



Bats in the Ghats: Agricultural intensification reduces functional diversity and increases trait filtering in a biodiversity hotspot in India



Claire F.R. Wordley^{a,*}, Mahesh Sankaran^{a,b}, Divya Mudappa^c, John D. Altringham^a

^a School of Biology, University of Leeds, Leeds LS2 9JT, United Kingdom

^b National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK, Bellary Road, Bangalore 560065, India

^c Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, Mysore 570002, India

ARTICLE INFO

Keywords:

Coffee plantations
Tea plantations
Riparian corridors
Forest fragmentation
Functional diversity
Trait filtering

ABSTRACT

The responses of bats to land-use change have been extensively studied in temperate zones and the neotropics, but little is known from the palaeotropics. Effective conservation in heavily-populated palaeotropical hotspots requires a better understanding of which bats can and cannot survive in human-modified landscapes. We used catching and acoustic transects to examine bat assemblages in the Western Ghats of India, and identify the species most sensitive to agricultural change. We quantified functional diversity and trait filtering of assemblages in forest fragments, tea and coffee plantations, and along rivers in tea plantations with and without forested corridors, compared to protected forests.

Functional diversity in forest fragments and shade-grown coffee was similar to that in protected forests, but was far lower in tea plantations. Trait filtering was also strongest in tea plantations. Forested river corridors in tea plantations mitigated much of the loss of functional diversity and the trait filtering seen on rivers in tea plantations without forested corridors. The bats most vulnerable to intensive agriculture were frugivorous, large, had short broad wings, or made constant frequency echolocation calls. The last three features are characteristic of forest animal-eating species that typically take large prey, often by gleaning.

Ongoing conservation work to restore forest fragments and retain native trees in coffee plantations should be highly beneficial for bats in this landscape. The maintenance of a mosaic landscape with sufficient patches of forest, shade-grown coffee and riparian corridors will help to maintain landscape wide functional diversity in an area dominated by tea plantations.

1. Introduction

The Western Ghats of India are, together with Sri Lanka, the eighth ‘hottest’ biodiversity hotspot in the world; but only 6% of the land remains under primary vegetation, and the human population density is higher than in any other hotspot (Cincotta et al., 2000; Sloan et al., 2014). To assess the impact of agricultural intensification on biodiversity we studied bats in a mosaic landscape typical of the Western Ghats, surrounded by protected, little disturbed forest. The landscape is dominated by intensive monoculture tea plantations under sparse shade from non-native trees, interspersed with forest fragments, forested riparian corridors, and coffee plantations which are mostly grown under a canopy of native trees (Mudappa and Raman, 2007). Since 2000 the Nature Conservation Foundation (NCF) has been working to extend and restore the forest fragments, and to encourage local coffee growers to maintain native shade trees rather than to shade their coffee with commercial timber trees (Mudappa and Raman, 2007). This is

predicted to benefit a wide range of taxa. NCF has also been working to understand the relative diversity of different taxa in protected forests, forest fragments, and different types of plantations: from spiders, frogs and birds to small carnivores, primates and elephants (Kapoor, 2008; Kumar et al., 2010; Mudappa et al., 2007; Murali and Raman, 2012; Raman, 2006; Sidhu et al., 2010; Umapathy and Kumar, 2000). We have recently assessed the taxonomic diversity of bats in this landscape in the Western Ghats (Wordley et al., 2017, in prep.) and now aim to understand the changes in bat functional diversity in different habitats.

Bats are a species-rich and functionally diverse mammalian order playing important roles in insect control, pollination and seed dispersal (Altringham, 2011; Boyles et al., 2011; Kunz et al., 2011). In addition to being a major component of vertebrate diversity across much of the world, they have been recognised as a valuable bioindicator group (Jones et al., 2009). Despite this, bats are a poorly studied taxon in the palaeotropics whose conservation is generally not prioritized, and this is certainly true in India (Meyer et al., 2016). Little is known about the

* Corresponding author.

E-mail address: cfw41@cam.ac.uk (C.F.R. Wordley).

vulnerability of most palaeotropical bat species to disturbance and habitat modification. In conserving bats, as with other taxa, it is important to protect both taxonomic and functional diversity (Mouillot et al., 2011; Tilman, 2001; Villéger et al., 2008). Functional diversity is the variability in morphological and ecological traits among species, and is thought to be more important than taxonomic diversity for ecosystem resistance, resilience and functioning (Petchey and Gaston, 2006). Measuring taxonomic diversity alone may underestimate the loss of functional diversity in modified habitats (Mouillot et al., 2013). Species richness may, for example, be high in areas of intermediate disturbance, but this disturbance may act as a filter, allowing only a narrower range of trait values to persist (Edwards et al., 2014; Gray et al., 2014; Hanspach et al., 2012; Mouillot et al., 2013).

The increasing number of studies relating bat functional traits with habitat use in different regions globally provides opportunities to assess the strength of global and regional patterns in trait filtering. So far, studies relating bat species traits and environmental associations have been undertaken in Australia (Hanspach et al., 2012; Threlfall et al., 2011), the neotropics (Bader et al., 2015; Cisneros et al., 2015; Farneda et al., 2015; Jung et al., 2007) and the USA (Duchamp and Swihart, 2008; Ford et al., 2005), but there are very few such studies from the palaeotropics of Africa and Asia (Meyer et al., 2004). Relationships between morphological traits and extinction risk have been found both globally (Jones et al., 2003) and in temperate European and North American assemblages (Safi and Kerth, 2004). Examining functional diversity and trait filtering in the palaeotropics will facilitate the identification of the types of palaeotropical bats sensitive to forest loss, and in doing so provide a starting point for prioritizing research and conservation actions for the most potentially vulnerable species.

Traits such as body size, wing morphology, echolocation call frequency and diet are related to foraging behaviour and habitat preferences in bats. These have been used to assess the impact of land use change on functional diversity in a range of studies (e.g. Bader et al., 2015; Hanspach et al., 2012; Threlfall et al., 2011). For example, bats with long, narrow wings and high wing loading (low wing area in relation to body weight) are better adapted to hawking for small to medium-sized insects in open areas, while those with short broad wings and low wing loading are better adapted to short, slow flights in cluttered habitats, often plucking large insects from vegetation (Norberg and Rayner, 1987). Higher frequency, broadband echolocation calls (which give more information but attenuate more rapidly) are better adapted to cluttered habitats than lower frequency, narrowband calls, while low frequency calls travel further and can thus give information over a wide area in open habitats (Altringham, 2011; Denzinger and Schnitzler, 2013; Schnitzler and Kalko, 2001).

