ORIGINAL PAPER

Bat diversity in Vietnamese limestone karst areas and the implications of forest degradation

Neil M. Furey · Iain J. Mackie · Paul A. Racey

Abstract Limestone karst ecosystems in Southeast Asia and Vietnam are important reservoirs for biodiversity and are currently experiencing habitat loss and degradation due to land use changes and increasing pressure from extractive and tourism industries. Recent reviews indicate that their biodiversity is poorly known and raise doubts about the extent to which karst can maintain its biodiversity in the face of ongoing degradation. We investigated this issue by examining the effects of forest degradation on bat species diversity, composition and abundance. Using mist nets and harp traps, we sampled bat assemblages in karst forests of differing integrity for a total of 240 net nights and 180 harp trap nights, capturing 694 bats representing 36 species and five families. Our results confirm that primary forests in Vietnamese karst are exceptionally important for bat diversity, supporting substantial proportions of the national fauna. Disturbed and heavily degraded karst forests also appear capable of supporting relatively high numbers of bat species at low abundances, but their ability to do so in the longer term is in doubt and requires further research. Our findings of bats in relict forests on karst hillsides and ridgetops provide justification for their protection and raise the possibility that these may provide corridors for the movement of forest-dwelling bats within anthropogenic landscapes. Since the majority of Vietnamese karst landscapes remain unprotected however, the future of their biodiversity remains uncertain.

Keywords Bats · Chiroptera · Habitat destruction · Karst · Vietnam

Introduction

Tropical forests in Southeast Asia are among the most threatened on earth (Mayaux et al. 2005; Laurance 2007), with some authors estimating that the region could lose three-quarters of its original forests and up to 42% of its biodiversity by 2100 (Sodhi et al. 2004). Predictions concerning the magnitude of forthcoming extinctions have provoked debate

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and have highlighted uncertainties regarding the extent to which regenerating and degraded habitats can sustain tropical biodiversity (Laurance 2006; Wright and Muller-Landau 2006; Gardner et al. 2007). Since the latter are dramatically increasing at the expense of old growth forests regionally (Laurance 2007), determining the biodiversity value of secondary and degraded habitats is crucial to improving the reliability of extinction projections and devising conservation policies to ameliorate their severity (Gardner et al. 2007).

Southeast Asia is a global priority for biodiversity conservation, containing four of the twenty-five 'biodiversity hotspots' originally identified by Myers et al. (2000). The region is further recognised as one of the world's premier regions for limestone karst, which covers ca. 400,000 km^2 and approximately twice this figure when southern China is included (Day and Urich 2000). While poorly known biologically, the importance of Southeast Asian karst regions as 'biodiversity arks' possessing high species diversity and levels of endemism has recently been revealed (Clements et al. 2006). Asian karst landscapes are also renowned for their spectacular topography and extensive cave networks, which have been subjected to archaeological and paleontological investigations (Vermeulen and Whitten 1999). In recognition of these values, IUCN has issued guidelines for wider karst conservation (Watson et al. 1997).

Vietnamese karst areas exemplify the aesthetic, cultural and biological values associated with Southeast Asian karst, including World Heritage Sites (Ha Long Bay and Phong Nha-Ke Bang), Global Centres of Plant Diversity (Cuc Phuong) and numerous sites of international biodiversity importance (World Bank 2005). Karst mainly occurs in the north and centre of the country, accounting for nearly a fifth (ca. 60,000 km^2) of its land area (Tuyet et al. 2004a). On the Vietnamese mainland, the karst form known as 'peak cluster-depression karst' dominates. These comprise often massive areas of pyramid or cone-shaped outcrops interspersed with valleys and closed depressions, both of which, where undisturbed, are overlain by closed-canopy forest (Tuyet et al. 2004a).

Bats constitute a substantial portion of mammalian diversity throughout the Asian tropics (30%, Corbet and Hill 1992). Vietnam supports high bat diversity with at least 104 species (Corbet and Hill 1992; Hendrichsen et al. 2001; Borissenko and Kruskop 2003; Lunde et al. 2003; Robinson et al. 2003; Kruskop et al. 2006; Thong et al. 2006; Bates et al. 2007; Csorba et al. 2007; Furey et al. 2009), representing over a third of the national mammal fauna (Can et al. 2008). Although species inventories are lacking for Southeast Asian karsts, formations across the region support extensive cave networks, which provide roosting sites for large aggregations and substantial numbers of bat species (Vermeulen and Whitten 1999; Mickeburgh et al. 2002). Moreover, due to their perceived significance for bat diversity and the multitude of threats they face, Asian karsts and their caves have been identified as one of four regional priorities for bat conservation research (Kingston 2008).

Reviews indicate that Southeast Asian biodiversity in general and karst ecosystems in particular are seriously threatened and critically understudied (Sodhi and Liow 1999; Sodhi et al. 2004; Clements et al. 2006). Few empirical studies have been undertaken to examine the effects of forest destruction on bat biodiversity in the region (Zubaid 1993; Lane et al. 2006; Struebig et al. 2008), in contrast to the neotropics (e.g. Medellin et al. 2000; Clarke et al. 2004; Willig et al. 2007). These issues collectively hinder assessment of the value of karst areas for bat conservation and highlight the need to evaluate the degree to which forested karsts can maintain bat diversity in the face of ongoing degradation. While comparative studies of bats in Southeast Asian karst ecosystems have yet to appear, it has been suggested that a substantial number of Asian bat species may depend upon intact forests for roosting and foraging habitat (Kingston et al. 2003; Kingston 2008) and Zubaid (1993) and Struebig et al. (2008) found that forest degradation and fragmentation has

negative effects on bat abundance, species richness and assemblage composition in Malaysia.

The aim of the present study was to investigate the species composition of bat populations inhabiting karst areas of differing integrity and to test the hypothesis that higher bat diversity is associated with primary forests in Vietnamese karst. As a consequence, we assess the extent to which forest degradation may negatively affect bat species diversity, composition and abundance. In view of the current paucity of information on Vietnamese bats, seasonal variations in assemblage diversity, composition and abundance were also determined. Our overall purpose is to provide baseline information to guide future conservation management of karst biodiversity in north Vietnam.

