

Structure and conservation of Sri Lankan land-snail assemblages in fragmented lowland rainforest and village home gardens

D. C. Raheem^{1,3*}, F. Naggs¹, R. C. Preece³, Y. Mapatuna⁴, L. Kariyawasam⁵ and P. Eggleton²

¹Department of Zoology and ²Soil Biodiversity Group, Department of Entomology, Natural History Museum, London SW7 5BD, UK; ³Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK; ⁴International Center for Geoinformatics Applications and Training, University of Moratuwa, Katubedda, Moratuwa, Sri Lanka; and ⁵Department of National Museums, Sir Marcus Fernando Mawatha, Colombo 7, Sri Lanka

Summary

1. Modified habitats have a profound impact on the biota of fragmented tropical forests. We investigated the structure of land-snail assemblages in Sri Lankan lowland rainforest and village home gardens, a habitat of the surrounding matrix of modified habitats. We focused on four questions, (i) How do the land-snail faunas of lowland rainforest and home gardens differ and can forest species persist in gardens? (ii) Can environmental variables such as altitude, canopy density and soil pH explain significant variation in species composition independent of the effects of habitat type? (iii) What is the extent of geographical species turnover? (iv) How valuable are the two habitats for the conservation of native land snails?

2. Sixty-nine standardized belt transects were sampled in 21 rainforest fragments and 12 gardens. Data were analysed using canonical and partial canonical correspondence analysis.

3. Land-snail species composition varied significantly between gardens and forest. Lowland rainforest was dominated by native snails, many of which were restricted to forest. Gardens contained a distinct component of exotic and native synanthropic snails, as well as many native forest species. Altitude, canopy density and soil pH explained significant variation in species composition independent of the effects of habitat type but were closely correlated with variation in species composition between gardens and forest. Longitude and latitude explained significant variation in species composition across both gardens and forest.

4. *Synthesis and applications.* Most rainforest snails were restricted to forest. This, together with the high level of geographical turnover and the scale of forest fragmentation, emphasizes the need to conserve all remaining rainforest cover. A substantial number of widespread and localized forest land-snail species can survive in gardens. Home gardens therefore offer great potential for restoring and increasing forest cover and connectivity.

Key-words: conservation, habitat fragmentation, home gardens, land snails, rainforest, tropics

Introduction

Land-use intensification and habitat fragmentation are major threats to global biodiversity (Laurance & Bierregaard 1997; Groombridge & Jenkins 2000; Foley *et al.* 2005). Biodiversity is concentrated in tropical forests (Groombridge & Jenkins 2000) but over the last decade the annual rate of tropical deforestation has been approximately 8.6 million ha and in south-east Asia, where forest clearance is greatest, a mean area of 0.8–0.9% is lost annually (Mayaux *et al.* 2005).

Modified habitats increasingly dominate many tropical landscapes and it is vital to understand how such habitats affect the survival and conservation of forest species. The matrix of modified habitats surrounding fragmented forest profoundly alters the composition and persistence of forest biota (Ewers & Didham 2006; Kupfer, Malanson & Franklin 2006). Matrix quality may influence dispersal of some organisms, leading to changes in colonization–extinction dynamics and species abundances (Wethered & Lawes 2005). Tropical forest species may use resources in the matrix (Ricketts 2004) and fragmented forest communities may be altered by native and exotic matrix species (Gascon *et al.* 1999).

*Correspondence author. E-mail: dinr@nhm.ac.uk.

Much of the existing literature on tropical forest species in matrix habitats is focused on vertebrates (but see Perfecto *et al.* 1996; Klein *et al.* 2002; Jones *et al.* 2003; Bobo *et al.* 2006). Moreover, current understanding of the persistence of tropical forest species in the matrix is poor. Matrix habitats are likely to be fundamental to the conservation of biological dynamism in natural landscapes fragmented by human activity; the management of matrix habitats to increase connectivity will be crucial for long-term conservation of fragmented biota (Lindenmayer & Franklin 2002; da Fonseca, Sechrest & Oglethorpe 2005). Matrix habitats that are based on agroforestry, such as home gardens, have a potentially important role to play in this context (Pimentel *et al.* 1992; Schroth *et al.* 2004). They offer additional habitat and resources for forest species in fragmented landscapes and, combined with active measures for forest protection, may help to reduce deforestation (Schroth *et al.* 2004). Home gardens are among the oldest tropical agro-ecosystems and are found in many parts of the tropics, where they generally occur at low to mid-altitudes in close proximity to forest, or in landscapes that were forested in historical times (McConnell 2003).

This study explored the capacity of a tropical forest invertebrate taxon to survive in a structurally complex matrix habitat by investigating the land-snail species composition of Sri Lankan lowland rainforest and home gardens. The Sri Lankan land-snail fauna is very diverse and at least 80% of the *c.* 300 recorded species are endemic (Raheem & Naggs 2006). The majority of endemic land-snail species occur in south-western Sri Lanka, the so-called wet zone, covering an area of about 12 000 km² (D. Raheem, unpublished data). Rainforest covered nearly all of this zone at the beginning of the 19th century but has declined to just 2135 km² of highly fragmented and degraded forest (Legg & Jewell 1995; Raheem 2005). Home gardens are a traditional element of the complex matrix of cultivated habitats surrounding these forests.

We focused on the following questions. (i) How different are the land-snail faunas of lowland rainforest and gardens and can forest species persist in home gardens? (ii) Can environmental variables such as altitude, canopy density and soil pH explain significant variation in species composition independent of the effects of habitat type? (iii) Given the geographically restricted ranges of many Sri Lankan land snails, what is the extent of geographical turnover in species across rainforest and gardens? (iv) How valuable are home gardens and rainforest for the conservation of native land snails?

Materials and methods

STUDY AREA AND SAMPLING STRATEGY

Sampling was conducted from December 2000 to June 2001 and March to September 2002 in 21 lowland rainforest fragments and 12 village home gardens in the southern part of Sri Lanka's wet zone (Fig. 1; see Table S1 in the supplementary material). Lowland