Many studies of functional diversity have measured functional group richness rather than functional diversity itself (Villéger et al., 2008). Assumptions must be made to fit species into groups and information is lost about the differences between species within each group (Villéger et al., 2008). Recently, multi-dimensional functional trait spaces have been used to calculate metrics such as functional richness, evenness, divergence and specialization that describe functional diversity (Villéger et al., 2011, 2010, 2008). These metrics correct many of the problems of older methods and have been used to study changes in communities due to human disturbance (Edwards et al., 2014; Mouillot et al., 2013). Here we use these metrics to assess functional changes in bat assemblages between habitats.

In this paper we quantify bat functional diversity in protected forests, forest fragments, coffee plantations under native shade and tea plantations. We also quantify bat functional diversity in riparian habitats; along rivers in protected forests, rivers with forested corridors and rivers with tea planted up to the banks. We assess the degree to which functionally important bat traits are filtered in these different habitats, with the aim of identifying the traits that affect bats' sensitivity to agricultural intensification.

We predict that functional diversity will decline and trait filtering

increase as habitat disturbance (relative to undisturbed protected forest) increases. Based on bat studies from other regions (Bader et al., 2015, Hanspach et al., 2012, Denzinger and Schnitzler, 2013) loss of structural diversity and native plant species are expected to lead to both trait filtering and a decline in functional diversity. Greatest diversity is expected in riparian areas due to the additional presence of riparian specialist bats. The greatest bat functional diversity is therefore expected on rivers in protected area forests, and lowest diversity and greatest trait filtering in tea plantations.

2. Methods

2.1. Study site

The study was conducted on the Valparai plateau and in the adjacent Anamalai Tiger Reserve in the state of Tamil Nadu in the southern Western Ghats (N 10.2–10.4°, E 76.8–77.0°). The Valparai plateau is an agricultural landscape approximately 800–1600 masl, dominated by tea plantations and interspersed with shade-grown coffee plantations, eucalyptus plantations, forest fragments and riparian vegetation (Mudappa and Raman, 2007). The native vegetation is mid-elevation tropical wet evergreen forest of the *Cullenia exarillata*–*Mesua ferrea*–*Palaquium ellipticum* type (Pascal, 1988; Raman et al., 2009). For detailed maps of the study area see Wordley et al. (2015) and Mudappa et al. (2007). The average annual rainfall is 3500 mm, of which about 70% falls during the southwest monsoon (June–September) (Raman et al., 2009).

In protected area forest we used a single lane road, several unpaved vehicle tracks and rough walking tracks to walk between the acoustic sampling points, so each site had experienced some level of disturbance. Small scale firewood collection by local people occurred in at least two protected forest sites. Forest fragments and riparian corridors were remnant forest patches or secondary forest/overgrown plantations dominated by mature native trees. Many of these fragments have received supplementary planting to restore and extend them (Mudappa and Raman, 2007).

2.2. Data collection

We chose five sites for each of the seven study habitats, and between January and May 2010 to 2013, and in November–December 2014, we spent two non-consecutive nights capturing bats and recording echolocation calls of free flying bats at each site. January–May is the driest time between monsoons, so this is when most of the work was done. Some data were gathered in November–December 2014, which was also quite dry, due to problems in obtaining forest permits in earlier years. We caught bats and recorded them on the same night to reduce the effects of inter-night variation. At every site we caught bats using five ground level (6 m × 2.5 m) mist nets (Avinet TB Mist Net (Bat Net), 38 mm mesh in 75 denier, 2-ply polyester, 4 shelves) 50–200 m from the nearest acoustic sampling point, and recorded at five points 100 m apart for 15 min per point. We started recording 40 min after sunset, using a Pettersson D240X ultrasound detector (www.batsound.com) with a sampling rate of 307 kHz and a range of 10–120 kHz recording onto an Edirol R-09 (www.roland.com) digital recorder sampling at 44.1 kHz in WAV format. Nets were opened at sunset and closed after 2.5 h. Bats were identified to species using Bates and Harrison (1997) and Srinivasulu et al. (2010).

In riparian habitats the nets were set over the river in all locations, and the recordings were taken at the river banks, pointing at the river, so only species close to the river would be recorded. All rivers were at least 4 m wide at the point and time of sampling.

2.3. Sound analysis

Echolocation calls were visualised as spectrograms to measure call

parameters using BatSound (www.batsound.com). Calls were identified using an echolocation call library for the area (Wordley et al., 2014). At each recording point a species was marked as present if a call unambiguously attributable to that species was recorded. Echolocation calls that we could not identify to species were removed from all further analyses, along with per habitat singletons, as very rare bats would be unlikely to play a major role in ecosystem functionality (McConkey and O'Farrill, 2015).

2.4. Functional metrics

We followed the methodology of Villéger et al. (2008) and Mouillot et al. (2013) in calculating functional metrics using trait-space based algorithms. Species were plotted in functional space for each habitat, based on their values for multiple functional traits. Functional richness refers to the volume of functional space occupied by all the species in a community. Functional divergence is defined as the proportion of total abundance or frequency of occurrence represented by those species with the most extreme trait values. Functional evenness is the regularity of the distribution of species and their relative abundance or frequency of occurrence in functional space. Functional specialization quantifies the mean distance of each species from the rest of the total species pool.

We measured traits relating to body size, echolocation call, diet and wing morphology to create our functional space (Table 1). Diet was established from the literature (Bates and Harrison, 1997; Baete, 2010). Echolocation call type and frequency of maximum energy (FMAXE) were taken from our own recordings (Wordley et al., 2014). Forearm length (a predictor of overall body size) was measured in the field. Photographs were taken in the field of outstretched wings against a background of known grid size. All wing variables were later calculated using the software ImageJ (Abramoff et al., 2004). Aspect ratio was calculated as $\text{wingspan}^2/\text{wing area}$, where wing area encompasses the tail membrane and the body between the wings. Relative wing loading was calculated as $((\text{body mass} \times \text{gravity})/\text{wing area})/\text{body mass}^{1/3}$.

We first generated a trait space on two axes to permit plotting the species, and to allow the calculations of functional diversity metrics. To do this we calculated a distance matrix between all species using Gower distance based on the traits measured, before running a principal coordinates analysis (PCoA) to calculate a new trait matrix of transformed coordinates using two axes, using the 'vegan' package in 'R'

Table 1
Traits of the species used in functional diversity analyses.