Methods

Study area

Kim Hy Nature Reserve (22°11′–22°18′N, 105°54′–106°08′E) is located in Bac Kan province, north-east Vietnam and covers an area of 15, 461 ha (Fig. 1) (Tordoff et al. 2004).
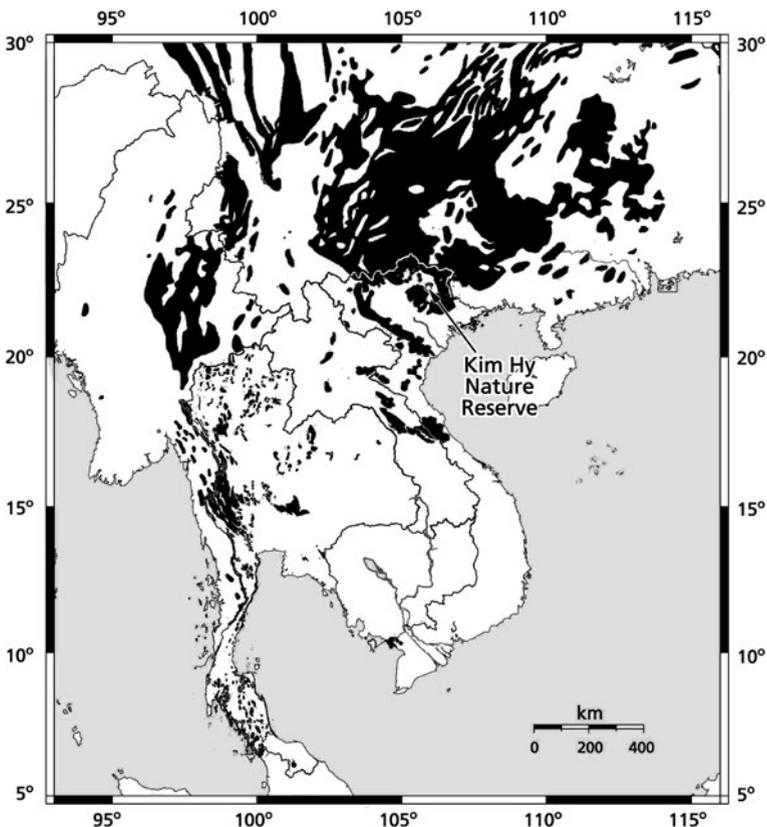

Fig. 1 Distribution of karst (*black*) in mainland Southeast Asia and location of Kim Hy Nature Reserve in north Vietnam. Created by Ricardo Insua-Cao using online map creation (http://www.aquarius.ifm-geomar.de/) and data from Hamilton-Smith and Ackroyd (2001)

Situated within the northern Indochina subtropical moist forest ecoregion (Olson and Dinerstein 1998), the site was designated as a nature reserve in 1998 and a management board established in 2003 (Tordoff et al. 2004). The core conservation area of Kim Hy comprises an uplifted and forested karst massif with elevations spanning 250–1000 metres above sea level (m a.s.l.). This is surrounded on all sides by generally lower elevation areas, which are given over to sedentary agriculture, remnant forest patches and residential areas. These collectively form the reserve's buffer zone, which encompasses an area of 20, 528 ha (Tordoff et al. 2004). Due to funding delays, activities to formalise and demarcate the boundaries of the core conservation area are ongoing (Kim Hy management board pers. comm. 2007). Surface water is absent from the core area. Local terrain is steep and highly dissected and comprises a mosaic of semi- to fully discrete valleys separated by steep to sheer karst ridges (peak cluster-depression karst). Forests at Kim Hy are regarded as seasonal broadleaved evergreen forests over limestone (Trung 1978). With the exception of peripheral areas, forests within the southern and central portions of the core conservation area are primary, whereas valley floors on the northern flank are largely cultivated for agriculture with remnant forest persisting mostly on hillsides and ridgetops. Although protection efforts are underway, illegal logging and fuel wood collection continue to degrade forests within the core conservation area, particularly those on its periphery. Wildlife hunting also remains commonplace, posing a major threat to forest biodiversity (Kim Hy management board pers. comm. 2007). Local climate is monsoonal with an average annual rainfall of 1593 mm, an average humidity of 81% and an average temperature of 20.1°C (data from the Ngan Son station in Van et al. 2000). The wet season typically lasts from May to September and the dry season from October to March, with April representing a transition between the two seasons.

Sampling sites

Fieldwork was undertaken between September 2006 and December 2007 at sites representative of three habitats: primary forest, disturbed forest, and agriculture/degraded forest. Due to access restrictions, a single site was available for sampling in each habitat. Each was located centrally within larger areas (≥300 ha) which were homogenous with respect to geology, landform and vegetation condition. To ensure spatial independence, sampling sites were located >8 km apart (Kingston 2009). Due to the difficulty of traversing highly-dissected karst terrain at night, sampling points at each site were confined to an area of 50–75 ha. Detailed information for forest and non-forest vegetation at Kim Hy is provided by Hardiman et al. (2002), but for indicative purposes, summary descriptions of each habitat sampled are given below.

Primary forest: Sampling of bat assemblages in primary forest was undertaken in a valley situated within the southern interior of the core conservation area (22°11.806′N, 106°02.216′E). Sampling elevations ranged from ca. 660 to 750 m a.s.l. The canopy and emergent forest layers were dominated by *Burretiodendron tonkinense* (Tiliaceae), and the middle storey dominated by shade-tolerant members of the Euphorbiaceae (*Mallotus*, *Antidema* and *Glochidion* spp.), Fagaceae (*Lithocarpus* spp.), and more locally, Moraceae (*Streblus* spp.) families (Hardiman et al. 2002). The understorey was relatively clear due to the predominantly scree substrate and density of the forest canopy (Fig. 2a).