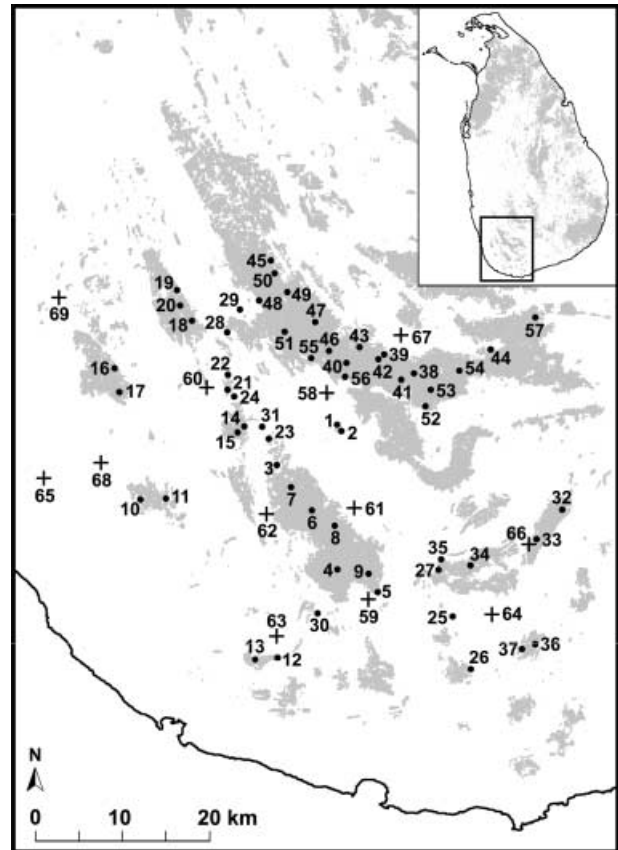


Fig. 1. The location of the 69 transects sampled in fragmented lowland rainforest (dots) and village home gardens (crosses). See Table S1 in the supplementary material for transect codes. Transects 23–31 correspond to the nine smallest (≤ 15 ha) fragments. Source of forest cover data: Legg & Jewell (1992, 1995).

rainforest is the characteristic natural vegetation type of the wet zone from sea level to an altitude of 1000 m (Legg & Jewell 1995). Village home gardens have formed a vital element of the island's agriculture from at least the 10th century AD, until the introduction of large-scale commercial plantations after 1815 (Raheem 2005). They are a system of agroforestry based on the perennial cropping of mixed tree species that provide food, fibre, timber, medicinal products and spices. Older and floristically diverse home gardens are structurally similar to forests, with a ground flora, understorey, subcanopy and main canopy.

Land-snail diversity and abundance were assessed using standardized 2×100 -m belt transects, each divided into twenty 2×5 -m sections. Sampling effort was standardized within each section to 30 person minutes (i.e. 10 person hours transect⁻¹). Within each section, the forest/garden floor (i.e. leaf litter, dead wood, stones and rocks) and then the understorey foliage and trees up to a height of 2 m were examined for snails. While searching the ground ten $15 \times 15 \times 10$ -cm leaf litter and soil samples were collected randomly from as wide an area of each section as possible. These litter and soil samples were searched in the field and all live snails and shells encountered were identified to species level. Representative samples were collected to verify field identifications.

Home gardens are generally less than 1 ha in size. One transect was sampled in each garden. Sampling of rainforest was approximately

standardized with respect to fragment area (see Table S1 in the supplementary material). The 12 largest fragments (182–29 229 ha) were sampled at a minimum of 200 m from the forest edge (edge effects for tropical forest invertebrates are strongest within 100 m of forest edges and do not usually penetrate beyond 200 m; Laurance *et al.* 2002). The nine smallest fragments (≤ 15 ha) were sampled at the centre. A total of 69 transects was sampled: 57 in rainforest and 12 in gardens (Fig. 1). Transects were positioned on ground not subjected to seasonal flooding and as far as possible on level terrain or parallel to contours. The direction of transects relative to aspect could not be held constant because of the complex topography of the study area.

SPECIES IDENTIFICATION

Species identifications were confirmed using characters of both shells and reproductive anatomy at the Natural History Museum (NHM), London, UK, and the National Museum, Colombo, Sri Lanka. Nomenclature follows Naggs & Raheem (2000) and Raheem (2005). The taxonomy of several species groups is poorly understood; such taxa are indicated by the suffix '-aggregate'. The worn condition of shells prevented identification of <4% of the 5496 specimens sampled.

In all analyses we used the total number of individuals (sum of shells and live animals). The pooling of shells and live animals is standard practice in land-snail ecology (de Winter & Gittenberger 1998; Cameron & Pokryszko 2004) and can be justified on several counts. Most shells probably decompose in less than 2 months in tropical rainforest conditions (de Winter & Gittenberger 1998). Generally, neither species richness of shells nor of live snails captures overall diversity at a site (Rundell & Cowie 2003; D. Raheem, personal observation). Moreover, land snails may exhibit seasonal variation in local density and patterns of aggregation and available data suggest that snail densities are often lower at low pH sites (e.g. rainforest; Cameron & Pokryszko 2005). Combining live snails and shells helps to partly overcome some of these problems and also increases sample size and statistical power.

MEASUREMENT OF ENVIRONMENTAL AND GEOGRAPHICAL VARIABLES

Habitat type was treated as a nominal variable with two classes, natural lowland rainforest and home garden. Seven quantitative environmental and geographical variables were recorded for each transect: altitude, slope, canopy density, aspect, soil pH, longitude and latitude. Altitude, slope and canopy density (i.e. the percentage canopy cover measured using a spherical densiometer) were recorded for every transect section. Soil pH was measured for six soil samples from each transect (i.e. two soil samples from the three sections, 0–5 m, 45–50 m and 95–100 m). The geographical coordinates and aspect of each transect were estimated using a global positioning system (GPS) and topographical maps.

ANALYSES

Species richness and composition

Sample-based rarefaction curves (*sensu* Gotelli & Colwell 2001) were calculated for each habitat using EstimateS (Colwell 2006). The two species accumulation curves were calculated from the Mao Tau in EstimateS and were computed from 50 randomizations of

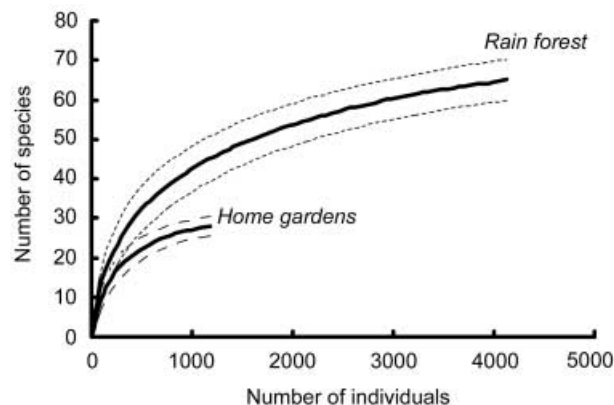


Fig. 2. Species accumulation curves for lowland rainforest and home gardens. Cumulative species richness (solid lines) and 95% confidence intervals (broken lines) were calculated from 50 random draws without replacement from a total of 57 forest transects and 12 garden transects.

sample order, without replacement, from 57 rainforest and 12 garden transects, respectively.