Species	Diet	FMAXE (kHz)	Call type	Wing aspect ratio	F.A. (mm)	Relative wing loading
<i>C. brachyotis</i>	Fru	NA	N	6.1	62	38.3
<i>H. pomona</i>	Ins	126	CF	5.2	41	32.4
<i>H. tickelli</i>	Ins	28	FM.QCF	6.9	55	40.9
<i>M. spasma</i>	Car	57	FMmult	4.7	56	31.4
<i>M. horsfieldii</i>	Ins	54	FM	6.7	39	35.8
<i>M. montivagus</i>	Ins	50	FM.QCF	6.5	45	35.8
<i>M. fuliginosus</i>	Ins	52	FM.QCF	7.1	47	34.1
<i>M. pusillus</i>	Ins	64	FM.QCF	7.3	40	32.9
<i>P. ceylonicus</i>	Ins	39	FM.QCF	7.3	39	45.3
<i>R. leschenaultii</i>	Fru	23	Clk	7	80	43.9
<i>R. beddomei</i>	Ins	42	CF	4.7	63	30.2
<i>R. indorouxii</i>	Ins	92	CF	5.8	51	33
<i>R. lepidus</i>	Ins	102	CF	6.1	41	31.8
<i>R. rouxii</i>	Ins	81	CF	5.4	49	36.4
<i>S. heathii</i>	Ins	41	FM.QCF	6.4	63	48.1
<i>S. kuhlii</i>	Ins	45	FM.QCF	6.1	50	44.5

N = no call, CF = constant frequency call, FM.QCF = frequency modulated call with a quasi-constant frequency tail, FMmult = multi-harmonic frequency modulated call, FM = frequency modulated call, Clk = click call. Fru = frugivore, Ins = insectivore, Car = insectivore and carnivore.

(Oksanen et al., 2013). Functional richness, evenness, specialization and divergence were calculated per site for acoustic and capture data combined using the functions provided by Villéger et al. (2008) and Mouillot et al. (2013) (<http://villegger.sebastien.free.fr/>). Data for both nights at each site were combined and analysis run per site as mixed models would not converge for these data. However, the mixed models did show that month, year and site, all added as random factors, accounted for little or no variation in the results.

All functional diversity metric data were tested for normality using Shapiro-Wilks tests. We then checked residuals versus fitted values to verify homogeneity, QQ-plots of the residuals for normality, and residuals versus each explanatory variable to check independence. We used linear models in the 'lme4' package in R to compare all the functional metrics between habitats. This was followed by false discovery rate (FDR) adjusted pairwise comparisons (Bates et al., 2014).

2.5. Traits

We took the mean trait values for each bat species (Table 1). We calculated community-weighted means (CWM) for each habitat ($\text{CWM} = \sum a_i \times \text{trait}_i$, where a_i is the relative abundance of species i and trait_i is the trait value of species i). All traits were tested for collinearity using R, but as none were correlated at 0.7 or above all were retained in the analysis.

As frugivores were among the largest bats in the assemblage, we compared the forearm length of bats in all habitats with frugivores both included and removed, to disentangle the effects of changes in recorded frugivore abundance and trait filtering for body size in the rest of the assemblage. All trait data were tested for normality using Shapiro-Wilks tests. We then checked residuals versus fitted values to verify homogeneity, QQ-plots of the residuals for normality, and residuals versus each explanatory variable to check independence.

We tested for differences between habitats in the abundance of frugivores, the mean relative wing loading and mean forearm length using Kruskal-Wallis tests followed by pairwise comparisons with FDR correction in R package 'agricolae' (Mendiburu and Simon, 2009). We tested for differences between habitats in the mean wing aspect ratio, the mean insectivore abundance, the FMAXE of echolocation call, and the number of individuals making frequency modulated calls with quasi-constant frequency tails (FM.QCF) using linear models followed by FDR correction in 'lsmeans'. Differences in the number of individuals making constant frequency (CF) calls in different habitats were assessed by taking the square root of the data and then using a linear model followed by FDR correction in 'lsmeans'.

3. Results

3.1. Functional metrics

One site in tea could not be used as too few species were detected for the analysis to run, so number of sites (n) = 5 for all habitats other than tea where n = 4. There were significant differences in functional richness ($F_{6,27} = 7.548$, $P < 0.001$), functional divergence ($F_{6,27} = 5.613$, $P < 0.001$), and functional specialization ($F_{6,27} = 4.241$, $P = 0.004$) between habitats, but there were no significant differences in functional evenness between habitats ($F_{6,27} = 0.395$, $P = 0.876$) (Figs. 1, 2, S1–S3, Tables S1–S5). Mean functional richness was significantly lower in tea plantations compared to all other habitats. Forest fragments, protected area forests and rivers in protected area forest had significantly greater functional richness than tea riparian habitats (rivers in tea with no riparian corridor). Mean functional divergence was significantly lower in tea plantations than in all habitats other than riparian corridors and tea riparian. Mean functional divergence was significantly higher in forest fragments than in riparian corridors. Functional specialization was greater in forest fragments than in tea and all riparian habitats.

