012 on butterflies). Clean weeding in these plantations induces soil erosion (Goonewardene et al. 2006), the leaf-litter levels were substantially reduced (Madduma Bandara 1991), added fertiliser may pollute water resources (Gunatilake et al. 1993) and forest regeneration is prevented due to the continuous removal of tree saplings (Goonewardene et al. 2006).

How then is it a critically endangered highland lizard still thrives in these modified and disturbed habitats? It is possible that most environmental attributes that change when cardamom is grown in the understory may not directly affect *C. tennentii*. Cardamom forests leave behind some structural complexity of forest ecosystems including, in the short term, a more or less intact canopy. In fact, Werner (2001) stated that cardamom has an ambivalent impact on nature conservation in Sri Lanka, given that protecting the canopy is essential for the survival of the crop. Our work shows that the microhabitat pockets occupied by these lizards within mixed cardamom forests and natural forests were largely alike. Canopy cover is a strong predictor of temperature and moisture levels in the Knuckles and the canopy cover in the mixed cardamom forests still manages to maintain the vital climatic conditions for this species. However, conditions were different within managed cardamom plantations, but were still sufficiently conducive for the species. This suggests that the changes in the microclimate within managed cardamom plantations are still within the microhabitat niche breath of *C. tennentii.* The adults of this species are largely arboreal and tend to prefer vertical perches; thus, cardamom stems provide ample perching substrates, even when clean weeding within the plantations has reduced the ground flora. This lizard buries its eggs in 30–40-mm-deep terrestrial nests (authors' pers. obs.): thus, even the reduced leaf-litter layer in cardamom plantations may provide sufficient conditions to lay eggs. Other potential impacts such as fertilisers polluting water resources (Gunatilake et al. 1993) may not be directly applicable for this species. Pethiyagoda and Manamendra-Arachchi (1998) found that *Ceratophora karu*, another critically endangered member of the genus restricted to a < 10 km^2 patch of montane forest in the Rakwana hills of Sri Lanka which is now under-planted with cardamom, has also managed to survive under these 'intermediate' alterations. However, the abundance of *C. tennentii* within managed cardamom plantations was significantly low. One possible reason for this low abundance could be the effect of agro-chemicals used in the plantations, that target the prey of lizards (Senanayake 1980). Another could be the continuous harvesting of other trees in and around these plantations to use as fire wood in cardamom-drying barns.

We did not encounter any *C. tennentii* in the pine plantations. The higher canopy openness arguably results in higher temperature and lower humidity regimes, and the open habitat potentially increases the vulnerability of the lizards to predators. Pine plantations in the area also lacked noticeable undergrowth; thus, the perch density was significantly low. However, pine plantations in the Sinharaja lowland rainforest were completely devoid of agamids despite a thick undergrowth of *Clidemia hirta* which could provide potential perches (Surasinghe and Wijesinghe 2005). Though only anecdotally surveyed, scrublands and tea plantations also lacked any *C. tennentii*. Despite having ample perches, both these habitats lack a canopy, there by resulting in unfavourable microclimatic conditions for this species. In these less complex habitats, specialists tend to decline and are replaced by generalist species such as *Calotes calotes* (Somaweera, pers. obs.).

Mixed cardamom forests vs natural forests

During the present study, the encounter rate of lizards within natural forests was less than that in mixed cardamom forests. This pattern could be attributed to several factors. As cardamom plantations were arguably located in areas with protection from wind, a large portion of the remaining natural forests (now more or less restricted to elevations over 1300 m) are in those lands unsuitable for cardamom plantations, partly due to their positioning in wind faces. The natural vegetation in these highly windy areas is stunted, and this stunted and thick vegetation (sometimes referred to as 'pygmy forests': Werner 2001) may not provide suitable conditions for the lizards. The weather in these wind faces also fluctuates rapidly.

Increased availability of niches through vegetation complexity generally promotes species coexistence and greater richness (Baker et al. 2002). Thus, the complex vegetation structures in the cardamom forests may support higher abundances of lizards, potentially due to increased availability of food, refuges and/or microhabitats (Attum et al. 2006). Similar trends have been observed in other plantation types that require the preservation of forest trees and canopy, with planting only at understory level. For example, on the Valparai plateau in the Western Ghats of India, Venugopal (2010) found that the encounter rates of the endemic *Calotes ellioti* were higher in vanilla plantations than in rainforest fragments. Similarly, in Soconusco Chiapaneco, Mexico, the diversity of lizards was higher in mixed coffee crops than in the primary vegetation such as rain forest and montane cloud forest (Macip-Rios and Munoz-Alonso 2008).