Multivariate analyses

The relationship between species composition and environmental variables was analysed with canonical correspondence analysis (CCA) and partial canonical correspondence analysis (pCCA) (CANOCO for Windows 4.5; ter Braak & Šmilauer 2002; for further details of the approach see Lepš & Šmilauer 2003). The relative importance of different environmental variables in explaining variation in species composition was assessed by forward selection. In pCCA the relative magnitude of specific observed variables or specific combinations of observed variables is assessed by eliminating or partialling out the effect of other observed variables (covariables; Lepš & Šmilauer 2003).

The geographical coordinates of the transects were incorporated into multivariate analyses following Borcard, Legendre & Drapeau (1992). The two-dimensional arrangement in space of the sampled sites is described by the nine terms of a cubic trend surface regression of the form:

$$z = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$$

where x is longitude, y is latitude and b is a constant. The terms x , y , x^2 , xy , y^2 , x^3 , x^2y , xy^2 and y^3 were computed for the geographical coordinates of each site and submitted as part of the matrix of environmental variables to analysis by CANOCO (this approach follows Davies *et al.* 2003).

Results

THE LAND-SNAIL FAUNA

A total of 5301 land-snail shells and live animals, representing 73 morphospecies (37 genera and 13 families), was recorded from the forest and garden transects. Undescribed taxa accounted for 39% of species and 8% of genera. At a standardized sample size of 1000 individuals, the species accumulation curve for the gardens was lower than the curve for lowland rainforest (Fig. 2), suggesting that the latter has greater total land-snail species richness.

RELATIONSHIP BETWEEN SPECIES COMPOSITION, ENVIRONMENTAL AND GEOGRAPHICAL GRADIENTS

In order to reduce noise only the 54 land-snail species (32 genera and 13 families) with ranges partly or completely overlapping the altitudinal range of the 12 home gardens sampled (20–280 m) were included in the multivariate analyses (Table 1). This omitted 19 exclusively rainforest species with a lower altitudinal limit exceeding 280 m.

Habitat type (forest/garden) explained significant variation in land-snail species composition in a CCA including all the environmental and geographical variables. Altitude, the geographical factors x and y , canopy density and soil pH were also significant (Fig. 3 and Tables 2 and 3). The variation in species composition explained by the environmental and geographical variables was 29%. The environmental arrows in CCA axes 1 and 2 ordination space accounted for 52.8% of the variance in the weighted averages of land-snail species composition with respect to the environmental variables. Species were ordered along the first axis primarily by habitat type and secondarily by altitude, canopy density and soil pH, and along the second axis by longitude (x) and latitude (y) (Table 3). Altitude, soil pH and canopy density varied with habitat type; altitude and canopy density were higher in forest sites than in gardens, and soil pH increased from forest to garden sites.

In a pCCA with the other initially significant environmental and geographical variables partialled out, habitat type retained a significant effect ($P = 0.001$) on land-snail composition; the explanatory power was 25.2%. The effect of habitat type ($\lambda_1 = 0.355$) was smaller than the sum of all the eigenvalues of the covariables ($\lambda_{\text{sum}} = 0.914$) but was similar in magnitude to significant individual environmental and geographical variables (Table 2).

The rainforest fauna was species rich and dominated by Sri Lankan endemics: 46 of the 54 species (85%) recorded occurred in forest and 89% (41 species) of these were endemic (Table 4). Moreover, 56% (26 species) of rainforest species were restricted to forest (Table 4). Home gardens were less diverse (28 species, 52% of the total fauna), had proportionately fewer endemics (17 species, 61% of the garden fauna; Table 4) and consisted of a mixture of exotic species (Table 1), native species characteristic of modified habitats in the lowlands of the wet zone (*Cryptozonia bistrialis*, *Pupisoma miccyla*-aggregate and *Sitala operiens*) and non-endemic native or endemic species occurring in both forest and gardens. The last category included two primarily forest species (*Glessula* sp. J and *Pterocyclus cumingi*-aggregate) that were recorded only from home gardens in this study.

Twenty species occurred in both habitats (Table 4). Of these 16 were endemic and non-endemic native wet zone species, two were native species characteristic of modified habitats and monsoon forest (*Pupisoma miccyla*-aggregate and *Sitala operiens*) and two were exotics (*Semperula maculata*-aggregate and *Subulina octona*). The last four species had a very restricted distribution in forest: they were recorded only from a few transects close to the edge of larger fragments and/

Table 1. Land-snail species recorded from lowland rainforest and home gardens. Species are grouped by family and are shown alongside the codes used in the ordination diagrams. Native non-endemic taxa are marked with an asterisk, exotic species by a cross. All other taxa are endemic

Land-snail species	Code	Forest	Garden
Vertiginidae			
<i>Pupisoma miccyla</i> -aggregate	Pum	+	+
Endodontidae			
<i>Philalanka circumsculpta</i> -aggregate	Phc	+	–
<i>Philalanka secessa</i> -aggregate	Phs	+	–
Ariophantidae			
<i>Cryptozonia bistrialis</i> *	Crb	–	+
<i>Cryptozonia chenui</i>	Crc	+	+
<i>Euplecta emiliana</i>	Eue	+	+
<i>Euplecta indica</i> -aggregate*	Eui	+	–
<i>Euplecta</i> sp. Y	EuY	+	–
<i>Euplecta</i> sp. Z	EuZ	+	–
<i>Euplecta travancorica praeeminens</i> *	Eut	+	+
<i>Ratnadvipia irradians</i>	Rai	+	+
<i>Ratnadvipia karui</i>	Rak	+	–
<i>Eurychlamys</i> sp. A	EuA	+	+
<i>Mariaella dussumieri</i> [†]	Mad	–	+
<i>Satiella</i> sp. A	SaA	+	+
<i>Sitala operiens</i>	Sio	+	+
<i>Kaliella barrakporensis</i> [†]	Kab	–	+
Macrochlamydiae sp. B	MaB	+	–
Glessulidae			
<i>Glessula</i> sp. A1	GIA1	+	–
<i>Glessula</i> sp. A2	GIA2	+	–
<i>Glessula</i> sp. A4	GIA4	+	–
<i>Glessula</i> sp. C	GIC	+	–
<i>Glessula</i> sp. G	GIG	+	–
<i>Glessula</i> sp. J	GIJ	–	+
Subulinidae			
<i>Subulina octona</i> [†]	Suo	+	+
<i>Allopeas gracile</i> [†]	Alg	–	+
<i>Eutomopeas layardi</i> -aggregate	Eul	+	+
Achatinidae			
<i>Lissachatina fulica</i> [†]	Lif	–	+
Acavidae			
<i>Acavus haemastoma</i>	Ach	+	+
<i>Acavus phoenix</i>	Acp	+	+
<i>Acavus superbis</i>	Acs	+	+
<i>Oligospira polei</i>	Olp	+	+
Corillidae			
<i>Corilla adamsi</i>	Coa	+	–
<i>Corilla colletti</i>	Coc	+	+
Camaenidae			
<i>Beddomea albizonata</i> -aggregate	Bea	+	+
Veronicellidae			
<i>Laevicaulis alte</i> [†]	Laa	–	+
<i>Semperula maculata</i> -aggregate [†]	Sem	+	+
Cyclophoridae			
<i>Cyclophorus involvulus</i> *	Cyi	+	+
<i>Cyclophorus menkeanus</i> -aggregate	Cym	+	+
<i>Aulopoma</i> sp. A	AuA	+	+
<i>Cyathopoma ceylanicum</i>	Cyc	+	–
<i>Cyathopoma</i> sp. A	CyA	+	–
<i>Japonia</i> sp. A	JaA	+	–
<i>Japonia</i> sp. B	JaB	+	–
<i>Leptopoma semiclausum</i>	Les	+	–
<i>Leptopomoides poecilus</i> -aggregate	Lep	+	–
<i>Theobaldius layardi</i>	Thl	+	–
<i>Theobaldius</i> sp. A	ThA	+	–
<i>Theobaldius</i> sp. B	ThB	+	–
<i>Theobaldius</i> sp. E	ThE	+	–
<i>Pterocyclus cumingi</i> -aggregate*	Ptc	–	+
Diplommatinidae			
<i>Nicida delectabilis</i>	Nid	+	–
Pupinidae			
<i>Tortulosa aurea</i>	Toa	+	–
<i>Tortulosa pyramidata</i>	Top	+	–

