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

Ruchira Somaweera\textsuperscript{a,b,*}, Nayana Wijayathilaka\textsuperscript{c,d}, Gayan Bowatte\textsuperscript{e} and Madhava Meegaskumbura\textsuperscript{c,d}

\textsuperscript{a}Biologic Environmental Survey, North Perth, Australia; \textsuperscript{b}CSIRO Land and Water Flagship, Floreat, Australia; \textsuperscript{c}Department of Zoology, Faculty of Science, University of Peradeniya, Peradeniya, Sri Lanka; \textsuperscript{d}Postgraduate Institute of Science, University of Peradeniya, Peradeniya, Sri Lanka; \textsuperscript{e}Centre for Molecular, Environmental, Genetic and Analytic (MEGA) Epidemiology, School of Population Health, University of Melbourne, Melbourne, Australia

(Received 18 February 2014; accepted 7 January 2015; first published online 20 February 2015)

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

\*Corresponding author. Email: ruchira.somaweera@gmail.com

© 2015 Taylor & Francis
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 (Gunatileke et al. 2008). Among the most biologically diverse but also highly disturbed habitats within the island are the montane forests (Wikramanayake and Gunatileke 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 km²) in April 2000 and then a National Man and Biosphere (MAB) Reserve. More recently, a 313-km² 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 km² 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-km² 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).](image-url)
(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 × 4 × 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
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 \( \times \) 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 \( \times \) 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 manamendrei*, *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     | $F_{3,795} = 180.9, \ p < 0.0001$ |
| RH (%)                  | 81.73 ± 8.07    | 81.69 ± 8.87           | 76.02 ± 10.59                | 69.55 ± 8.43     | $F_{3,795} = 57.6, \ p < 0.0001$ |
| Solar radiation (Mj/m²) | 6.19 ± 2.78     | 11.06 ± 3.89           | 22.29 ± 6.63                 | 24.66 ± 3.87     | $F_{3,795} = 695.18, \ p < 0.0001$ |
| **Structural features** |                 |                        |                              |                  |                 |
| Perch density (m⁻²)     | 8.04 ± 2.98     | 16.45 ± 9.50           | 36.07 ± 18.15                | 3.55 ± 1.86      | $F_{3,797} = 337.73, \ p < 0.0001$ |
| 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, p < 0.0001 |

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

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.)
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, $p < 0.001$ | LR = 17.20, df = 3, $p < 0.001$          |
| RH (%)                       | 82.31 ± 8.14      | 76.89 ± 10.38        | LR = 28.45, df = 1, $p < 0.001$ | LR = 2.69, df = 3, $p = 0.44$           |
| Solar radiation (MJ/m²)      | 8.93 ± 2.51       | 16.47 ± 8.23         | LR = 346.55, df = 1, $p < 0.001$ | 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, $p = 0.02$   | LR = 72.51, df = 3, $p < 0.001$         |
| Ground vegetation Present in | 28.49%            | 26.78%               | LR = 0.25, df = 1, $p = 0.61$   | LR = 3.03, df = 3, $p = 0.39$           |
| Leaf litter                  | 40.46%            | 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
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...
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 km² 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 intermediateely 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 (Palihowardana 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.
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.

**Acknowledgements**

We would like to thank H.R. Rathnayake, S.R.B. Dissanayake, A. Sathurusinghe, J. Wimalasiri, R. Rajakaruna and S. Gunathilake for assistance with permits and allowing access to the sites; Dushantha Kandambi, Tharindu Gunathilake, Waruna Agalawatte, Chinthaka Munasinghe, Samantha Bommuwalage, Sumith, Janaka Kudahewa, Gamini Gunaratne and the staff members of the regional Forest Department office for support given during the field work; and Bruno Buzatto, Nimal Gunatileke, Rohan Pethiyagoda, Anslem de Silva, Thilanka Gunaratne, Hasula Wickremasinghe and Inoka Karunaratne for providing literature and supporting data, and assisting in the preparation of the manuscript. Two anonymous reviewers provided useful comments on an early version of the manuscript.