Disturbed forest: Sampling was undertaken in a valley located to the west of the core conservation area (22°14.789′N, 105°58.469′E) between elevations of 720–790 m a.s.l. Forests on valley floors within the area were heavily disturbed by selective logging and small scale mining activities (Fig. 2b). Due to selective removal of mature timber and other trees, the original emergent forest layer was largely removed and canopy cover reduced
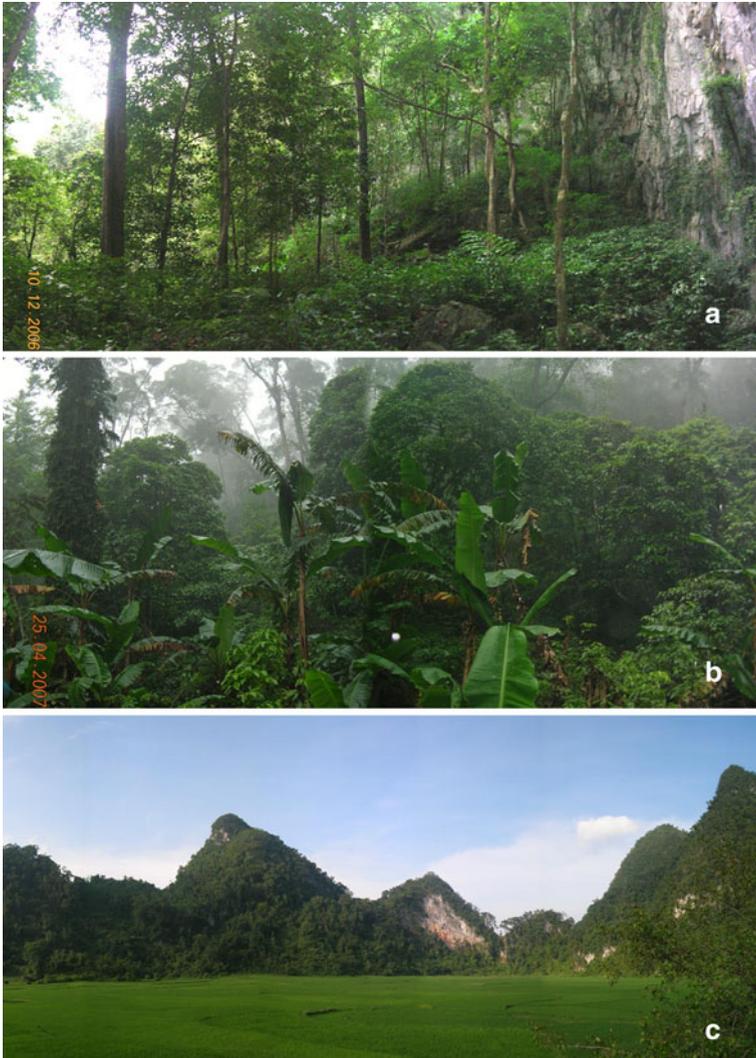
Fig. 2 Habitats sampled at Kim Hy Nature Reserve: **a** primary seasonal broadleaved evergreen forests over limestone; **b** disturbed forests over limestone; **c** agriculture/degraded forests over limestone

with distinctions between remaining forest-strata blurred. The understorey was densely vegetated due to greater light penetration and included an abundance of wild banana (*Musa* spp.) on valley floors. Forests on surrounding hillsides and ridgetops were comparatively less disturbed and retained more of their canopy cover.

Agriculture/degraded forest: Sampling was undertaken in a valley located in the northern buffer zone of Kim Hy (22°16.288′N, 106°02.994′E) between elevations of 440–582 m a.s.l. Valley floors within the area are permanently given over to paddy rice which is cultivated from April to November and fallowed outside this period. The lowest portion of hillsides were characterised by woody vegetation, while heavily degraded forests were present above these and on ridgetops (Fig. 2c). Being unsuitable for cultivation, karst

hillsides and ridgetops in settled areas at Kim Hy typically support corridors of forest vegetation of variable quality which encircle denuded valley floors.

Capture methods and sampling protocols

Bat species vary in their relative susceptibility to capture with mist nets and harp traps (Francis 1989; Berry et al. 2004). As our aim was to maximise inventory completeness, both capture devices were consequently employed for sampling bat assemblages in each of the three habitats. Two sizes of mist nets were used depending on local topography (12×2.5 m and/or 10×3 m), both being equal in net area. All nets were 70 denier with a mesh size of 16×16 mm. Four-bank harp traps with a capture surface of 2.4 m^2 were employed. To standardise units of sampling effort between these capture devices, sampling effort for mist nets was calculated as m^2 of net multiplied by the number of hours for which they were set (m^{2}nh) (Kingston 2009), while harp trap effort was similarly calculated as m^2 of harp trap multiplied by the number of hours of use (m^{2}hth) (Francis 1989). Sampling effort with both capture devices was carefully standardised to ensure equal effort across the three habitats, and within each habitat, between the dry and wet season. Sampling was suspended during heavy rain and was avoided on consecutive nights at the same location and during full moon periods.

As the topography of sample sites consisted of relatively small (<100 ha) and mostly closed valleys which were encircled by steep to sheer karst ridges (i.e. the dominant landform at Kim Hy), sampling points at each site were separated into two types, those on ridgetops and those on valley floors. Sampling points on ridgetops were situated in inter-valley passes (i.e. low points between adjacent high ground). Five discrete inter-valley passes were sampled at each site, each of which were located at least 100 m apart. At each of two nightly sampling points, two mist nets were erected end to end or combined in a trap array comprising a single harp trap flanked on either side by a single net. All were opened at sunset, remained so for an average of 5 h each night (typically until 2300 h) and were attended constantly. Eighty net nights and 20 harp trap nights of ridgetop sampling were consequently undertaken in each habitat, divided equally between the dry and wet season.

Sampling points on valley floors were located ≥50 m apart in a variety of microhabitats within understorey vegetation in primary and disturbed forest, and in the margins between cultivated areas and hillside vegetation in agricultural/degraded forest. Due to the need for constant attendance of mist nets on ridgetops to minimise stress to captured bats and lack of personnel, mist nets were not employed on valley floors. Harp traps, which do not necessitate constant attendance, were solely used instead. To allow sampling of potential bat activity prior to dawn, these were left open overnight and checked hourly until midnight and then again the following morning. Forty harp trap nights were undertaken on valley floors in each habitat, divided equally between the dry and wet season.