Previous studies of lizard populations experiencing disturbance have provided some support for the idea that the abundance of lizards could be highest under disturbance regimes. For example, in southeastern Spain, *Chamaeleo chamaeleon* were most common in areas of intermediate disturbance, such as cultivated areas and near roads (Hodar et al. 2000). *Ameiva ameiva* in the Amazonian of Brazil preferentially used disturbed habitats rather than closed-canopy forests within the region (Sartorius et al. 1999), while the density of *Acanthocercus atricollis atricollis* in South Africa was higher in villages than that in adjacent communal rangelands and in a nearby protected area (Whiting et al. 2009). Previous studies also have shown similar patterns with lizard diversities. For example, in South Africa, the terrestrial lizard diversity was higher in degraded communal lands that contained significantly fewer large trees and less ground cover than an adjoining protected area (Smart et al. 2005). In Tucson, Arizona, the abundance and species richness of lizards peaked at intermediate levels of urbanisation (Germaine and Wakeling 2001). Hence, it is possible that 'intermediate disturbance' could sometimes facilitate greater abundance and diversity of lizards. However, the definition of 'intermediate disturbance' is subjective and, in our case, we consider mixed cardamom forests to be of intermediately disturbed compared to natural forest (not disturbed) and cardamom or pine plantations (relatively fully disturbed). Our study complements the growing body of literature that suggests that some Sri Lankan lizards may benefit from certain disturbances and maintain viable populations in disturbed habitats (Palihawardana 1996; de Silva 2001; Goonewardene et al. 2006; Samarawickrama et al. 2006; Asela et al. 2012; Somaweera et al. 2012; Karunarathna and Amarasinghe 2013).

Determinants of habitat selection by C. tennentii

Collectively, these findings show that *C. tennentii* seeks specific climatic and structural microhabitat features, many which are common in natural and mixed cardamom forests; only a few are common in natural and managed cardamom plantations, and none are common in natural forests and pine plantations.

Spatial heterogeneity in food supply can also be an important determinant of habitat use (Somaweera et al. 2011). Our preliminary assessment of the availability of potential food items did differ among habitat types and showed the pine plantations to contain less potential food items than did the three other habitats. Most pine plantations in the area lack structural complexity in microhabitats and thus may not support a large assemblage of arthropods in the potential food categories. Managed cardamom plantations harboured a lesser abundance of potential food items compared with mixed cardamom forests and natural forests. In a study assessing the bee fauna in Knuckles, Karunaratne and Edirisinghe (2008) reported fewer bees in a managed cardamom plantation compared to a natural forest. However, given that *C. tennentii* has a catholic diet feeding on a wide variety of foods including caterpillars, cockroaches, bees, moths, large ants and their own young (Rodrigo and Jayantha 2004; de Silva et al. 2005), an accurate and more detailed assessment of food availability is logistically difficult. Given that this species largely follows a sit-and-wait foraging strategy and actively forages only in a small area (authors' pers. obs.), it could be inferred that they select habitat pockets with a sufficient supply of food, and that even some disturbed habitats provide a sufficient amount of food. Future work could usefully examine potential differences in food quality among habitats as, arguably, the usage of pesticides in the cardamom plantations has an impact on some prey utilised by lizards.

It is unlikely that direct killing by local farmers affects habitat selection in this species. Cardamom farmers (i.e., paid workers from villages in the region) have good identification skills, are well aware of *C. tennentii* and managed to distinguish the superficially similar *C. stoddartii* (which is absent in the Knuckles range) from *C. tennentii*. Unlike some other rural regions where agamids are used as food or in traditional medicine (Smart et al. 2005), they are not consumed in Sri Lanka and hence are not under threat of direct mortality by humans. Nevertheless, some farmers do believe that the lizards cause damage to the cardamom plants and thus kill lizards in managed plantations. The impact of this haphazard killing of lizards is likely to be low, given that the vast majority of respondents did not see the lizards as a threat.

A limitation in our study is the failure to determine the importance of predator pressure in shaping the distribution of *C. tennentii*. Nonetheless, the potential predators of lizards in the region (arboreal snakes, raptors, etc.) are widespread and it could be assumed that they are present in all three habitat types, excluding those at the highest peaks. Another potential limitation is the lack of fire histories for the different sites, as fires could have a profound impact on the distribution of lizards (Braithwaite 1987; Russell et al. 1999). Fire is a recent yet integral part of the Knuckles' ecology, and species such as pines, which produce slowly-decomposing, often resinous litter that is flammable, are thus more prone to fire (Shibayama et al. 2006).