Fig. 3. Land-snail species distributions in relation to habitat type. (a) CCA ordination diagram with species (+), transects in lowland rainforest (solid circles) and home gardens (upright triangles) and environmental and geographical variables (quantitative variables, arrows; nominal variables, large inverted triangles). The environmental variables are habitat type (FOREST, rainforest; GARDEN, home gardens), altitude (ALTI), slope (SLOPE), canopy density (CANO), aspect (ASPECT) and soil pH (SOILpH), and the geographical factors are longitude (x) and latitude (y). Only species referred to in the Results and Discussion are labelled and only a selection of the forest transects are shown. Transect codes follow Table S1 in the supplementary material. Species names follow Table 1. (b) Detail of (a) showing all 57 rainforest transects.

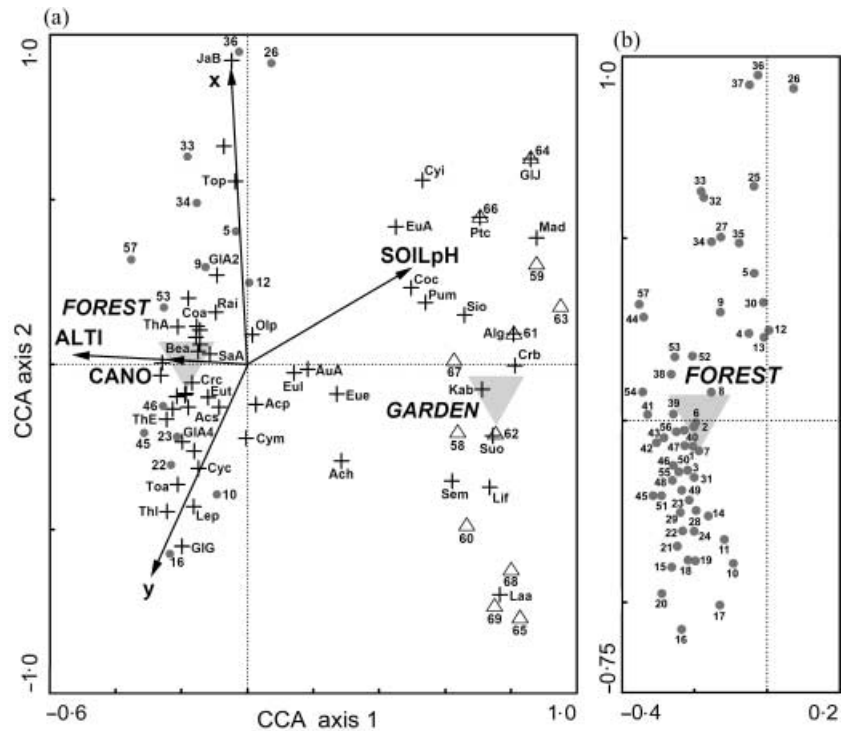


Table 2. Importance of environmental and geographical variables in explaining variation in land-snail species composition across 69 transects as shown by their marginal (left) and conditional (right) effects. λ_1 , eigenvalue of ordination when each variable is considered alone; λ_a , increase in the sum of all canonical eigenvalues of the ordination when the variable is added to the variables already included; cum(λ_a), cumulative increase in λ_a with sequential addition of variables; *P*, level of significance as obtained from a Monte Carlo permutation test under the null model (999 unrestricted permutations). The sum of all eigenvalues is 5.03 and the sum of all canonical eigenvalues is 1.452. Only the significant variables are shown in the conditional effects section

Marginal effects			Conditional effects			cum (λ_a)
Variable	λ_1	<i>P</i>	Variable	λ_a	<i>P</i>	
1 FOREST/ GARDEN	0.52	0.001	1 FOREST/ GARDEN	0.52	0.001	0.52
2 ALTI	0.29	0.001	2 x	0.21	0.001	0.73
3 y	0.23	0.001	3 ALTI	0.20	0.001	0.93
4 y ²	0.23	0.001	4 y	0.16	0.001	1.09
5 xy ²	0.23	0.001	5 CANO	0.09	0.033	1.18
6 y ³	0.23	0.001	6 SOILpH	0.09	0.047	1.27
7 xy	0.23	0.001				
8 x ² y	0.22	0.001				
9 SOILpH	0.22	0.001				
10 x	0.22	0.001				
11 x ²	0.22	0.001				
12 x ³	0.22	0.001				
13 CANO	0.12	0.019				
14 SLOPE	0.12	0.031				
15 ASPECT	0.09	0.121				

Table 3. Correlation of environmental and geographical variables to the ordination axes of Fig. 3. Inter-set coefficients show the correlation between the environmental and geographical variables (abbreviations as Fig. 3) and the first two ordination axes derived from the species data and intraset coefficients show the correlation between the environmental and geographical variables and the first two ordination axes derived from the environmental data. Significant correlations are shown in bold. The interset and intraset coefficients for the environmental variables FOREST and GARDEN are directly inversely correlated and only the former set is listed

Environmental/ geographical variables	Inter-set coefficients		Intraset coefficients	
	CCA axis 1	CCA axis 2	CCA axis 1	CCA axis 2
CANO	-0.230	0.014	-0.241	0.016
ALTI	-0.504	0.026	-0.528	0.028
SLOPE	-0.354	-0.074	-0.371	-0.084
ASPECT	-0.215	0.079	-0.226	0.088
SOILpH	0.477	0.262	0.500	0.295
x	-0.049	0.795	-0.051	0.895
y	-0.279	-0.571	-0.292	-0.643
x ²	-0.048	0.795	-0.051	0.895
xy	-0.290	-0.517	-0.304	-0.581
y ²	-0.279	-0.569	-0.293	-0.640
x ³	-0.048	0.795	-0.050	0.895
x ² y	-0.300	-0.456	-0.315	-0.513
xy ²	-0.285	-0.542	-0.299	-0.610
y ³	-0.279	-0.566	-0.293	-0.638
FOREST	-0.924	0.097	-0.968	0.109

or from several of the smallest fragments. Together these four taxa accounted for just 2.4% of the total sample for the 54 species (3719 live snails and shells) from the 21 forest fragments.