Bats were measured, photographed and identified in the field using Borissenko and Kruskop (2003), Hendrichsen et al. (2001) and unpublished field keys developed from taxonomic literature by N. Furey. All bats captured were marked on their toe claws with temporary non-toxic paint and released as near as possible to their capture site. Recaptures were low at 0.02% ($n = 16$) and are excluded from analyses. Species representing <0.5% of the total captures were defined as locally rare. Where required to confirm species identifications, a single adult male and non-reproductively active adult female were retained as voucher specimens. Voucher specimen skulls and bacula (where taxonomically important) were subsequently prepared for the purposes of measurement and examination. Finally, to maximise species inventory data, specimens previously collected at Kim Hy Nature Reserve in 2001 by Hardiman et al. (2002) and in 2003 by Vu Dinh Thong

(unpublished data) were prepared and examined. Additional species records made during other studies at Kim Hy (N. Furey unpublished data) were similarly utilised for the purposes of assessing inventory completeness. Museum accession numbers for all specimens reviewed are available from the first author. Taxonomy follows Simmons (2005).

Statistical analysis

To determine the completeness of sampling effort at each site, we estimated true species richness using abundance data and multinomial prediction methods developed by Solow and Polasky (1999) and Shen et al. (2003). Many of the available species richness predictors can substantially overestimate bat species richness (Kingston 2009), whereas those used here are considered reliable in most situations (Shen et al. 2003). To create upper and lower bound estimates of species richness, predictions were based upon a doubling of sampling effort (after Kingston 2009) and inventory completeness was calculated as the ratio of species observed to those estimated i.e. *Sobs*/*Smax* × 100. Data were analysed with SPADE (Chao and Shen 2003–2005).

To assess differences in observed species richness between habitats, we constructed sample-based rarefaction (Mao Tao) curves using abundance data with EstimateS vers. 7.5 (Colwell 2005) and plotted species richness as a function of the accumulated number of individuals (Gotelli and Colwell 2001). Statistical comparisons were undertaken by plotting the 95% confidence intervals of the sample with the greatest abundance and assessing whether these overlapped with curves for the remaining samples (Colwell et al. 2004). To further assess potential differences in species diversity, we employed the reciprocal form of Simpson's Index (1/D). Assemblage evenness ($E_{1/D}$) was calculated by dividing index values by S (number of species). Variations in species diversity between habitats and seasons were statistically compared using randomisation tests with 10,000 partitions (Solow 1993). Diversity tests were performed with Species Diversity and Richness vers. 2.65 (Pisces Conservation Ltd., UK).

Species composition between habitats and seasons was compared using the Chao-Jaccard Abundance-based Similarity Index and Estimator (Chao et al. 2005) in EstimateS. To investigate species abundance distributions between habitats, we constructed rank abundance (Whittaker) plots and statistically compared abundance distributions using a Kolmogorov–Smirnov two-sample test. An initial test was performed on the entire dataset for each habitat, followed by a second test which was restricted to the 15 most common species in each habitat to exclude the stochastic effects of rare species. Seasonal variations in bat abundance were assessed using the non-parametric Wilcoxon signed rank test (T). As sampling effort each night occasionally varied for logistical reasons, we partitioned species abundance data from each habitat into 40 samples of equal mist net and harp trap effort for the purposes of comparing capture rates between habitats (rather than use nightly capture rates). Though data were normally distributed, variances were not homogenous ($P < 0.0001$). Non-parametric Kruskal–Wallis tests were therefore employed for comparisons, with *post hoc* testing using pairwise Mann–Whitney U tests.

Results

Inventory completeness

A total of 694 bats representing 36 species were captured over the course of 39,994 m^2 trap hours (Tables 1 and 2). Estimates of total species richness (*Smax*) at Kim Hy ranged from

39.0 to 39.8, indicating an overall completeness ratio of 90–92%. The highest bat species richness was recorded in primary forest (29 species), followed by agriculture/degraded forest (25) and disturbed forest (24). Completeness ratios within these habitats ranged from 88–89%, 72–74% and 59–69%, respectively (Table 1). Ninety percent of species were recorded in these habitats after 54%, 91% and 71% of trap effort respectively.

Species richness and diversity

As the sample-based rarefaction curves for disturbed forest and agriculture/degraded forest fell within the 95% confidence intervals for primary forest (Fig. 3), differences in bat species richness between habitats were not statistically significant. Trends in species richness between the three habitats were mirrored in indices of species diversity, with primary forest obtaining the highest index (1/D = 9.40), followed by agriculture/degraded forest (8.58) and disturbed forest (8.05) (Table 1). As with species richness, differences in species diversity between the three habitats were not statistically significant (all comparisons, $P \geq 0.05$). Estimates of assemblage evenness ($E_{1/D}$) were similar and relatively low across all three bat assemblages (Table 1).

Species richness was consistently higher during the dry season in all three habitats, although indices for species diversity during the dry season were lower in disturbed forest, due to lower evenness within this assemblage relative to the wet season. With the exception of bat assemblages in agriculture/degraded forest however, differences in species diversity between seasons were not statistically significant (Table 3).

Species composition and abundance

The Vespertilionidae was best represented in terms of species richness with 16 species, although it accounted for fewer captures (21.6% of total) relative to the Pteropodidae (25.2%), Rhinolophidae (25.4%) and Hipposideridae (25.9%). Species richness within the latter families was lower with four, eight and seven species recorded respectively. The Megadermatidae was represented by *Megaderma lyra* and accounted for the lowest proportion of captures (1.9%). The single most abundant species, *Hipposideros larvatus*, accounted for 14.7% of total captures and was the commonest species in primary forest. The most abundant species in disturbed forest and agriculture/degraded forest were *Murina cyclotis* and *Rousettus leschenaultii*, respectively. Thirteen species were locally rare (<0.5% of total captures, $n \leq 3$), with five species represented by a single individual (Table 1 and Fig. 4).