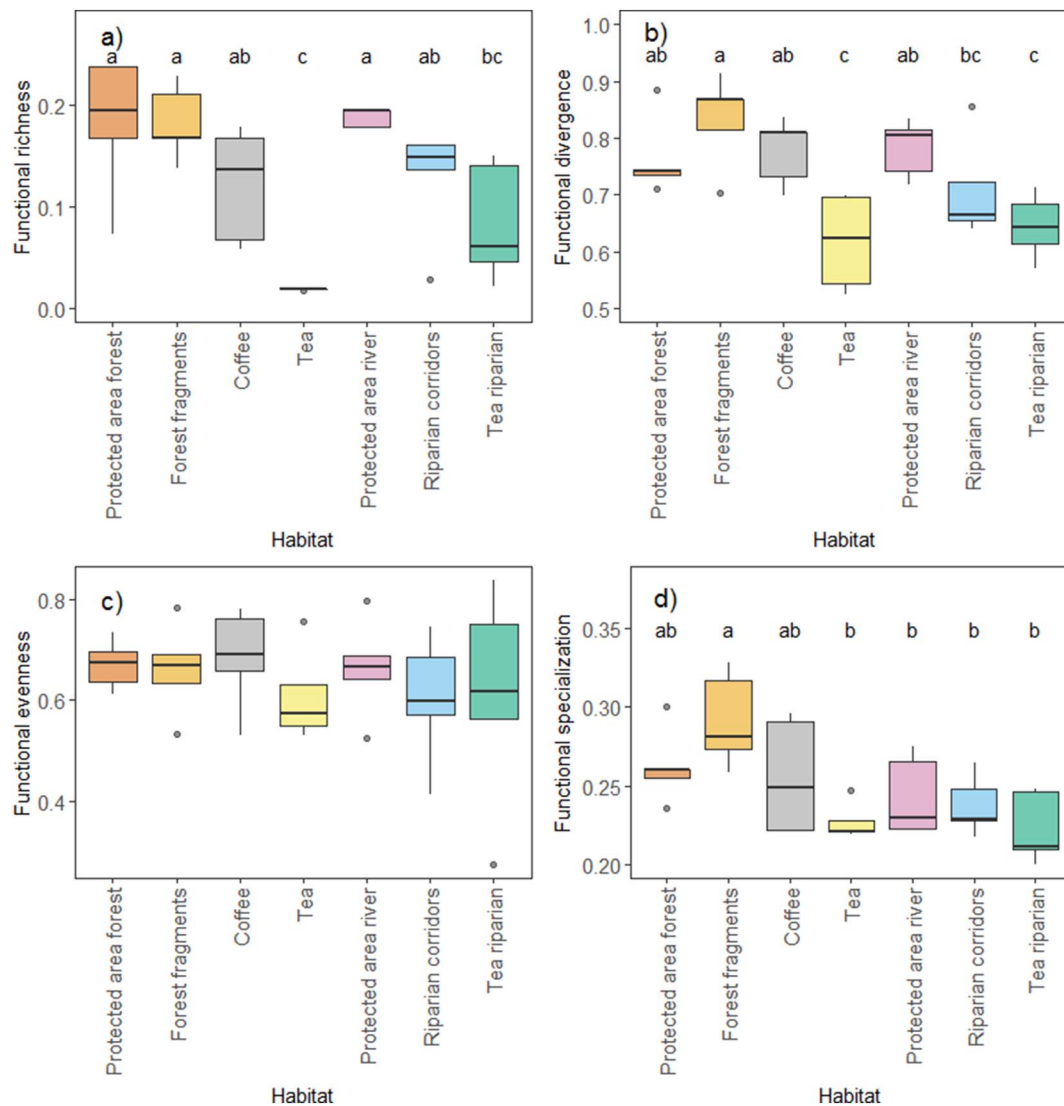


Fig. 1. a) Functional richness, b) functional divergence, c) functional evenness and d) functional specialization by habitat. Boxplots shown as quartiles with whiskers extending to 1.5 times the interquartile range of the nearest hinge and outliers as points. Within a graph, habitats sharing a letter are not significantly different at $P = 0.05$, those not sharing a letter are significantly different.

3.2. Functional traits

No traits were correlated at a value of 0.7 or greater, so all were retained in the analysis. There were significant differences among the bat assemblages of different habitats in community-weighted mean (hereafter referred to as mean) wing aspect ratio ($F_{6,1043} = 30.272$, $P < 0.001$), forearm length of all bats ($\chi^2 = 89.672$, $df = 6$, $P < 0.001$), forearm length of insectivorous and carnivorous bats only ($F_{6,917} = 9.724$, $P < 0.001$), FMAXE ($F_{6,926} = 7.469$, $P < 0.001$), and relative wing loading ($\chi^2 = 41.464$, $df = 6$, $P < 0.001$) (Fig. 3). Mean wing aspect ratio of the assemblage increased significantly in modified habitats (a shift to longer, narrower wings) as compared to protected forest, and the range of wing aspect ratio values declined. Mean forearm length declined in modified habitats compared to protected forest, and was lower in riparian habitats. When frugivores were removed from the analysis, all other habitats still had bat assemblages with shorter forearm lengths than protected forest. FMAXE was higher, and relative wing loading was lower, in protected forests compared to plantations.

The number of insectivores ($F_{6,28} = 5.051$, $P = 0.001$) and frugivores ($\chi^2 = 13.954$, $df = 6$, $P = 0.03$) also varied between habitats, as did the number of bats using FM.QCF calls ($F_{6,28} = 5.486$, $P < 0.001$)

and CF calls ($F_{6,28} = 4.98$, $P = 0.001$) (Fig. 3, Tables S6–S11). No frugivores were seen in tea plantations, and the number of insectivores was greatest on rivers in protected forests and lowest in forest fragments. The number of bats using FM calls with a QCF sweep was lower in protected forests and forest fragments than in other habitats, but the number of bats making CF calls was greatest in protected forests and rivers in protected forests and lowest in tea plantations.

4. Discussion

4.1. Trait filtering

To our knowledge this is the first study linking both echolocation and morphological traits to habitat use by bats in the palaeotropics, and thus provides an opportunity to assess the universality of bat trait-habitat relationships. Wing aspect ratio and forearm length were the strongest predictors of species responses to different habitats in this study (Fig. 3b). Wing aspect ratio was also a strong determinant of habitat use by bats in other studies, with bats with shorter, broader wings declining in deforested and urban areas while the abundance of bats with long, narrow wings increased (Bader et al., 2015; Farneda et al., 2015; Hanspach et al., 2012; Threlfall et al., 2011). In this study,

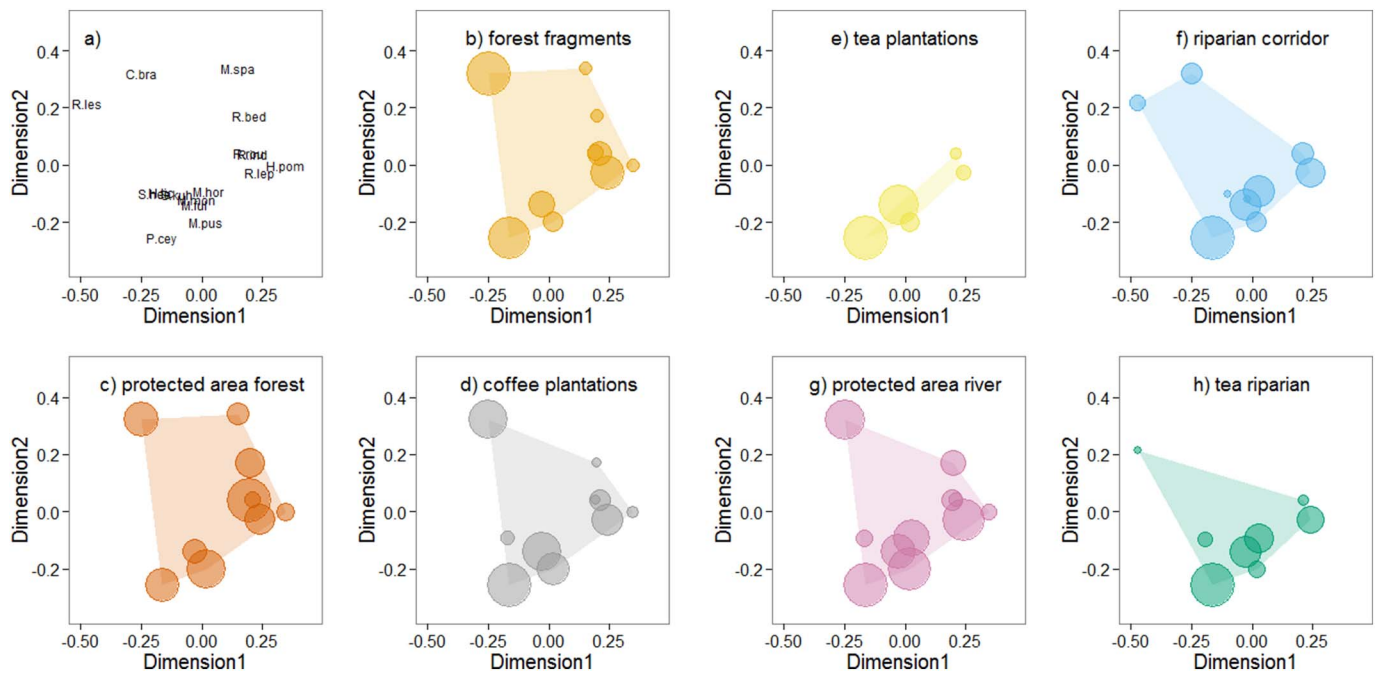


Fig. 2. Principal coordinates analysis plot of all the species in the assemblage (a), followed by plots of functional richness using the total data from each habitat. Circles indicate the recorded frequency of occurrence of each species, and the shaded polygon indicates the area of functional space occupied by the assemblage.

the range in wing aspect ratio values also declined as habitats were modified. This trait could be used as an indicator of species vulnerability to inform the conservation status and prioritize action for little-studied bats, and indeed wing morphology is a good predictor of extinction risk in bats based on IUCN threat criteria (Jones et al., 2003).