Of the 16 native rainforest species common to both gardens and forest, nine (*Acavus phoenix*, *Aulopoma* sp. A, *Beddomea albizonata*-aggregate, *Cryptozona chenui*, *Euplecta travancorica praeeminens*, *Eutomopeas layardi*-aggregate, *Oligospira polei*,

Table 4. Contribution of endemic, native non-endemic and exotic snails to the faunas of rainforest and home gardens and the distribution of species across the two habitats

	Number of species			Total
	Endemic	Native non-endemic	Exotic	
Fauna by habitat				
Rainforest	41	3	2	46
Home gardens	17	4	7	28
Distribution of species				
Rainforest only	25	1	0	26
Home gardens only	1	2	5	8
Both habitats	16	2	2	20
Total	42	5	7	54

Ratnadvipia irradians and *Satiella* sp. A) were widespread across the study area. The seven remaining species included six snails with geographically localized distributions in the study area (*Acavus haemastoma*, *Acavus superbus*, *Corilla colletti*, *Cyclophorus involvulus*, *Cyclophorus menkeanus*-aggregate, *Eurychlamys* sp. A) and one widely but sparsely distributed species (*Euplecta emiliana*). Interestingly, the local abundances of some of these widespread and localized taxa in gardens were comparable to or greater than abundances at forested sites (Fig. 4).

In a pCCA with the other initially significant variables as covariables, the effect of the geographical factors alone (longitude, latitude $P = 0.001$) was highly significant (Fig. 5). The first axis was defined by longitude and the second axis by latitude. Geographical turnover in species, along both latitudinal and longitudinal gradients, was high. This reflected the presence of a number of native land snails with restricted distributions in the study area (see above). A substantial number of these localized species were confined to rainforest and were restricted to single fragments or groups of geographically adjacent fragments (e.g. *Cyathopoma ceylanicum*, *Cyathopoma*

sp. B, *Glessula* sp. A1, *Glessula* sp. A2, *Glessula* sp. G, *Japonia* sp. B, *Theobaldius layardi*, *Theobaldius* sp. E, *Tortulosa aurea* and *Tortulosa pyramidata*). A smaller, but nevertheless important, element of the study area's localized rainforest land-snail fauna occurred in both forest and garden habitats. *Corilla colletti*, for example, was restricted to forest and gardens in the extreme south-east and north-east of the study area; it was replaced by the forest species *Corilla adamsi* to the south and west. *Cyclophorus involvulus* and *Cyclophorus menkeanus*-aggregate occurred in forest and gardens in the southern and northern parts of the study area, respectively. *Acavus haemastoma* and *Acavus superbus* had a similar pattern of distribution.

Partial CCA quantifying the sole effects of altitude and soil pH showed these environmental variables to be highly ($P = 0.001$) and weakly significant ($P = 0.042$), respectively. In a pCCA the sole effect of canopy density was not significant ($P = 0.062$).

Discussion

VARIATION IN LAND-SNAIL SPECIES COMPOSITION IN RELATION TO HABITAT

There were marked differences in the structure of the land-snail assemblages of rainforest and home gardens. The more diverse lowland rainforest fauna is almost entirely composed of Sri Lankan endemic snails, with 56% of species being restricted to forest. In contrast, although gardens were dominated by native snails, a distinct component of exotic species was present. These exotics were almost entirely absent from forest; even the land-snail faunas of the nine smallest fragments were dominated by native forest species. This suggests that the lowland rainforest fauna has in the short term been relatively resilient to invasion by species from outside the forest. We are aware that these findings might have been confounded by sampling effort: 57 transects were in forest and just 12 in gardens. However, casual field observations and

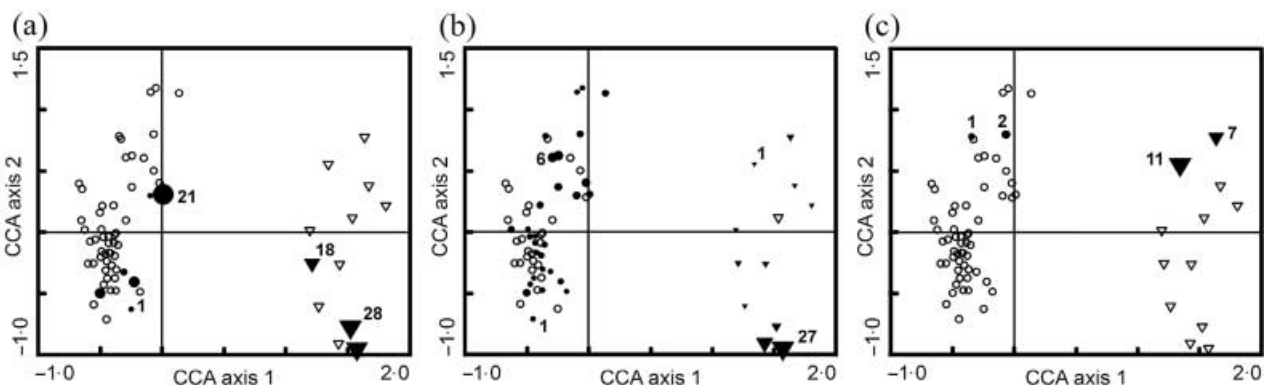


Fig. 4. CCA attribute plots showing abundance of (a) *Acavus haemastoma*, (b) *Cyclophorus involvulus* and (c) *Aulopoma* sp. A across rainforest and garden transects. Species presences and absences are denoted by solid and open symbols, respectively (circles, forest; triangles, gardens). Species abundances (total number of individuals) are proportional to the size of the solid symbols. Minimum and maximum abundances in each habitat are shown alongside relevant transects (e.g. *Acavus haemastoma* ranges in abundance from 1 to 21 individuals in forest and 18–28 individuals in gardens).