Quantitative similarities in species composition between habitats were modest to relatively high and higher still between all habitats when the effects of unseen shared species were incorporated (Table 3). Species abundance distributions did not significantly differ between the three habitats (Fig. 4), (Kolmogorov–Smirnov test in primary forest vs. disturbed forest maximum difference: 0.1027, $P > 0.05$; primary forest vs. agriculture/degraded forest maximum difference: 0.0687, $P > 0.05$; disturbed forest vs. agriculture/degraded forest maximum difference: 0.0364, $P > 0.05$). The same was true when Kolmogorov–Smirnov tests were restricted to the 15 most common species in each habitat (greatest difference: 0.1096, $P > 0.05$).

No significant difference was detected in the abundance of bats between the dry and wet seasons either within each of the three habitats (Table 3) or collectively (Wilcoxon's T = 367.0, $n = 35$, $P = 0.399$). Quantitative similarities in species composition between seasons in all three habitats were also high and slightly greater when the effects of unseen

Table 1 Bat species composition, abundance and diversity for habitats sampled at Kim Hy Nature Reserve

Taxon	Species abbreviations	Primary forest	Disturbed forest	Agriculture/ degraded forest
Pteropodidae				
Rousettus leschenaultii[a]	Rle	49		37
Cynopterus sphinx[a]	Csp			15
Sphaerias blanfordi[a]	Sbl		3	1
Eonycteris spelaea[a]	Esp	69	1	
Megadermatidae				
Megaderma lyra[a]	Mly	3	2	8
Rhinolophidae				
Rhinolophus paradoxolophus	Rpa	52		2
Rhinolophus macrotis	Rma	13	1	8
Rhinolophus pearsoni	Rpe	26	13	12
Rhinolophus yunanensis	Ryu	4	5	2
Rhinolophus pusillus	Rpu	3	3	3
Rhinolophus stheno	Rst	1	4	1
Rhinolophus sinicus[†]	Rsi	3		
Rhinolophus affinis	Raf	2	16	2
Hipposideridae				
Hipposideros pomona	Hpo	5	1	7
Hipposideros cineraceus[b,†]	Hci	1		2
Hipposideros lylei[a,†]	Hly	1		2
Hipposideros armiger	Har	22	10	1
Hipposideros larvatus	Hla	73	3	26
Aselliscus stolitzkanus	Ast	18	1	5
Coelops frithii[b,†]	Cfi	2		
Vespertilionidae				
Myotis chinensis[a]	Mch	2	1	1
Myotis siligorensis[†]	Msi	1	1	1
Myotis ater[b,†]	Mat			1
Myotis muricola[b,†]	Mmu	1		
Scotomanes ornatus[a]	Sor	7		
Tylonycteris pachypus[a,†]	Tpa		1	
Pipistrellus javanicus[a,†]	Pja	2		
Hypsugo pulveratus[a,†]	Hpu		1	1
Hypsugo cadornae	Hca	1	3	
Murina tubinaris	Mtu	6	10	
Murina cyclotis	Mcy	16	41	8
Murina tiensa[†]	Mti	2	1	
Murina eleryi	Mel	3	4	1
Harpiocephalus harpia	Hha	13	17	1
Kerivoula hardwickii[b,†]	Kha			1
Kerivoula titania[b,†]	Kti		1	

Table 1 continued

Taxon	Species abbreviations	Primary forest	Disturbed forest	Agriculture/degraded forest
Number of species (*Sobs*)		29	24	25
Estimated species richness (*Smax*)				
Solow and Polasky (1999)		32.5	40.5	33.7
Shen et al. (2003)		32.9	34.8	34.9
Inventory completeness (%)		88–89	59–69	72–74
Simpson's diversity index (1/D)		9.40	8.05	8.58
Evenness ($E_{1/D}$)		0.32	0.34	0.34

Exclusively caught in [a] mist nets and [b] harp traps; [†] locally rare ($n = \leq 3$)

Table 2 Capture rates according to trapping methods for habitats sampled at Kim Hy Nature Reserve

Habitat	Ground mist nets					Harp traps				
	S	N	m^2nh	spp./m^2nh	Bats/m^2nh	S	N	m^2hth	spp./m^2hth	Bats/m^2hth
Primary forest	22	313	11,871	0.002	0.026	18	88	1,380.1	0.013	0.064
Disturbed forest	18	71	11,928	0.002	0.006	14	73	1,391.8	0.010	0.052
Agriculture/degraded forest	21	114	12,030	0.002	0.009	11	35	1,393.2	0.008	0.025
Sum	30	498				25	196			

Sampling effort in each habitat was divided equally between the dry and wet season

S number of species, *N* number of individuals, m^2nh metres squared mist net hour, m^2hth metres squared harp trap hour
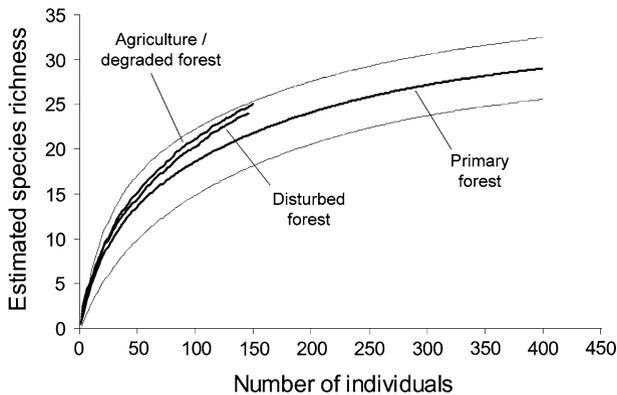

Fig. 3 Sample-based rarefaction curves with data rescaled to individuals for habitats sampled at Kim Hy Nature Reserve. *Thinner lines* are the 95% confidence intervals for primary forest