**Funding**

This work was funded by the National Geographic Society under grant 9002-11 (to RS) and was conducted under research permits from the Department of Wildlife Conservation of Sri Lanka (WL/3/2/1/7) and the Forest Department of Sri Lanka (R&E/RES/NFSRC/10).
References

Ambagahaduwa IM, Prasad N, Gunatileke IAUN, Seneviratne G, Gunatileke CVS. 2009. Estimation of above ground biomass of a Pinus caribaea Morelet stand in lower Hantana. J Natl Sci Found Sri Lanka. 37:195–201.

Asela MDC, Ukuwela KDB, Bandra IN, Kandambi HKD, Surasinghe TD, Karunarathna DMSS. 2012. Natural history and current distribution patterns of Calotes liolepis Boulenger, 1885 (Reptilia: agamidae: Draconinae) in Sri Lanka. Herpetotropicos. 8:39–47.

Ashton P, Gamage S, Gunatileke I, Gunatileke C. 1997. Restoration of a Sri Lankan rainforest: using Caribbean pine Pinus caribaea as a nurse for establishing late-successional tree species. J Appl Ecol. 34:915–925.

Attum O, Eason P, Cobbs G, El Din SMB. 2006. Response of a desert lizard community to habitat degradation: do ideas about habitat specialists/generalists hold? Biol Conserv. 133:52–62.

Badenoch N. 2008. Improving Forest Governance in Knuckles: dialogue and development for better outcomes. Bangkok: IUCN.

Bahir MM, Surasinghe TD. 2005. A conservation assessment of the Sri Lankan Agamidae (Reptilia: Sauria). Raffles B Zool. 12:407–412.

Baker J, French K, Whelan RJ. 2002. The edge effect and ecotonal species: bird communities across a natural edge in southeastern Australia. Ecology. 83:3048–3059.

Balasubramaniam S. 1988. The major forest formations of the Knuckles region. Paper presented on the preliminary workshop for the preparation of a conservation plan for the Knuckles range of forests. Colombo: Forest Department.

Bambaradeniya CNB, Ekanayake SP. 2003. A guide to the biodiversity of Knuckles forest region. Colombo: IUCN.

Bambaradeniya CNB, Fonseka KT, Ambagahawatte CL. 1998. A preliminary study of fauna and flora of a rice field in Kandy, Sri Lanka. Cey J Sci (Bio Sci). 25:1–22.

Bates D, Maechler M, Bolker BM, Walker S. 2014. lme4: Linear mixed-effects models using Eigen and S4 [Internet]. R package version 1.1–7. [cited 2014 Dec 27]. Available from: http://CRAN.R-project.org/package=lme4

Bierregaard Jr RO. 2001. Lessons from Amazonia: the ecology and conservation of a fragmented forest. New Haven (CT): Yale University Press.

Böhm M, Collen B, Baillie JEM, Bowles P, Chanson J, Cox N, Hammerson G, Hoffmann M, Livingstone SR, Ram M, et al. 2013. The conservation status of the world’s reptiles. Biol Conserv. 157:372–385.

Bossuyt F, Meegaskumbura M, Beenerts N, Gower DJ, Pethiyagoda R, Roeplants K, Mannaert A, Wilkinson M, Bahir MM, Manamendra-Arachchi K, et al. 2004. Local endemism within the western Ghats-Sri Lanka biodiversity hotspot. Science. 306:479–481.

Braithwaite RW. 1987. Effects of fire regimes on lizards in the wet-dry tropics of Australia. J Trop Ecol. 3:265–275.

Brook BW, Sudhi NS, Ng PKL. 2003. Catastrophic extinctions follow deforestation in Singapore. Nature. 424:420–423.

Brooks TM, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, et al. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conserv Biol. 16:909–923.

Chokkalingam U, Vanniaraachchy SA. 2011. Sri Lanka’s REDD potential: myth or reality? Colombo: Forest Carbon Asia.