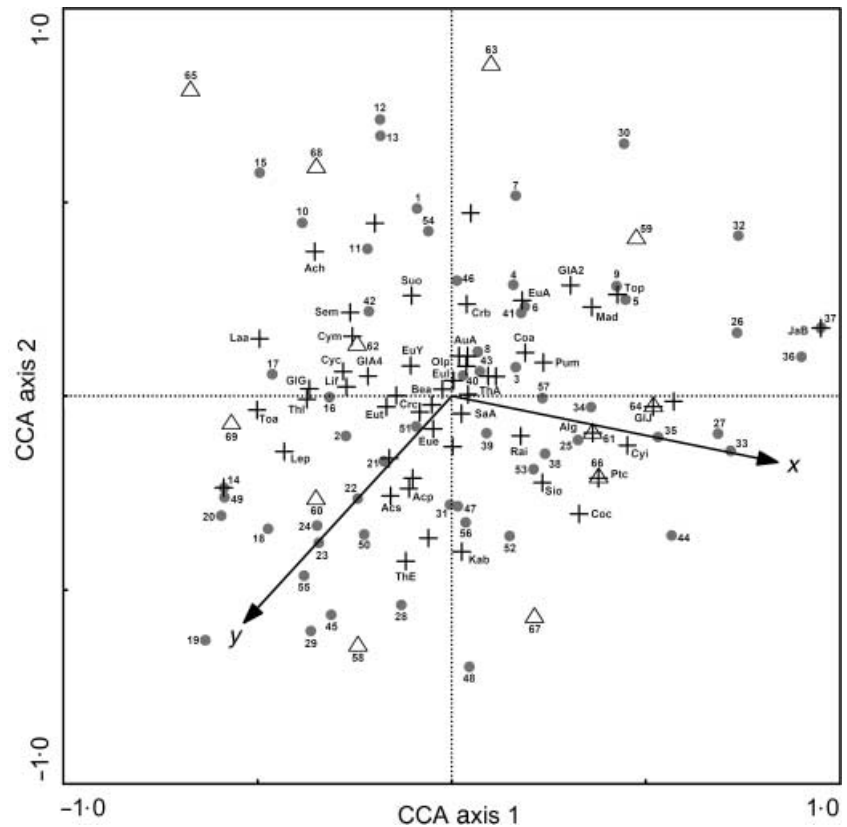


Fig. 5. Land-snail species distributions in relation to geographical variables: pCCA ordination diagram showing species, transects in lowland rainforest and home gardens, and the geographical variables, x and y . The covariables were FOREST/GARDEN, ALTI, SOILpH and CANO. Symbols and labels as Fig. 3.

recent data from a wide range of modified habitats emphasize that many Sri Lankan snail species have an absolute requirement for forest (Raheem 2005).

A surprisingly large proportion of native land snails are apparently able to survive in home gardens. Such species represent approximately 45% of the native, largely endemic land-snail fauna occurring at low altitudes in the study area, and include snails with a widespread distribution in the study area or across the lowlands of the wet zone, as well as geographically localized species. Some of these forest species seem to thrive in gardens and high population densities were recorded. For example, the density of *Corilla colletti* was nearly three times the highest density sampled from a forested site for this genus, and a small home garden (≤ 0.1 ha) may contain 50–200 live juveniles and adults of the large snails of the genus *Acavus* (maximum adult shell dimension of 4.5–7 cm). Even rainforest species with very sparse and patchy distributions may successfully colonize gardens (e.g. *Pterocyclus cumingi*-aggregate). Home gardens therefore are clearly valuable for the conservation of some Sri Lankan lowland rainforest snails.

VARIATION IN LAND-SNAIL SPECIES COMPOSITION IN RELATION TO ALTITUDE, SOIL PH AND CANOPY DENSITY

Although altitude, canopy density and soil pH explained significant variation in species composition independent of the effects of habitat type, these three environmental variables

were closely correlated with variation in species composition between gardens and forest. Canopy density was generally a weak predictor of species composition; the difference in canopy density between gardens and forest is small (see Table S1 in the supplementary material).

The correlation between land-snail composition and altitude was strong. Home gardens have traditionally been cultivated in low-lying areas and on the lower slopes of otherwise largely forested hills (Raheem 2005). In contrast, despite widespread loss of forest cover over the last two centuries, rainforest occurs almost throughout the altitudinal range of the study area. This difference may explain why some rainforest species were absent from gardens. The observed effect of altitude may also reflect altitudinal differences in the abundances of species restricted to rainforest. However, some snails restricted to forest (e.g. *Theobaldius* sp. A and *Tortulosa pyramidata*), although more abundant at higher altitudes, were recorded at comparable altitudes to the garden sites. This suggests that unmeasured environmental variation, such as differences in microclimatic conditions (e.g. soil and leaf litter moisture, and temperature), resource availability, habitat structure (e.g. density of plant stems and canopy height) and habitat configuration (e.g. fragment/garden area and distance to edge), may have a more important role than altitude in accounting for variation in species composition between gardens and forest.

The correlation between soil pH and species composition was weak. All our study gardens were originally forested and passed through an intervening phase of shifting agriculture.

Surface soil may show marked increases in pH because of the accumulation of base cations from the decomposition and burning of above-ground vegetation during the shifting cultivation cycle (McGrath *et al.* 2001). Those rainforest species occurring at higher densities in gardens may be responding to the higher pH of garden soils (see Table S1 in the supplementary material) as several temperate studies show that total snail abundance and/or the density of individual species increases with increasing soil pH (Martin & Sommer 2004).

GEOGRAPHICAL SPECIES TURNOVER AND THE CONSERVATION VALUE OF RAINFOREST AND HOME GARDENS

Rainforest covers just 15–20% of the study area and is clearly vital for the survival of many native species. The striking level of geographical turnover across forest sites implies that long-term conservation of the land-snail fauna will require protection of most or all of the remaining forest. Although the proportion of rainforest land snails able to persist in home gardens is relatively high, it must be emphasized that the study area contains a substantial number of localized Sri Lankan endemic rainforest snails (19 species) with ranges that fall outside the altitudinal range (20–280 m) of the gardens sampled. These taxa were excluded from our analyses to reduce noise, but their inclusion increases the proportion of native species restricted to forest to 70% and correspondingly reduces the proportion of native species able to persist in gardens to 30% (Raheem 2005). Furthermore, many land-snail taxa (e.g. the families Ariophantidae, Acavidae and Cyclophoridae, and the genera *Glessula* and *Tortulosa*) show marked geographical variation at the intraspecific level. *Acavus haemastoma* and *Acavus superbus*, for example, are each represented by at least two morphologically well-defined and geographically different forms within the study area.