Table 3 Seasonal variation in bat species diversity, abundance and composition, and similarity indices for habitats sampled at Kim Hy Nature Reserve

| Habitat	Primary forest		Disturbed forest		Agriculture/degraded forest	
Season:	Dry	Wet	Dry	Wet	Dry	Wet
Number of species	24	20	18	16	19	16
Simpson's index (1/D)	9.64	7.72	7.41	9.04	13.89	6.59
Simpson's evenness ($E_{1/D}$)	0.40	0.39	0.41	0.57	0.73	0.41
Randomisation tests (p)	0.0877		0.481		0.0015	
Number of individuals	216	185	81	63	58	91
Wilcoxon signed rank tests (p)	0.439		0.394		0.370	
Chao-Jaccard abundance-based similarity index/ estimator	0.852/0.872		0.758/0.84		0.722/0.779	
Number of shared species	15		10		10	
Chao-Jaccard abundance-based similarity index/estimator			Disturbed forest		Agriculture/ degraded forest	
	Primary forest		0.685/0.986		0.691/0.769	
	Disturbed forest				0.553/1	
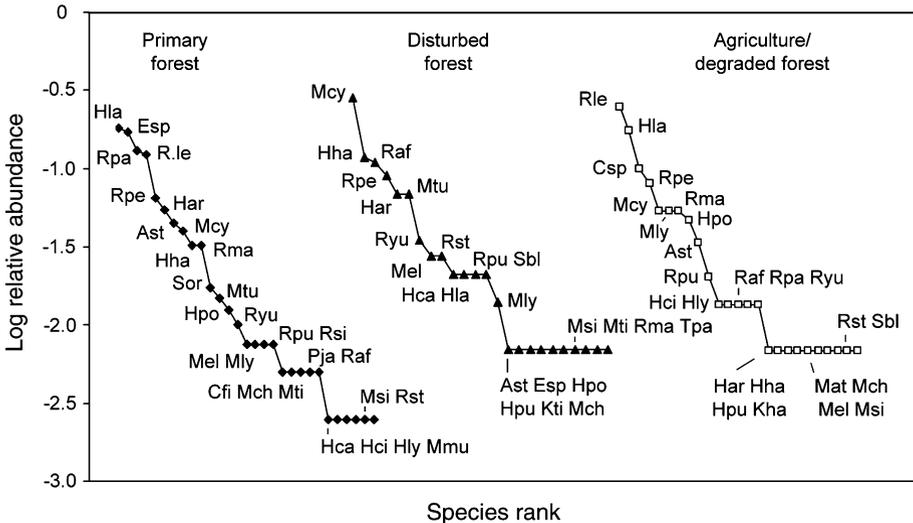
Fig. 4 Rank abundance (Whittaker) plots for bats recorded in three habitats at Kim Hy Nature Reserve. Species abbreviations are given in Table 1

shared species were incorporated. Notwithstanding this, approximately half or less of the species observed in each habitat were recorded in both seasons: primary forest (15 spp. = 52%), disturbed forest (10 spp. = 42%) and agriculture/degraded forest (10 spp. = 40%) (Table 3).

Capture success

Capture rates between habitats were significantly different (Kruskal–Wallis: H = 34.1, $P < 0.001$), as numbers of bats captured in primary forest were significantly greater than those captured in disturbed forest (Mann–Whitney: W = 2145.5, $P < 0.0001$) and agriculture/degraded forest (Mann–Whitney: W = 2138.0, $P < 0.0001$). Capture rates in the latter two habitats did not significantly differ (Mann–Whitney: W = 1582.5, $P > 0.5$) (Table 2). When expressed by area (individuals/species per m^2 trap hour), harp traps caught more bats and species than mist nets in all three habitats (Table 2), although this may reflect the fact that mist nets were only employed on ridgetops.

Thirty bat species were caught in mist nets including 11 species exclusively, while 25 species were captured in harp traps including six species exclusively (Table 1). All Pteropodidae, Megadermatidae and 85% of captures of larger hipposiderids and vespertilionids (body mass $\geq$15 g) were recorded in nets, while harp traps accounted for 71% of captures of smaller species (<15 g) within the latter two families. Mist nets similarly accounted for a greater proportion of larger rhinolophids ($\geq$15 g = 74%), while captures of smaller rhinolophids (<15 g) were also greater in mist nets (59%).

Discussion

Inventory completeness

Bat assemblages in north Vietnam (>20°N) include at least 73 species, although knowledge concerning the species composition and biogeography of Vietnamese bats is incomplete (Corbet and Hill 1992; Hendrichsen et al. 2001; Borissenko and Kruskop 2003; this study). This is illustrated by the fact that our study provides the first confirmed occurrence of seven species in north Vietnam, including three species new to science: *Kerivoula titania*, *Murina tiensa* and *Murina eleryi* (Bates et al. 2007; Csorba et al. 2007; Furey et al. 2009). Two additional species provide the first records for Vietnam (*Rhinolophus yunanensis* and *M. formosus*), while the remaining two (*M. annectans* and *M. huttoni*) represent the second and fourth confirmed in-country records respectively (Hendrichsen et al. 2001; Borissenko and Kruskop 2003; Lunde et al. 2003). Notwithstanding this, in confirming 42 bat species, more than any other community study undertaken in Vietnam, our inventory provides the most complete representation of bat assemblages at a Vietnamese site to date.

We carefully standardised trapping methods and sampling effort in order to ensure that valid quantitative comparisons could be made between habitats and seasons. Our results suggest that field surveys during both the dry and wet seasons coupled with combined use of mist nets and harp traps are required to maximise completeness of inventory surveys in northern Vietnam. The latter is demonstrated by the exclusive capture of eleven species in mist nets and six species exclusively in harp traps and is attributable to interspecific variation in susceptibility to capture with these trapping methods.