Cooray PG. 1961. Geology of the country around Rangala. Ceylon Geol Surv Dept Mere. 2:138.

de Silva A. 2001. The herpetofauna of Sri Lanka: historical aspects and current status. Battaramulla: Ministry of Environment.
de Silva A, Goonewardene S, Bauer A, Drake J. 2005. Ceratophora tennentii Gunther & Grey, in Tennent, 1861 (Reptilia: Agamidae): some notes on its ecology. Lyriocephalus. 6:55–62.
Dela JDS. 2009. Fourth country report from Sri Lanka to the United Nations Convention on Biological Diversity. Colombo: Government of Sri Lanka.
Dhakal B, Pinard MA, Gunatilke IAUN, Gunatilke CVS, Weerasinghe HMSPM, Dharmaparakrama ALS, Burslem DFRP. 2012. Impacts of cardamom cultivation on montane forest ecosystems in Sri Lanka. Forest Ecol Manag. 274:151–160.
Dharmaparakrama S. 2006. Carbon sequestration in major land use types in the Knuckles forest and surrounding region, Sri Lanka [PhD thesis]. Vienna: University of Natural Resources and Applied Life Sciences.
Eedelen WR. 2012. Conservation of biodiversity in a hotspot: Sri Lanka’s amphibians and reptiles. Amphib Reptile Conserv. 5:33–51.
Forestry Department. 2010. Global forest resources assessment 2010: country report. Battaramulla: Food and Agriculture Organization of the United Nations.
Franco AMA, Hill JK, Kitschke C, Collingham YC, Roy DB, Fox R, Huntley B, Thomas CD. 2006. Impacts of climate warming and habitat loss on extinctions at species’ low-latitude range boundaries. Global Change Biol. 12:1545–1553.
Frazer GW, Canham CD, Lertzman KP. 1999. Gap light analyzer (GLA) Version 2.0. Imaging software to extract canopy structure and gap light transmission indices from true-color fisheye photographs. New York: Users manual and program documentation: Simon Fraser University, Burnaby, British Columbia, Canada, and Institute of Ecosystem Studies, Millbrook.
Frazer GW, Fournier RA, Trofymow J, Hall RJ. 2001. A comparison of digital and film fisheye photography for analysis of forest canopy structure and gap light transmission. Agricult Forest Meterol. 109:249–263.
Gamage SN, Weerakoon DK, Gunawardena A. 2011. Current status of vertebrate diversity in anthropogenic and natural ecosystems in south-western Sri Lanka. J Natl Sci Found Sri Lanka. 39:383–389.
Germaine SS, Wakeling BF. 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biol Conserv. 97:229–237.
Goonewardene S, Drake J, De Silva A. 2006. The herpetofauna of the Knuckles range: project Knuckles 2004 and 2005. Gampola: University of Edinburge, Amphibia and Reptile Research Organisation of Sri Lanka (ARROS).
Greer AE. 1989. The biology and evolution of Australian lizards. Baulkham Hills: Surrey Beatty & Sons.
Gunaratne AMTA, Gunatilke CVS, Gunatilke IAUN. 2010. Barriers to tree seedling emergence on human-induced grasslands in Sri Lanka. J Appl Ecol. 47:157–165.
Gunatilake HM, Senaratne D, Abeygunawardena P. 1993. Role of non-timber forest products in the economy of peripheral communities of Knuckles national wilderness area of Sri-Lanka - a farming systems-approach. Econ Bot. 47:275–281.
Gunatilke N, Pethiyagoda R, Gunatilke S. 2008. Biodiversity of Sri Lanka. J Natl Sci Found Sri Lanka. 36:25–62.
Hitinayake HMGBS. 1998. Agroecosystems as habitats for amphibians and reptiles in Sri Lanka. In: de Silva A, editor. Proceedings of the international conference on the biology and conservation of the amphibians and reptiles of South Asia. Gampola: Amphibian and Reptile Research Organisation of Sri Lanka.
Hodor JA, Pleguzuelos JM, Poveda JC. 2000. Habitat selection of the common chameleon (Chamaeleo chamaeleon) (L.) in an area under development in southern Spain: implications for conservation. Biol Conserv. 94:63–68.
IUCN. 1994. Management plan for the conservation of the Knuckles forest. Phase II. Ceratophora tennentii <http://www.iucnredlist.org/details/4178/0>. Gland: International Union for Conservation of Nature and Natural Resources.
IUCN. 1996. *Ceratophora tennentii* <http://www.iucnredlist.org/details/4178/0>: The IUCN Red List of Threatened Species. Gland: International Union for Conservation of Nature and Natural Resources.