Our view that all remaining forest cover in the study area should be conserved is consistent with three lines of evidence. First, unlike some parts of the tropics, the scale of forest loss in Sri Lanka has been dramatic over recent centuries. Rainforest cover has declined from *c.* 80–90% of the wet zone's area in 1815 to *c.* 15% in 1992 (estimated from Legg & Jewell 1995; Raheem 2005). Secondly, a 5-year survey of the biodiversity of Sri Lankan natural forests has shown that the remaining rainforests of the wet zone are crucial for the conservation of woody plant and animal diversity and/or for the protection of watersheds (Green & Gunawardena 1997). Thirdly, the study area represents the most forested lowland rainforest landscape in Sri Lanka (Raheem 2005) and thus the best hope for expanding forest connectivity in the short to medium term in the lowland wet zone.

The failure to consider a number of potentially important environmental variables (see above) may have influenced our results. We hope to tackle this in a later study involving a more complex series of analyses incorporating a range of variables not considered in this study (e.g. fragment area, age, extent of surrounding forest cover and edge, and distance from edge).

However, it seems likely that the geographical variation in species composition reported here reflects substantial natural turnover. The occurrence of some geographically localized rainforest species in gardens within their ranges, and the fact that most of the localized species restricted to forest (e.g. *Tortulosa pyramidata* and *Theobaldius* sp. E) occur in fragments varying widely in area, history and surrounding forest cover, are consistent with this view (Raheem 2005; D. Raheem, unpublished data).

THE CONSERVATION VALUE OF HOME GARDENS

Research interest in the role of home gardens in biodiversity conservation has grown in recent decades (Kumar & Nair 2004) but quantitative data on the value of gardens for conserving forest species are still scarce. Our finding that gardens can contribute positively to the conservation of forest species agrees with the available data for tropical home-garden systems (Klein *et al.* 2002; Marjokorpi & Ruokolainen 2003; Schroth, Harvey & Vincent 2004) and with studies showing the conservation value of other types of tropical polyculture agroforests (e.g. shaded coffee, shaded cocoa and jungle rubber) for forest biota (Perfecto *et al.* 1996; Rice & Greenberg 2000; Jones *et al.* 2003; Schroth, Harvey & Vincent 2004; Somaribba *et al.* 2004). Although home gardens and other agroforests may contain a substantial subset of natural forest species, their conservation value is closely linked to the level of disturbance to which they are subjected. Less intensively cultivated, structurally complex and more forest-like coffee and cocoa agroforests, for example, have a richer forest biota than intensively managed, structurally simple systems (Rice & Greenberg 2000; Somaribba *et al.* 2004). Moreover, even low-intensity, biologically rich agroforests contain only a subset of the species present in natural forest. Thus agroforestry systems, such as home gardens, can support and complement the conservation of natural forest but should not be viewed as a substitute for natural habitats (Schroth *et al.* 2004).

In many parts of Sri Lanka's wet zone, home gardens are threatened by habitat fragmentation and conversion to commercial monoculture cultivation. Nevertheless, they represent an important type of land use on the margins of larger rainforest fragments and still occur in landscapes where natural forest is scarce. Home gardens therefore offer great potential for restoring and increasing forest cover and connectivity.

MANAGEMENT RECOMMENDATIONS

On the basis of our findings we make the following general management recommendations.

1. Sustain efforts to conserve Sri Lanka's remaining lowland rainforest. Measures must include continued active protection of forest cover and, crucially, the development and implementation of strategies to increase connectivity between existing forest fragments.
2. Secure conservation of home gardens through state- or non-governmental sector schemes of land purchase and

subsidies. Priority areas for conservation include gardens along the margins of larger fragments (e.g. Sinharaja and Rammalakanda), which presently act as forest buffer zones, and gardens in landscapes where natural forest is scarce, and which thus represent virtually the last available habitat for matrix-tolerant forest species.

3. Explore the potential of home gardens for reforesting the extensive areas of highly degraded, deforested and currently uncultivated land that occur on the edges of many forest fragments. Gardens cultivated in such areas, along with existing gardens on forest margins, can be used in the short to medium term for low-level extraction by local communities and allowed to revert to forest in the long term. Developing forest corridors from home gardens in this way may be a relatively fast and cost-effective way of restoring and increasing connectivity in fragmented forest landscapes.

Acknowledgements

This study was funded by the UK Government's Defra Darwin Initiative (grant numbers 162/08/214 and EI DPO 1) with additional financial support from the Natural History Museum, London, Special Funds, the John Stanley Gardiner Fund (Department of Zoology, University of Cambridge) and the Percy Sladen Memorial Fund. The Forest Department and Department of Wildlife Conservation (Government of Sri Lanka) provided the necessary permits. David Reid, David Gower and four anonymous referees commented on the manuscript. L. W. Perera, N. H. Chithrasekera and the 1999–2002 Darwin Initiative team assisted with fieldwork. Rohan Pethiyagoda, Harold Taylor and Jim Chimonides generously assisted us at various stages.