Although the predictive methods we employed to estimate true species richness (Smax) are considered reliable in most situations (Shen et al. 2003), estimates for total species richness at Kim Hy (39–39.8) were overly conservative as data from other studies at Kim Hy indicate the presence of six additional bat species (raising the confirmed site total from 36 to 42). Two of these (*Myotis annectans* and *Kerivoula kachinensis*), were collected by Hardiman et al. (2002), while the remainder (*M. formosus*, *M. ricketti*, *Ia io* and *Murina*

huttoni) were recorded in 2006/7 (N. Furey unpublished data). Conversely, while the *Smax* ranges for agriculture/degraded forest (33.7–34.9) seem reasonable in suggesting a completeness ratio of 72–74%, the upper *Smax* value of 40.5 for disturbed forest is improbable and likely represents a substantial overestimate. As tests with a variety of other non-parametric estimators failed to shed further light by producing a wide range of *Smax* values, as in other studies (Kingston 2009), we regard the lower value for disturbed forest (34.8) as more realistic in suggesting a completeness ratio of 69%, similar to that of our agriculture/degraded forest sample.

Since our sampling methods were ground-based, bat species yet to be recorded at Kim Hy likely include species which habitually forage in unobstructed airspaces above or away from the forest canopy. As such species tend to use high-intensity echolocation calls (Neuweiler 1990), acoustic methods may prove valuable in sampling members of this group (MacSwiney et al. 2008). Possible under-representation of species which habitually fly within the forest canopy may have been offset by our intensive sampling on ridgetops however, as this occurred at the level of the forest canopy in the immediate vicinity due to the steep terrain surrounding ridgetops. The fact that pteropodids, for whom vertical stratification is known (Hodgkison et al. 2004), were only caught on ridgetops would appear to support this suggestion.

Assemblage composition

The majority of bat species recorded in our study (26/36) occasionally or exclusively depend upon caves and/or rock crevices for roosting habitat (Bates and Harrison 1997; Hendrichsen et al. 2001; Borissenko and Kruskop 2003; N. Furey unpublished data). While these resources therefore influence the overall composition of bat assemblages at Kim Hy, they are unlikely to underlie the differences in species composition we observed between habitats due to their abundance at all our sampling sites and throughout the reserve. The proximity of caves to sampling sites also appears unlikely to have unduly influenced our results. For instance, intensive sampling of all caves known around the primary forest sampling site throughout the study period resulted in the capture of only one individual of *H. larvatus* (an exclusive cave dweller), whereas this proved the single most abundant species in primary forest.

After *H. larvatus*, *Eonycteris spelaea* was the most abundant bat in primary forest, while the commonest species in agriculture/degraded forest were *Rousettus leschenaultii* and *H. larvatus* (Table 1 and Fig. 4). All three are widely distributed and common in Southeast Asia, occurring in both primary and heavily disturbed habitats (Corbet and Hill 1992; Bates and Harrison 1997). Being colonial and dependent upon caves for roosting habitat however, local populations are potentially vulnerable to direct persecution such as harvesting for consumption and disturbance from a variety of human cave uses (Mickeburgh et al. 1992, 2002).

Tube-nosed bats (subfamily Murininae), *M. cyclotis* and *Harpiocephalus harpia*, were the most abundant species in disturbed forest (Table 1 and Fig. 4). *M. cyclotis* is the commonest tube-nosed bat in Vietnam and is adapted to foraging within densely vegetated habitats, whereas little is known about the natural history of *H. harpia* (Hendrichsen et al. 2001; Kingston et al. 2003). Both species are perceived as being potentially at risk from forest clearance (IUCN 2008), although our results suggest that, in Vietnam at least, both appear to tolerate a significant degree of habitat disturbance.

Thirteen species recorded in our study were locally rare ($n \leq 3$ individuals). This may represent their true abundance within the wider assemblage or partially reflect methods

used in sampling. The latter might occur due to interspecific variation in local distributions, microhabitat preferences and/or ability to perceive and avoid harp traps and mist nets. Discriminating between these possibilities requires ecological information which is lacking for most Southeast Asian bat species.

Importance of forest for bat species

Though figures are unavailable for karst forest *per se*, natural forest cover is currently increasing in Vietnam and represented 10.1 million ha or 30.6% of land area in 2004 (World Bank 2005). However, natural forests continue to be more fragmented and degraded. In 2004, over two-thirds of natural forests were considered poor quality secondary forests, while rich and closed canopy forests constituted 4.6% of the total (World Bank 2005). Although differences in bat species diversity between habitats were not statistically significant, our results nonetheless support the hypothesis that remaining primary forests in Vietnamese karst are important for bats, in harbouring higher species diversity and significantly greater bat abundances.

Bats respond to habitat alteration in a species-specific manner, with the result that abundances of some species can be expected to increase (tolerant species), while others decrease (intolerant species) and yet others are seemingly unaffected (Willig et al. 2007). Tolerant species include *Cynopterus sphinx* (Bates and Harrison 1997), which we recorded only in agriculture/degraded forest. Kingston et al. (2003) predict that intolerant species should include insectivorous bat species that habitually forage within cluttered environments such as the forest interior, as their adaptations constrain their ecological flexibility, rendering them dependent on intact forest and therefore particularly susceptible to habitat disruption. Since these represent a substantial portion of Southeast Asian bat diversity, including members of the Rhinolophidae, Hipposideridae, Kerivoulinae and Murininae, (together accounting for 22 species in our sample), this has considerable conservation relevance.

We found that members of the Rhinolophidae and Hipposideridae were significantly less abundant in disturbed forest and agriculture/degraded forest relative to primary forest (57 & 73 vs. 226 individual bats respectively), while species richness within these families was also slightly less in the former habitats (10 & 13 vs. 15 species respectively). Since both families comprise predominantly cave-dwelling species, the availability of such sites undoubtedly influences their presence or absence in a given area. Given the abundance of caves and countless passageways and rock cavities that characterise the Kim Hy karst however, our sampling sites were likely to be similar in terms of roost availability. Our results therefore support the hypothesis that both families are negatively affected by habitat alteration.