Jayasuriya AHM. 2008. Biodiversity profile and conservation action plan - Central Province. Battaramulla: Ministry of Environment & Natural Resources.

Kariyawasam D. 1991. Resource use and settlement in the forests of the Knuckles Range. The Sri Lanka Forester. 10:3–13.

Karunarathne DMSS, Amarasinghe AAT. 2013. Behavioral ecology and microhabitat use by *Lyriocephalus scutatus* (Linnaeus, 1758): a monotypic genus in Sri Lanka (Reptilia: Agamidae: Dracaonidae) with notes on the taxonomy. Russ J Herpetol. 20:1–15.

Karunarathne WAIP, Edirisinghe JP. 2008. Diversity of bees at different altitudes in the Knuckles forest reserve. Cey J Sci (Bio Sci). 37:61–72.

Kawecki TJ. 2008. Adaptation to marginal habitats. Annu Rev Ecol Evol Syst. 39:321–342.

Kudavidanage EP, Wanger TC, de Alwis C, Sanjeewa S, Kotagama SW. 2012. Amphibian and butterfly diversity across a tropical land-use gradient in Sri Lanka: implications for conservation decision making. Anim Conserv. 15:253–265.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv Biol. 16:605–618.

Lindström S, Mattsson E, Nissanka SP. 2012. Forest cover change in Sri Lanka: the role of small scale farmers. Appl Geogr. 34:680–692.

Louzada J, Gardner T, Peres C, Barlow J. 2010. A multi-taxon assessment of nestedness patterns across a multiple-use Amazonian forest landscape. Biol Conserv. 143:1102–1109.

Macip-Rios R, Munoz-Alonso A. 2008. Lizard diversity in coffee crops and primary forest in the Soconusco Chiapaneco. Rev Mex Biodivers. 79:185–195.

Maduma Bandara CM. 1991. Climate and hydrology of the Dumbara Hills. Annual Review 1990. Kandy: Institute of Fundamental Studies; p. 51.

Manamendra-Arachchi K, Liyanage S. 1994. Conservation and distribution of the agamid lizards of Sri Lanka with illustrations of the extant species. J South Asian Nat Hist. 1:77–96.

Mazerolle MJ, Bailey LL, Kendall WL, Royle JA, Converse SJ, Nichols D. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. J Herpetol. 41:672–689.

Medawatte WWMAB, Ekanayake EMB, Tennakoon KU, Gunatilleke CVS, Gunatilleke IAUN. 2011. A floristic survey of a unique lowland rain forest in Moraela in the Knuckles valley, Sri Lanka. Cey J Sci (Bio Sci). 40:33–51.

Meegaskumbura M, Bossuyt F, Pethiyagoda R, Manamendra-Arachchi K, Bahir M, Milinkovitch MC, Schneider CJ. 2002. Sri Lanka: an amphibian hot spot. Science. 298:398.

Meyer E. 1998. Forests, chena cultivation, plantations and the colonial state in Ceylon 1840–1940. In: Sangwan RHG, Grove D, Vinita S, editors. Nature and the orient: the environmental history of south and southeast Asia. New Delhi: Oxford University Press; p. 793–827.

Miththapala S. 2006. The ecology of the wild cats of Sri Lanka: status of taxonomy, research and conservation. In: Bambaradeniya CNB, editor. The fauna of Sri Lanka. Colombo: World Conservation Union & Government of Sri Lanka; p. 235–256.

MoE. 2012. The national red list 2012 of Sri Lanka; conservation status of the fauna and flora. Battaramulla: Ministry of Environment.

Moller AP. 2009. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. Oecologia. 159:849–858.

Noon BR, Ishwar NM, Vasudevan K. 2006. Efficiency of adaptive cluster and random sampling in detecting terrestrial herpetofauna in a tropical rainforests. Wildl Soc Bull. 34:59–68.
Palihawardana A. 1996. An ecological study of the *Cophotis ceylanica*. In: de Silva A, editor. Proceedings of the biology and conservation of the amphibians, reptiles and their habitats in South Asia. Gampola: Amphibian and Reptile Research Organisation of Sri Lanka.