Contrary to studies in Australia (Hanspach et al., 2012; Threlfall et al., 2011), which found larger bats in more disturbed environments, we found that trait filtering removed large bats from the assemblage in modified habitats. This was partly driven by the loss of relatively large frugivorous species, but even after frugivores were removed from the analysis, protected area forests had a bat assemblage with a significantly longer mean forearm length than other habitats (Fig. 3). This fits results from tropical Brazil, where body size declined as fragmentation increased (Farneda et al., 2015). However, in Brazil this was driven by a loss of large gleaning carnivores and an increase in small fruit bats able to exploit resources in secondary forests. Ford et al. (2005) in North America, and Meyer et al. (2008) in Panama, found no relationship between body mass and response to habitat modification. Therefore, the relationship between body size and disturbance tolerance depends on the composition of the regional species pool, and so body size may not be a useful metric for predicting disturbance tolerance in poorly studied assemblages.

In this study, we saw few frugivorous bats in tea and tea riparian habitats, likely due to the lack of food, but frugivore numbers were high in shade coffee plantations (Fig. 3a). Neotropical studies have often reported declines in large carnivores but increases in the abundance of frugivores with disturbance, underscoring the need for more palaeotropical studies, and study of a wider variety of modified habitats (Farneda et al., 2015; Meyer et al., 2008; Williams-Guillen and Perfecto, 2010).

We found that mean call frequency was higher in forested habitats (Fig. 3h), in line with other studies. However, in the tropics the call frequency for most bat species is unknown as there are few comprehensive call libraries, so call frequency may currently be less useful than wing morphology as a predictive variable (Threlfall et al., 2011; Hanspach et al., 2012).

Bats using constant frequency calls used protected forest more than even the moderately altered habitats, forest fragments and coffee

plantations (although the latter was not significant, Fig. 3c). These species are adapted to detecting fluttering wings close to vegetation (Denzinger and Schnitzler, 2013; Schnitzler and Kalko, 2001). In the palaeotropics two families use constant frequency calls; Rhinolophidae and Hipposideridae. This may be a factor to consider in combination with other factors, such as wing morphology, when attempting to identify bats that are likely to be sensitive to disturbance.

In contrast, bats using frequency modulated calls with a quasi-constant-frequency component were least abundant in the dense, cluttered forest fragment understory, and most abundant in open tea riparian habitats (Fig. 3d). Some of these species, such as pipistrelles and miniopterids which comprised the majority of this assemblage, have quite 'flexible' calls which can be adjusted to suit different habitats (Denzinger and Schnitzler, 2013; Schnitzler and Kalko, 2001). Bats using this call type were the most abundant in the assemblage overall, so may be normally of least conservation concern in relation to habitat alteration.

4.2. Comparison of habitats

Many studies of bat species richness have found no differences between forest fragments and minimally disturbed forest (Mendenhall et al., 2014). However, species richness may not reveal changes in species composition and/or the occurrence of trait filtering, as seen here (Cisneros et al., 2015; Edwards et al., 2014; Gray et al., 2014). In another study from this area, we found that protected area forests did not differ significantly from shade coffee plantations and forest fragments in terms of bat species richness or composition (Wordley et al., 2017 in prep). However, the trait based analyses reported here did uncover differences between bat assemblages. Trait filtering has resulted in fewer bats with low aspect ratio wings and low relative wing loading, such as *Rhinolophus beddomei* and *Megaderma spasma*, in forest fragments and coffee plantations relative to protected area forests. There were significantly fewer bats making constant frequency (CF) calls (Rhinolophidae and Hipposideridae) in forest fragments, and significantly fewer large bats in coffee plantations, as compared to protected forests. Bats with these trait combinations may be particularly vulnerable to forest loss if they are declining in even moderately