The bigger picture

There is a growing body of literature that signifies the importance of disturbed land in protecting threatened fauna in Sri Lanka: including agricultural lands (Bambaradeniya et al. 1998; Hitinayake 1998; Gamage et al. 2011; Kudavidanage et al. 2012), novel ecosystems (Pethiyagoda and Manamendra-Arachchi 2012), lands planted with exotic trees (Palihawardana 1996) and land invaded by alien invasive species (Somaweera R et al. 2012), some of which relates to the montane region. Pethiyagoda (2012) showed that among the Sri Lankan terrestrial vertebrates assessed as 'endangered' or 'critically endangered' in the IUCN Red List, 12 of 14 mammal species, three of four reptile species and 40 of 48 amphibian species occur also in once heavily disturbed lands. These disturbed lands may sometimes harbour high levels of faunal diversity (Smart et al. 2005) or higher abundance of a given species (Venugopal 2010); thus, the sustainable use and management of these habitats is a key to ensuring conservation of species outside natural forests.

Although *C. tennentii* exists in mixed cardamom forests as well as cardamom plantations, the eventual removal of the canopy from lack of regeneration may result in these habitats being hostile in future. Longer term survival of the forest must include provision for the canopy trees to replace themselves. If cardamom cultivations use clear weeding, then the canopy is not sustainable in the long term, to the detriment of the habitat for this lizard and, presumably, a raft of other species. It will be crucial to study whether mixed cardamom forests are capable of sustainable regeneration with an unmanaged cardamom understory. Additionally, with the expansion of human settlements and large-scale development programmes, the rate of habitat fragmentation is increasing in the Knuckles range. This process modifies the structure of an original community, favouring species that are matrix tolerant and harming species that are continuous habitat dependent (Laurance et al. 2002). Given that *C. tennentii* seeks specific microhabitat conditions (that are absent in most monocultures) and more open habitats such as grasslands, habitat fragmentation would arguably result in genetic isolation of this and many other forest-dependent species. Studies elsewhere in the tropics (e.g. Bierregaard 2001) have shown that fragmentation can have negative impacts on faunas even in the decadal time frame. Hence, a broader approach that improves and increases landscape-level connectivity among the remaining habitat patches is a priority.

Wikramanayake and Gunatilleke (2002) suggested that future *in situ* biodiversity-conservation measures in the montane zone will likely require the establishment of habitat corridors across the altered landscape so as to provide connectivity between 'island forests'. Pine plantations in the Knuckles range are barriers to the dispersal of many species, but with human intervention it is likely that these could be used for forest restoration and to bring about connectivity (Medawatte et al. 2011). Selective replacement of pine with native species (i.e. *Shorea*, *Calamus* and *Coscinium* spp.) to increase structural and floristic complexity has been shown to be successful in trials (Ashton et al. 1997; Wijesooriya and Gunatilleke 2003). Conversion of monocultures of pine to mixed-species stands enriched with medicinal plants, food crops and timber species may have not only economic significance to rural communities but also other ecological benefits such as a significant increase in the total carbon stored (Dharmaparakrama 2006). From a faunal perspective, such replacement will create corridors with potentially favourable habitat for the dispersal of species

(Miththapala 2006). Given that juvenile *C. tennentii* are largely terrestrial, they could potentially use these corridors to disperse. Alternatively, under-planting cardamom in *Pinus* plantations has proven to be successful at an experimental level and has been shown to produce a higher yield higher than under natural forest (Wickremasinghe and Kularatne 1998). Properly managed, this practice could reduce the burden on natural forests and make better use of the pine plantations. Then again, experimental removal of cardamom to restore natural forest has shown that though treatments involving relatively severe disturbance to the soil (e.g. uprooting cardamom) effectively reduce subsequent cardamom densities, they also facilitate the establishment of weedy herbaceous species such as *Lantana camara* (Goonewardene et al. 2006), a phenomenon also observed after removing tea plants from highland habitats (Gunaratne et al. 2010; Pethiyagoda and Nanayakkara 2011).

The success of any conservation programme for a threatened species depends on a sound understanding of its habitat requirements. If the habitat that is critical for a species' persistence is understood, important areas can be identified and protected, and searches for further populations may be efficiently targeted. Our study shows that *C. tennentii* inhabit forest patches with adequate canopy cover despite the undergrowth being disturbed, but avoid habitats that lack the structural complexity and/or the specific shade and moisture levels. Ideally, the preservation of biodiversity and ecosystem functioning would occur in undisturbed habitats protected from human exploitation. However, the most practical conservation tactic in many cases may be for humans to take an active role in managing ecosystems. Such management aims to allow for some level of human use while maintaining maximal biodiversity. However, in order to avoid the criticisms of previous management attempts, future strategies will require the prior acquisition of detailed knowledge about the ecological effects of human disturbance. Ultimately, comparative surveys in disturbed landscapes may be useful in determining how much native biodiversity can be maintained in disturbed habitats and may facilitate attempts to tailor human practices to sustain maximal biodiversity.

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