Peres CA, Gardner TA, Barlow J, Zuanon J, Michalski F, Lees AC, Vieira ICG, Moreira FMS, Feeley KJ. 2010. Biodiversity conservation in human-modified Amazonian forest landscapes. *Biol Conserv.* 143:2314–2327.

Pethiyagoda R. 2012. Biodiversity conservation in Sri Lanka’s novel ecosystems. *Cey J Sci (Bio Sci).* 41:1–10.

Pethiyagoda R. 2013. Want to avert extinctions in Sri Lanka? Empower the citizenry! In: Sodhi NS, Gibson L, Raven PH, editors. Conservation biology: voices from the tropics. Chichester: John Wiley & Sons, Ltd.

Pethiyagoda R, Manamendra-Arachchi K. 1998. A revision of the endemic Sri Lankan agamid lizard genus *Ceratophora* Gray, 1835, with description of two new species. *J South Asian Nat Hist.* 3:1–50.

Pethiyagoda Jr. RS, Manamendra-Arachchi K. 2012. Endangered anurans in a novel forest in the highlands of Sri Lanka. *Wildlife Res.* 39:641–648.

Pethiyagoda RS, Nanayakkara S. 2011. Invasion by *Austroeupatorium inulifolium* (Asteraceae) arrests succession following tea cultivation in the highlands of Sri Lanka. *Cey J Sci (Bio Sci).* 40:175–181.

Pimm SL, Askins RA. 1995. Forest losses predict bird extinctions in eastern North America. *Proc Natl Acad Sci USA.* 92:9343–9347.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2015. *nlme*: Linear and nonlinear mixed effects models [Internet]. R package version 3.1-119. [cited 2015 Jan 15]. Available from: [http://CRAN.R-project.org/package=nlme](http://CRAN.R-project.org/package=nlme)

Pyron RA, Kandambi HKD, Hendry CR, Pushpamal V, Burbrik FT, Somaweera R. 2013. Genus-level phylogeny of snakes reveals the origins of species richness in Sri Lanka. *Mol Phylogenet Evol.* 66:969–978.

R core team. 2013. R: A language and environment for statistical computing. Austria, Vienna: R core team.

Rajapaksha DRNS, Samarawickrama VAMPK, Ranawana KB. 2006. Herpetofaunal diversity in Dothalugala man and Biosphere Reserve, of the Knuckles Forest Range, Sri Lanka. *Russ J Herpetol.* 13:120–134.

Ranawana KB, Priyadarshana TGM. 2012. The taxonomy and conservation status of the land snails in Sri Lanka. In: Weerakoon DK, Wijesundara S, editors. The national red list 2012 of Sri Lanka: conservation status of the fauna and flora. Battaramulla: Ministry of Environment; p. 65–76.

Rodrigo RK, Jayantha D. 2004. An observation of the foraging behavior of *Ceratophora tennentii* Günther, 1861 Knuckles forest range in Sri Lanka. *Reptile Rap.* 6:11.

Russell KR, Lear DHV, Guynn DC. 1999. Prescribed fire effects on herpetofauna: review and management implications. *Wildl Soc Bull.* 27:374–384.

Samarawickrama VAMPK, Ranawana KB, Rajapaksha DRNS, Ananjeva NB, Orlov NL, Ranasinghe JMAS, Samarawickrama VAP. 2006. A new species of the genus *Cophotis* (Squamata: Agamidae) from Sri Lanka. *Russ J Herpetol.* 13:207–214.

Samarawickrama VAMPK, Samarawickrama DRNS, Kumburegama S. 2012. Herpetofauna in the Kaluganga upper catchment of the Knuckles Forest Reserve, Sri Lanka. *Amphib Reptile Conserv.* 5:81–89.

Sartorius SS, Vitt LJ, Colli GR. 1999. Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*. *Biol Conserv.* 90:91–101.

SAS Institute Inc. 2013. *JMP®* 11. Cary (NC): SAS Institute Inc.

Scherr SJ, McNeely JA. 2008. Biodiversity conservation and agricultural sustainability: towards a new paradigm of ‘ecoagriculture’ landscapes. *Phil Trans R Soc B.* 363:477–494.
Senanayake FR. 1980. The status of the endemic lizards, genus: *Ceratophora*, in Sri Lanka. Tiger Paper. 7:26–28.