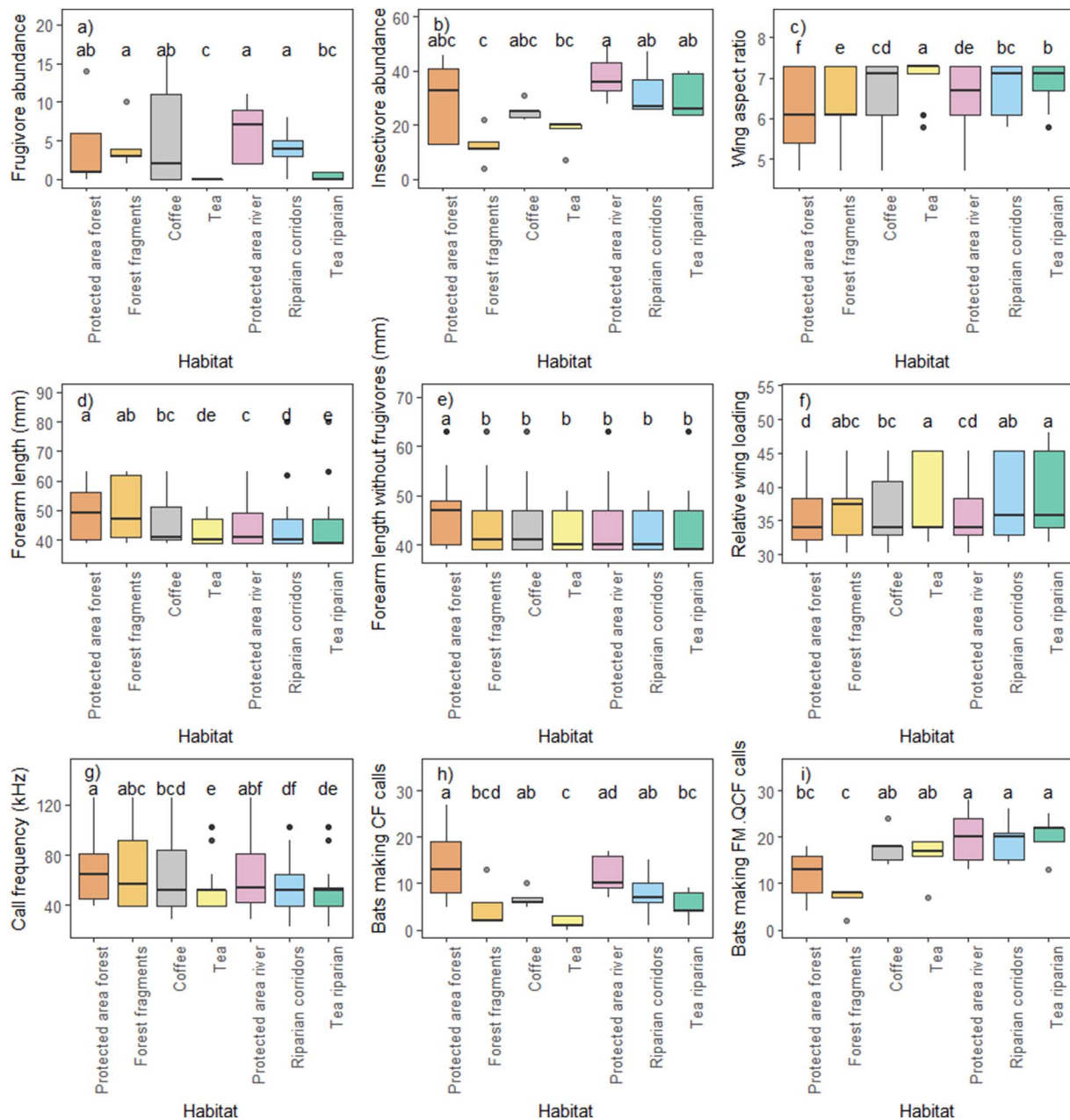


Fig. 3. Changes in values of functional traits: a) frugivore abundance, b) insectivore abundance, c) wing aspect ratio, d) forearm length e) forearm length without frugivores, f) relative wing loading, g) call frequency (frequency of maximum energy of echolocation call, FMAXE), h) number of bats making CF (constant frequency) calls and i) number of bats making FM-QCF (frequency modulated with a constant frequency tail) calls. Within a graph, habitats sharing a letter are not significantly different at $P = 0.05$, those not sharing a letter are significantly different.

modified forest habitats. Even declines in these species without local extinction may alter ecosystem function, especially if functional redundancy is low (McConkey and O'Farrill, 2015).

Functional specialization was higher (but not significantly) in forest fragments than in protected area forests and coffee plantations, and significantly higher than in all other habitats, (Fig. 1). Similarly, functional divergence was highest in forest fragments, although not significantly higher than protected area forests, coffee and protected area rivers. This is because forest fragments had few bats overall, but many of these showed more 'extreme' trait values associated with forest environments, such as frugivory and low aspect ratio wings. This may be because forest fragments in this area typically have a thinned canopy compared to protected forest, leading to a dense understory, which may be too cluttered for some of the species with more average trait values, which can thrive in the more open structure of protected area forests.

Bat assemblages in tea plantations showed the lowest functional richness, lowest functional divergence and the most extreme trait filtering of all habitats (Figs. 1 and 2). The species found in tea plantations were closer to each other in trait space than expected by chance, with no species far from the 'mean' trait values of the assemblage. Bat species that survived in tea plantations tended to be small insectivores with long, narrow wings, high wing loadings, and mid-to-low call frequencies, and to use frequency modulated calls with a quasi-constant-frequency sweep at the end. Many of these traits are typical of bats able to survive in highly modified habitats in other regions (Bader et al., 2015; Hanspach et al., 2012; Threlfall et al., 2011), however as pointed out by Maas et al. (2015), there do not appear to be any agricultural specialist bats in the same way that there are agricultural specialist birds; all the species seen in tea were seen in all other habitats. While slightly less numerous in protected forests, the

typical species abundant in tea (making frequency modulated calls with a quasi-constant frequency tails) were as abundant in the more open spaces of rivers within protected forests as in tea plantations (Fig. 3). Only a single frugivorous bat was recorded in tea plantations, likely due to the lack of foraging opportunities in this environment (Wordley et al., 2017, in prep.). Further work is needed to determine whether fruit bats in the assemblage cross tea plantations between forest fragments, and how far they travel in such open habitats, in order to advise on the maximum distances that should exist between fragments in modified landscapes.

Rivers with riparian corridors had bat assemblages of similar overall functional diversity to rivers in protected area forest (Fig. 1). However, some trait filtering was observed, with bats in riparian corridor assemblages being on average smaller, with longer, narrower wings and higher relative wing loading compared to assemblages on rivers in protected forests. Tea riparian habitats showed further altered assemblages, with significantly lower functional richness and divergence than rivers in protected forest. Assemblages on rivers in tea without riparian corridors showed further trait filtering from those along rivers with riparian corridors; the number of frugivores was significantly reduced, and the bats were on average smaller. It appears that the riparian corridors in this landscape improve the habitat for bats, but do not replicate continuous forest on each side of the river. Both habitat suitability modelling studies and studies of taxonomic diversity have previously highlighted the value of riparian vegetation in this landscape (Wordley et al., 2015, Wordley et al., 2017 in prep).

4.3. Conservation implications

The high level of protection given to protected area forests should be maintained and extended to other forests in the Western Ghats. Forest fragments are worth maintaining and restoring for bat conservation, and shade coffee under native trees is preferable to tea plantations for maintaining bat diversity in biodiversity hotspots such as the Western Ghats. Our results are similar to those from spiders, which found that forest fragments and shade coffee plantations retained high levels of diversity and many rare species, even if they were less diverse than protected forests in the same landscape (Kapoor, 2008). In contrast, lower frog and bird species richness were seen in shade coffee than in forest fragments in this landscape (Raman, 2006; Murali and Raman, 2012), so coffee plantations are not a substitute for forest fragments.

Ways to improve tea plantations for bats should be investigated. In Valparai, NCF is encouraging tea planters to use native trees for shade rather than the exotic Australian silver oak. Shade will always be sparser for tea than for *Coffea arabica* since tea bushes need more sun, but replacing exotic trees with native species may benefit bat diversity.

While riparian corridors are not equivalent to rivers through protected area forest for bats, they are preferable to rivers without riparian corridors for maintaining functional diversity in the landscape. Legislation requiring tea plantation owners to leave a buffer of native trees on both sides of every river would greatly benefit bats, and probably other species in the landscape (Wordley et al., 2017a in prep., Gray et al., 2014; Kumar et al., 2010). Work should be undertaken to assess the minimum width of buffer for a variety of taxa.

Bats with very short, broad wings are especially vulnerable to habitat loss and modification, especially when this trait is found in combination with others such as low wing loading, high frequency and/or constant frequency echolocation calls and (in this study) large size and frugivory. Across much of Asia little is known about the vulnerability of bats to different types of habitat modification, or even about the basic ecology of many species. Bats with short, broad wings, especially relatively large members of Rhinolophidae and Hipposideridae, should be the target of conservation efforts through the maintenance and extension of forests, and preventing the conversion of shade-grown to sun-grown coffee.