Of the remaining two subfamilies, Murininae were similarly diverse and notably more abundant in disturbed forest compared to primary forest (73 vs. 40 individual bats; six species in each habitat), but rather less abundant and diverse in agriculture/degraded forest (10 bats, three species). Sample sizes for Kerivoulinae were insufficient for comparison. In contrast to the above families, all Vietnamese members of the Murininae are foliage-dwelling species (Furey et al. 2009). Our results thus suggest that differences may exist in ecological tolerances at species and higher taxonomic levels in Vietnam. Further research is required to elucidate specific susceptibilities to habitat degradation and loss.

Our results suggest that disturbed and degraded habitats in Vietnamese karst may be capable of supporting high bat species diversity, albeit at significantly reduced abundances. These low abundances may reflect the fact many forest-dwelling species (particularly those in the above families) combine wing morphologies and echolocation call designs which are ill-suited for prey detection and capture in the more open habitats typical of degraded

landscapes (Kingston et al. 2003; Kingston 2008). As low abundances may render species more vulnerable to stochastic events, studies assessing their resilience in such circumstances are required to elucidate the long term conservation value of degraded karsts. Notwithstanding this, as the region surrounding our agriculture/degraded forest sampling site had been intensively cultivated for at least three human generations (e.g. 60 years, Kim Hy management board pers. comm.), extinction debts (Tilman et al. 1994) are unlikely to exist or to have influenced our findings in this instance. Lack of detailed historical data for vegetation at our disturbed forest sampling site unfortunately precluded assessments in this regard. Nonetheless, the fact that the overwhelming majority of bats in agriculture/degraded forest were recorded on ridgetops (23 out of 25 species, 19 species exclusively so) is likely to be significant. We attribute this to the ubiquitous presence of remnant forest belts upon the karst hillsides and ridgetops which encircle denuded valley floors in settled areas surrounding Kim Hy (Fig. 2c). This provides a justification for their conservation and raises the possibility that forested karst ridges could act as corridors for the movement of bats within otherwise anthropogenic landscapes.

Conservation implications

In documenting well over a third of the national bat fauna (42/104) at a single protected area covering ca. 150 km^2, our study suggests that karst areas harbouring intact expanses of primary forest are particularly important for Vietnamese bats. Kim Hy Nature Reserve is by no means unique in this regard, as preliminary studies at other forested karst sites in Vietnam have demonstrated similarly high species richness (e.g. Cuc Phuong with 38 species, Phong Nha Ke Bang with 36 species) (Hendrichsen et al. 2001; Borissenko and Kruskop 2003; Robinson et al. 2003). Our results emphasize the importance of undertaking field surveys during both the dry and wet season and employing harp traps and mist nets to maximise inventory completeness.

    The importance of forested karsts for bat diversity is undoubtedly a partial consequence of their countless rock fissures and subterranean passageways. Of the 73 bat species currently known to occur north of 20°N in Vietnam, over two-thirds frequently or occasionally roost in caves and/or rock crevices (Bates and Harrison 1997; Hendrichsen et al. 2001; Borissenko and Kruskop 2003; Csorba et al. 2003; N. Furey unpublished data). Studies from 3°N in Malaysia reveal that other forest types (e.g. lowland dipterocarp forest) also support exceptional bat diversity (Kingston et al. 2003), although latitudinal variations in bat species richness (Findley 1993) preclude direct comparisons. Comparisons within Vietnam are hampered by the current lack of published inventories, although to our knowledge, levels of species richness comparable to this study have yet to be recorded in non-karst forest types. Intensive multi-seasonal sampling with harp traps and mist nets in such forests e.g. Pu Hoat with 24 species (19°N: Osborn et al. 2000) and Huong Son with 25 species (18°N: Hurley 2002; N. Furey unpublished data) supports this. Irrespectively, the fact that primary karst forests in Vietnam are capable of supporting substantial portions of the national bat fauna, together with high levels of species diversity and endemism in other groups (Vermeulen and Whitten 1999; Clements et al. 2006), justifies their consideration as a conservation priority.

    Our findings suggest that disturbed and degraded karst forests in Vietnam may have the potential to support relatively high levels of bat diversity at low abundances provided sufficient vegetation cover is retained. However, we emphasize the need for additional and preferably long term studies at a range of karst sites to elucidate these findings. Nonetheless, as Vietnamese karst substrates are generally unsuitable for farming, land

conversion is typically confined to valley floors in the first instance, leaving a latticework of forests on hillsides and ridgetops which can maintain habitat connectivity within the wider landscape. This phenomenon has been observed in many areas, perhaps most noticeably in the Pu Luong-Cuc Phuong limestone range, a narrow belt of forested karst surrounded by agricultural lands which extends >50 km across north Vietnam, linking protected areas at either end (Furey and Infield 2005). As forested karst ridges appear to support relatively high levels of bat species richness and may provide corridors for the movement of forest-dwelling bats and other species within anthropogenic landscapes, further confirmation of this would considerably elevate their conservation value. While this has less relevance for karst endemic taxa with low dispersal capabilities e.g. molluscs, the rarity of forested lowlands outside of Vietnamese protected areas and high levels of forest dependency in rural areas (World Bank 2005) has led to karst hillside forests becoming ever more threatened. Though figures are unavailable, the fact that bare karst hills are increasingly commonplace in many part of the country attests to the growing seriousness of this issue (Tuyet et al. 2004b; N. Furey pers. obs.). We therefore advocate conservation of forested karst ridges in Vietnam, with particular emphasis on those connecting relict forest stands in otherwise degraded landscapes.

Southeast Asian karst ecosystems face unprecedented pressures due to their massive potential for tourism and extractive industries e.g. quarrying (Vermeulen and Whitten 1999; Clements et al. 2006). The threat posed by forest degradation is exacerbated in Vietnamese karsts due to their susceptibility to desertification and the extreme difficulty of rehabilitation (Tuyet et al. 2004b). Experiences from southwest China provide a salutary reminder of the devastating impact of karst desertification upon biodiversity and human livelihoods (Wang et al. 2004), and this issue has yet to receive the international attention it deserves. Since environmental pressures exerted by the recent massive economic and demographic changes in Vietnam show little sign of abating and ca. 90% of in-country karsts remain outside the protected area system (Day and Urich 2000), the future for Vietnamese karst biodiversity appears uncertain.

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