References

- Bobo, K.S., Waltert, M., Fermon, H., Njokagbor, J. & Muhlenberg, M. (2006) From forest to farmland: butterfly diversity and habitat associations along a gradient for forest conversion in southwestern Cameroon. *Journal of Insect Conservation*, **10**, 29–42.
- Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.
- ter Braak, C.J.F. & Šmilauer, P. (2002) *CANOCO Reference Manual and CanoDraw for Windows User's Guide. Software for Canonical Community Ordination*, Version 4.5. Biometris, Wageningen and Ěeské Budejovice.
- Cameron, R.A.D. & Pokryszko, B.M. (2004) Land mollusc faunas of Białowieża forest (Poland), and the character and survival of forest faunas in the North European Plain. *Journal of Molluscan Studies*, **70**, 149–164.
- Cameron, R.A.D. & Pokryszko, B.M. (2005) Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. *Journal of Conchology*, **38**, 529–547.
- Colwell, R.K. (2006) *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples*, Version 8. purl.oclc.org/estimates, accessed January 2008.
- Davies, R.G., Hernandez, L.M., Eggleton, P., Didham, R.K., Fagan, L.L. & Winchester, N.N. (2003) Environmental and spatial influences upon species composition of a termite assemblage across neotropical forest islands. *Journal of Tropical Ecology*, **19**, 509–524.
- Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570–574.
- da Fonseca, G.A.B., Sechrest, W. & Oglethorpe, J. (2005) Managing the matrix. *Climate Change and Biodiversity* (eds T.E. Lovejoy & L. Hannah), pp. 346–358. Yale University Press, New Haven and London.
- Gascon, C., Lovejoy, T.E., Bierregaard, R.O. Jr, Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M. & Borges, S. (1999) Matrix habitat and species richness in tropical forest remnants. *Biological Conservation*, **91**, 223–229.
- Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- Green, M.J.B. & Gunawardena, E.R.N. (1997) *Designing an Optimum Protected Areas System for Sri Lanka's Natural Forests. I. Environmental Management in Forestry Development Project*. Forest Department, Government of Sri Lanka, Colombo, Sri Lanka.
- Groombridge, B. & Jenkins, M.D. (2000) *Global Biodiversity. Earth's Living Resources in the 21st Century*. UNEP-World Conservation Monitoring Centre.
- Jones, D.T., Susilo, F.X., Bignell, D.E., Hardiwinto, S., Gillison, A.N. & Eggleton, P. (2003) Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. *Journal of Applied Ecology*, **40**, 380–391.
- Klein, A., Steffan-Dewenter, I., Buchori, D. & Tschardt, T. (2002) Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology*, **16**, 1003–1014.
- Kumar, B.M. & Nair, P.K.R. (2004) The enigma of tropical homegardens. *Agroforestry Systems*, **61**, 135–152.
- Kupfer, J.A., Malanson, G.P. & Franklin, S.B. (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*, **15**, 8–20.
- Laurance, W.F. & Bierregaard, R.O. Jr (1997) *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. The University of Chicago Press, Chicago, IL.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*, **16**, 605–618.
- Legg, C. & Jewell, N. (1992) *A New 1: 50 000 Scale Forest Map of Sri Lanka*. Forest and Land Use Mapping Project. Forest Department, Colombo, Sri Lanka.
- Legg, C. & Jewell, N. (1995) A 1: 50 000-scale forest map of Sri Lanka: the basis for a National Forest Geographic System. *The Sri Lanka Forester (The Ceylon Forester)*, Special Issue (Remote Sensing), 3–24.
- Lepš, J. & Šmilauer, P. (2003) *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, Cambridge.
- Lindenmayer, D.B. & Franklin, J.F. (2002) *Conserving Forest Biodiversity*. Island Press, Washington, DC.
- McConnell, D.J. (2003) *The Forest Farms of Kandy and other Gardens of Complete Design*. Ashgate Publishing, Hampshire, UK.
- McGrath, D.A., Smith, C.K., Gholz, H.L. & de Assis Oliveira, F. (2001) Effects of land-use change on soil nutrient dynamics in Amazonia. *Ecosystems*, **4**, 625–645.
- Marjokorpi, A. & Ruokolainen, K. (2003) The role of traditional forest gardens in the conservation of tree species in West Kalimantan, Indonesia. *Biodiversity and Conservation*, **12**, 799–822.
- Martin, K. & Sommer, M. (2004) Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. *Journal of Biogeography*, **31**, 531–545.
- Mayaux, P., Holmgren, P., Achard, F., Eva, H., Stibig, H.-J. & Branthomme, A. (2005) Tropical forest cover change in the 1990s and options for future monitoring. *Philosophical Transactions of the Royal Society of London*, **B360**, 373–384.
- Naggs, F. & Raheem, D. (2000) Land snail diversity in Sri Lanka. The Natural History Museum, London, UK.
- Perfecto, I., Rice, R.A., Greenberg, R. & Van der Voort, M.E. (1996) Shade coffee: a disappearing refuge for biodiversity. *Bioscience*, **46**, 598–608.
- Pimentel, D., Stachow, U., Takacs, D.A., Brubaker, H.W., Dumas, A.R., Meaney, J.J., O'Neil, J.A.S., Onsi, D.E. & Corzilius, D.B. (1992) Conserving biological diversity in agricultural/forestry systems. *Bioscience*, **42**, 354–362.
- Raheem, D. (2005) *Land-snail diversity in Sri Lankan rainforest fragments*. PhD Thesis. University of Cambridge, Cambridge, UK.
- Raheem, D. & Naggs, F. (2006) *An Illustrated Guide to the Land Snails of Sri Lankan Natural Forest and Cultivated Habitats*. The Natural History Museum, London, UK.
- Rice, R.A. & Greenberg, R. (2000) Cacao cultivation and the conservation of biological diversity. *Ambio*, **29**, 167–173.
- Ricketts, T.H. (2004) Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology*, **18**, 1262–1271.
- Rundell, R. & Cowie, R.H. (2003) Preservation of species diversity and abundances in Pacific Island land snail death assemblages. *Journal of Conchology*, **38**, 155–170.
- Schroth, G., da Fonseca, G.A.B., Harvey, C.A., Gascon, C., Vasconcelos, H.L., Izac, A.N., Angelsen, A., Finegan, B., Kaimowitz, D., Krauss, U., Laurance, S.G.W., Laurance, W.F., Nasi, R., Naughton-Treves, L., Niessen, E., Richardson, D., Somarriba, E., Tucker, N.I.J., Vincent, G. & Wilkie, D.S. (2004) Agroforestry and biodiversity conservation in tropical land-

- scapes. *Agroforestry and Biodiversity Conservation in Tropical Landscapes* (eds G. Schroth, G.A.B. da Fonseca, C.A. Harvey, C. Gascon, H.L. Vasconcelos & A.N. Izac), pp. 487–501. Island Press, Washington, DC.
- Schroth, G., Harvey, C.A. & Vincent, G. (2004) Complex agroforests: their structure, diversity, and potential role in landscape conservation. *Agroforestry and Biodiversity Conservation in Tropical Landscapes* (eds G. Schroth, G.A.B. da Fonseca, C.A. Harvey, C. Gascon, H.L. Vasconcelos & A.N. Izac), pp. 227–260. Island Press, Washington, DC.
- Somaribba, E., Harvey, C., Samper, M., Anthony, F., González, J., Staver, C. & Rice, R.A. (2004) Biodiversity conservation in neotropical coffee (*Coffea arabica*) plantations. *Agroforestry and Biodiversity Conservation in Tropical Landscapes* (eds G. Schroth, G.A.B. da Fonseca, C.A. Harvey, C. Gascon, H.L. Vasconcelos & A.N. Izac), pp. 198–226. Island Press, Washington, DC.
- Wethered, R. & Lawes, M.J. (2005) Nestedness of bird assemblages in fragmented Afromontane forest: the effect of plantation forestry in the matrix. *Biological Conservation*, **123**, 125–137.
- de Winter, A.J. & Gittenberger, E. (1998) The land snail fauna of a square kilometre of rainforest in southwestern Cameroon: high species richness, low abundance and seasonal fluctuations. *Malacologia*, **40**, 231–250.

Received 9 May 2007; accepted 29 January 2008
Handling Editor: Justin Brashares

Supplementary material

The following supplementary material is available for this article.

Table S1. Lowland rainforest fragments and home gardens sampled

This material is available as part of the online article from:
<http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2008.01470.x>

(This link will take you to the article abstract.)

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.