Frugivores are vulnerable to the loss of habitat containing fruiting trees: although the number of frugivores in coffee plantations was not significantly lower than in protected area forests, very few frugivores were seen in tea and tea riparian habitats. Since the Endangered Salim Ali's fruit bat *Latidens salimalii* has been found in this landscape (Wordley et al., 2016), it is imperative that the landscape is improved for frugivores, for example by planting more riparian corridors with fruit-bearing native trees, by protecting forest fragments and extending them where possible, and by encouraging planters to use fruiting native trees as shade in coffee plantations.

Acknowledgements

Funding was provided by NERC (Natural Environment Research Council) (NE/1528393/1), the British Ecological Society (4863/5903), the University of Leeds, and UKIERI (UK India Education and Research Initiative). We thank the Tamil Nadu Forest Department, the Tamil Nadu Electricity Board and managers of Peria Karamalai Tea Company, Bombay Burmah Trading Corporation, Tata Coffee Ltd., Parry Agro Industries Ltd., Altaghat Estate and Thalanan Estate for permissions and local support. We would like to thank the field assistants Satish Kumar A., Dinesh T., Pandi, Sunderaj, Karthik and Anand Kumar. We are also grateful to Emma Rigby, Sarah Proctor, Aurelie Laurent, Ruth Angell, Kate Parker, and Aditya Malgaonkar for help in the field. Finally, we thank T.R. Shankar Raman, M. Ananda Kumar, and Ganesh Raghunathan for logistical support and advice, Keith Hamer and Zoe Davies for their comments on CFRW's thesis, and three reviewers for their comments on the original manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.03.026>.

References

- Abramoff, M.D., Magalhães, P.J., Ram, S.J., 2004. Image processing with ImageJ. *Biophoton. Int.* 11, 36–42.
- Altringham, J.D., 2011. *Bats: From Evolution to Conservation*, second ed. Oxford University Press, New York.
- Bader, E., Jung, K., Kalko, E.K.V., Page, R.A., Rodriguez, R., Sattler, T., 2015. Mobility explains the response of aerial insectivorous bats to anthropogenic habitat change in the Neotropics. *Biol. Conserv.* 186, 97–106. <http://dx.doi.org/10.1016/j.biocon.2015.02.028>.
- Baete, D.S., 2010. Food and roosting habits of the lesser false vampire bat, *Megaderma spasma* (Chiroptera: Megadermatidae), in a Philippine lowland forest. *Asia Life Sci. Suppl.* 4, 111–129.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. In: R Package Version 1, pp. 1–6.
- Bates, P.J.J., Harrison, D.L., 1997. *Bats of the Indian Subcontinent*. Harrison Zoological Museum Publications.
- Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.H., 2011. Economic importance of bats in agriculture. *Science* 332, 41–42.
- Cincotta, R.P., Wisniewski, J., Engelman, R., 2000. Human population in the biodiversity hotspots. *Nature* 404 (6781), 990–992.
- Cisneros, L.M., Fagan, M.E., Willig, M.R., 2015. Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Divers. Distrib.* 21, 523–533.
- Denzinger, A., Schnitzler, H.-U., 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Front. Physiol.* 4, 164. <http://dx.doi.org/10.3389/fphys.2013.00164>.
- Duchamp, J.E., Swihart, R.K., 2008. Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landsc. Ecol.* 23, 849–860.
- Edwards, F.A., Edwards, D.P., Larsen, T.H., Hsu, W.W., Benedick, S., Chung, A., Vun Khen, C., Wilcove, D.S., Hamer, K.C., 2014. Does logging and forest conversion to oil palm agriculture alter functional diversity in a biodiversity hotspot? *Anim. Conserv.* 17, 163–173. <http://dx.doi.org/10.1111/acv.12074>.
- Farneda, F.Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J.M., Bobrowiec, P.E.D., Meyer, C.F.J., 2015. Trait-related responses to habitat fragmentation in Amazonian bats. *J. Appl. Ecol.* 52, 1381–1391. <http://dx.doi.org/10.1111/1365-2664.12490>.
- Ford, W.M., Menzel, M.A., Rodrigue, J.L., Menzel, J.M., Johnson, J.B., 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biol. Conserv.* 126, 528–539. <http://dx.doi.org/10.1016/j.biocon.2005.07.003>.
- Gray, C.L., Slade, E.M., Mann, D.J., Lewis, O.T., 2014. Do riparian reserves support dung