Shibayama T, Ashton MS, Singhakumara B, Griscom HP, Ediriweera S, Griscom BW. 2006. Effects of fire on the recruitment of rain forest vegetation beneath *Pinus caribaea* plantations, Sri Lanka. Forest Ecol Manag. 226:357–363.

Smart R, Whiting MJ, Twine W. 2005. Lizards and landscapes: integrating field surveys and interviews to assess the impact of human disturbance on lizard assemblages and selected reptiles in a savanna in South Africa. Biol Conserv. 122:23–31.

Somaweera R, Somaweera N. 2009. Lizards of Sri Lanka: a colour guide with field keys. Chimaira: Buchhandelsgesellschaft mbH.

Somaweera R, Webb JK, Shine R. 2011. Determinants of habitat selection by hatchling Australian freshwater crocodiles. Plos One. 6:e28533.

Somaweera R, Wijayathilaka N, Bowatte G. 2012. Does the invasive shrub *Ulex europaeus* benefit an endemic Sri Lankan lizard? Herpetol Conserv Biol. 7:219–226.

Surasinghe T, Wijesinghe MR. 2005. The influence of habitat disturbance on agamid lizards: evidence from a study along a disturbance gradient in Sinharaja. Lyricephalus. 6:291–302.

UNESCO. 2014. Central highlands of Sri Lanka [Internet]. United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage Centre; [cited 2014 Mar 3]. Available from: http://whc.unesco.org/en/list/1203/

Ujvari B, Shine R, Madsen T. 2011. Detecting the impact of invasive species on native fauna: Cane toads (*Bufo marinus*), frillneck lizards (*Chlamydosaurus kingii*) and the importance of spatial replication. Austral Ecol. 36:126–130.

van der Poorten G. 2012. The taxonomy and conservation status of the butterflies of Sri Lanka. In: Weerakoon DK, Wijesundara S, editors. The national red list 2012 of Sri Lanka: conservation status of the fauna and flora. Battaramulla: Ministry of Environment; p. 26–41.

Venugopal PD. 2010. Population density estimates of agamid lizards in human-modified habitats of the Western Ghats, India. Herpetol J. 20:69–76.

Webb GJW, Manolis SC, Buckworth R. 1982. *Crocodylus johnstoni* in the McKinlay river area, N.T. I. variation in the diet, and a new method of assessing the relative importance of prey. Aust J Zool. 30:877–899.

Weerawardhena SR, Russell AP. 2012. Cover-dependency of anurans in the Riverstone, Knuckles mountain forest range, Sri Lanka. Taprobanica. 4:12–19.

Werner W. 2001. Sri Lanka’s magnificent cloud forests. Colombo: WHT Publications.

Whiting MJ, Chetty K, Twine W, Carazo P. 2009. Impact of human disturbance and beliefs on the tree agama *Acanthocercus atricollis atricollis* in a South African communal settlement. Oryx. 43:586–590.

Wickremasinghe PJ, Kularatne RS. 1998. Prospects of cultivating cardamom under Pinus in mid country wet zone of Sri Lanka. Multipurpose tree species in Sri Lanka: multipurpose trees for environment conservation. In: Gunasena HPM, National Research Network on Multipurpose Trees, editors. Proceedings of the Eighth National Workshop on Multipurpose Trees; 1997 Oct 23–25; Kandy.

Wijesooriya W, Gunatilleke C. 2003. Buffer zone of the Sinharaja biosphere reserve in Sri Lanka and its management strategies. J Natl Sci Found Sri Lanka. 31:57–71.

Wijesundara S. 2012. Present status of montane forests in Sri Lanka. In: Weerakoon DK, Wijesundara S, editors. The national red list 2012 of Sri Lanka: conservation status of the fauna and flora. Battaramulla: Ministry of Environment; p. 181–185.

Wikramanyake ED, Gunatilleke S. 2002. Sri Lanka’s montane rain forests. In: Wikramanyake E, Dinerstein E, Loucks CJ, editors. Terrestrial ecoregions of the Indo-Pacific: a conservation assessment. Washington (DC): Island Press; p. 290–293.