- beetle biodiversity and ecosystem services in oil palm-dominated tropical landscapes? *Ecol. Evol.* 4, 1049–1060. <http://dx.doi.org/10.1002/ece3.1003>.
- Hanspach, J., Fischer, J., Ikin, K., Stott, J., Law, B.S., 2012. Using trait-based filtering as a predictive framework for conservation: a case study of bats on farms in southeastern Australia. *J. Appl. Ecol.* 49, 842–850. <http://dx.doi.org/10.1111/j.1365-2664.2012.02159.x>.
- Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R., Racey, P.A., 2009. Carpe noctem: the importance of bats as bioindicators. *Endanger. Species Res.* 8 (1–2), 93–115.
- Jones, K.E., Purvis, A., Gittleman, J.L., 2003. Biological correlates of extinction risk in bats. *Am. Nat.* 161, 601–614.
- Jung, K., Kalko, E.K.V., Helversen, O. Von, 2007. Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. *J. Zool.* 272, 125–137. <http://dx.doi.org/10.1111/j.1469-7998.2006.00250.x>.
- Kapoor, V., 2008. Effects of rainforest fragmentation and shade-coffee plantations on spider communities in the Western Ghats, India. *J. Insect Conserv.* 12 (1), 53–68.
- Kumar, M.A., Mudappa, D., Raman, T.R.S., 2010. Asian elephant *Elephas maximus* habitat use and ranging in fragmented rainforest and plantations in the Anamalai Hills, India. *Trop. Conserv. Sci.* 3, 143–158.
- Kunz, T.H., de Torrez, E.B., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. *Ann. N. Y. Acad. Sci.* 1223, 1–38. <http://dx.doi.org/10.1111/j.1749-6632.2011.06004.x>.
- Maas, B., Karp, D.S., Bumrungsri, S., Darras, K., Gonthier, D., Huang, J.C.C., Lindell, C.A., Maine, J.J., Mestre, L., Michel, N.L., Morrison, E.B., Perfecto, I., Philpott, S.M., Şekercioğlu, Ç.H., Silva, R.M., Taylor, P.J., Tschardtke, T., Van Bael, S.A., Whelan, C.J., Williams-Guillén, K., 2015. Bird and bat predation services in tropical forests and agroforestry landscapes. *Biol. Rev.* 43. <http://dx.doi.org/10.1111/brv.12211>.
- McConkey, K.R., O’Farrill, G., 2015. Cryptic function loss in animal populations. *Trends Ecol. Evol.* 30, 182–189. <http://dx.doi.org/10.1016/j.tree.2015.01.006>.
- Mendenhall, C.D., Karp, D.S., Meyer, C.F.J., Hadly, E.A., Daily, G.C., 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature* 509, 213–217. <http://dx.doi.org/10.1038/nature13139>.
- Mendiburu, Simon, 2009. *Agricolae - A Free Statistical Toolbox for Agricultural Experiments*. (ISTR conference).
- Meyer, C.F.J., Schwarz, C.J., Fahr, J., 2004. Activity patterns and habitat preferences of insectivorous bats in a West African forest – savanna mosaic. *J. Trop. Ecol.* 20, 397–407. <http://dx.doi.org/10.1017/S0266467404001373>.
- Meyer, C.F.J., Frund, J., Lizano, W.P., Kalko, E.K.V., 2008. Ecological correlates of vulnerability to fragmentation in Neotropical bats. *J. Appl. Ecol.* 45, 381–391.
- Meyer, C.F., Struebig, M.J., Willig, M.R., 2016. Responses of tropical bats to habitat fragmentation, logging, and deforestation. In: *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, pp. 63–103.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28, 167–177. <http://dx.doi.org/10.1016/j.tree.2012.10.004>.
- Mouillot, D., Villéger, S., Scherer-Lorenzen, M., Mason, N.W.H., 2011. Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS One* 6, e17476. <http://dx.doi.org/10.1371/journal.pone.0017476>.
- Mudappa, D., Raman, T.R.S., 2007. Rainforest restoration and wildlife conservation on private lands in the Western Ghats. In: Rangarajan, G.S., M. (Eds.), *Making Conservation Work*. Permanent Black, Uttaranchal, pp. 210–240.
- Mudappa, D., Noon, B.R., Kumar, A., Chellam, R., 2007. Responses of small carnivores to rainforest fragmentation in the southern Western Ghats, India. *Small Carniv. Conserv.* 36, 18–26.
- Murali, R., Raman, T.R.S., 2012. CEPF Western Ghats Special Series: Streamside amphibian communities in plantations and a rainforest fragment in the Anamalai hills, India. *J. Threat. Taxa* 4 (9), 2849–2856.
- Norberg, U.M., Rayner, J.M.V., 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos. Trans. R. Soc. B* 316, 335–427.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2013. *Vegan: community ecology package*. In: R Package Version 2, pp. 0–10.
- Pascal, J.P., 1988. *Wet Evergreen Forests of the Western Ghats of India: Ecology, Structure, Floristic Composition and Succession*. Pondicherry Inst, Français Pondichéry.
- Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9, 741–758. <http://dx.doi.org/10.1111/j.1461-0248.2006.00924.x>.
- Raman, T.S., 2006. Effects of habitat structure and adjacent habitats on birds in tropical rainforest fragments and shaded plantations in the Western Ghats, India. In: *Forest Diversity and Management*. Springer Netherlands, pp. 517–547.
- Raman, T.R.S., Mudappa, D., Kapoor, V., 2009. Restoring rainforest fragments: survival of mixed-native species seedlings under contrasting site conditions in the Western Ghats, India. *Restor. Ecol.* 17, 137–147. <http://dx.doi.org/10.1111/j.1526-100X.2008.00367.x>.
- Safi, K., Kerth, G., 2004. A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conserv. Biol.* 18, 1293–1303. <http://dx.doi.org/10.1111/j.1523-1739.2004.00155.x>.
- Schnitzler, H.-U., Kalko, E.K.V., 2001. Echolocation by insect-eating bats. *Bioscience* 51, 557–569.
- Sidhu, S., Raman, T.R.S., Goodale, E., 2010. Effects of plantations and home-gardens on tropical forest bird communities and mixed-species bird flocks in the southern Western Ghats. *J. Bombay Nat. Hist. Soc.* 107 (2), 91.
- Sloan, S., Jenkins, C.N., Joppa, L.N., Gaveau, D.L.A., Laurance, W.F., 2014. Remaining natural vegetation in the global biodiversity hotspots. *Biol. Conserv.* 177, 12–24.
- Srinivasulu, C., Racey, P.A., Mistry, S., 2010. *Monograph A key to the bats (Mammalia: Chiroptera) of South Asia*. *J. Threat. Taxa* 2, 1001–1076.
- Threlfall, C., Law, B., Penman, T., Banks, P.B., 2011. Ecological processes in urban landscapes: mechanisms influencing the distribution and activity of insectivorous bats. *Ecography* 34, 814–826. <http://dx.doi.org/10.1111/j.1600-0587.2010.06939.x>.
- Tilman, D., 2001. Functional diversity. In: *Encyclopedia of Biodiversity*. 3.
- Umapathy, G., Kumar, A., 2000. The occurrence of arboreal mammals in the rain forest fragments in the Anamalai Hills, south India. *Biol. Conserv.* 92 (3), 311–319.
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301.
- Villéger, S., Ramos Miranda, J., Flores Hernández, D., Mouillot, D., 2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecol. Appl.* 20, 1512–1522.
- Villéger, S., Novack-Gottshall, P.M., Mouillot, D., 2011. The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecol. Lett.* 14, 561–568. <http://dx.doi.org/10.1111/j.1461-0248.2011.01618.x>.
- Williams-Guillén, K., Perfecto, I., 2010. Effects of agricultural intensification on the assemblage of leaf-nosed bats (Phyllostomidae) in a coffee landscape in Chiapas, Mexico. *Biotropica* 42, 605–613. <http://dx.doi.org/10.1111/j.1744-7429.2010.00626.x>.
- Wordley, C.F.R., Foui, E.K.F., Mudappa, D., Sankaran, M., Altringham, J.D., 2014. Acoustic identification of bats in the southern Western Ghats, India. *Acta Chiropterologica* 16, 213–222.
- Wordley, C.F.R., Sankaran, M., Mudappa, D., Altringham, J.D., 2015. Landscape scale habitat suitability modelling of bats in the Western Ghats of India: bats like something in their tea. *Biol. Conserv.* 191, 529–536. <http://dx.doi.org/10.1016/j.biocon.2015.08.005>.
- Wordley, C.F.R., Foui, E.K.F., Mudappa, D., Sankaran, M., Altringham, J.D., 2016. New location for the endangered Salim Ali’s fruit bat *Latidens salimalii* (Chiroptera: Pteropodidae) in the Anamalai Hills, Tamil Nadu. *J. Threat. Taxa* 8, 9486–9490.
- Wordley, C.F.R., Sankaran, M., Mudappa, D., Altringham, J.D., 2017. Comparing bat assemblages using acoustic and capture data in the Western Ghats of India: Heard but not Seen. (in prep.).