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Sustaining biodiversity conservation in human-modified landscapes in the Western Ghats: Remnant forests matter

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A B S T R A C T

Human-modified tropical landscapes under semi-natural or agro-ecosystems often harbor biodiversity of significant conservation value. In the Western Ghats of India, these ecosystems also provide connectivity between protected areas and other remnant forests. We investigated the conservation value of these landscapes and agro-ecosystems using results from 35 studies covering 14 taxonomic groups. Large, conspicuous taxonomic groups and tree-covered land-use types have received much focus in this area of research in the Western Ghats. We computed a response ratio defined as the log ratio of species richness in human land use to species richness in forest control site from 17 studies. In a meta-analysis, we investigated variation of this ratio across studies with respect to three variables: taxonomic group, the land-use type sampled and the extent of forest cover within the study landscape. Higher forest cover within the landscape emerged as a major positive influence on biodiversity in human-modified landscapes for vertebrates and vegetation while no patterns emerged for invertebrates. Our results suggest that loss of remnant forest patches from these landscapes is likely to reduce biodiversity within agro-ecosystems and exacerbate overall biodiversity loss across the Western Ghats. Conservation of these remnant forest patches through protection and restoration of habitat and connectivity to larger forest patches needs to be prioritized. In the densely populated Western Ghats, this can only be achieved by building partnerships with local land owners and stakeholders through innovative land-use policy and incentive schemes for conservation.

1. Introduction

It is becoming widely accepted that protected areas (PAs), although the most effective way to conserve biodiversity (Terborgh et al., 2002), are by themselves inadequate to conserve tropical biodiversity in the long-term (Rosenzweig, 2003). PAs cover less than 12% of the Earth's surface, and are concentrated in temperate and montane zones (Hoekstra et al., 2005). In the light of increasing demand for resources by a growing human population, human-use production systems that also serve to conserve some components of biodiversity are pragmatic additions to conservation efforts in PAs (Bhagwat et al., 2008; Vandermeer and Perfecto, 1997). Human use landscapes managed in a biodiversity-friendly manner not only serve as habitat but can provide a high quality matrix that facilitates the dispersal of biodiversity across landscapes of fragmented natural habitat (Perfecto and Vandermeer, 2008). There is thus an urgent need to view PAs and human-modified landscapes, not as independent entities but as ecologically interacting components of a single system (Gardner et al., 2009). Such a strategy can potentially ensure effective biodiversity conservation over large landscapes. This is particularly so for the Western Ghats mountain ranges of India (Fig. 1) – by far the most densely populated global biodiversity hotspot (Cincotta et al., 2000) – which has a mosaic of natural, semi-natural and agroecosystems in close proximity to one another.

Our goal in this paper is to survey the literature and conduct a meta-analysis in order to identify the major ecological factors that influence the status of biodiversity in human-modified landscapes in the Western Ghats. An understanding of the extent to which

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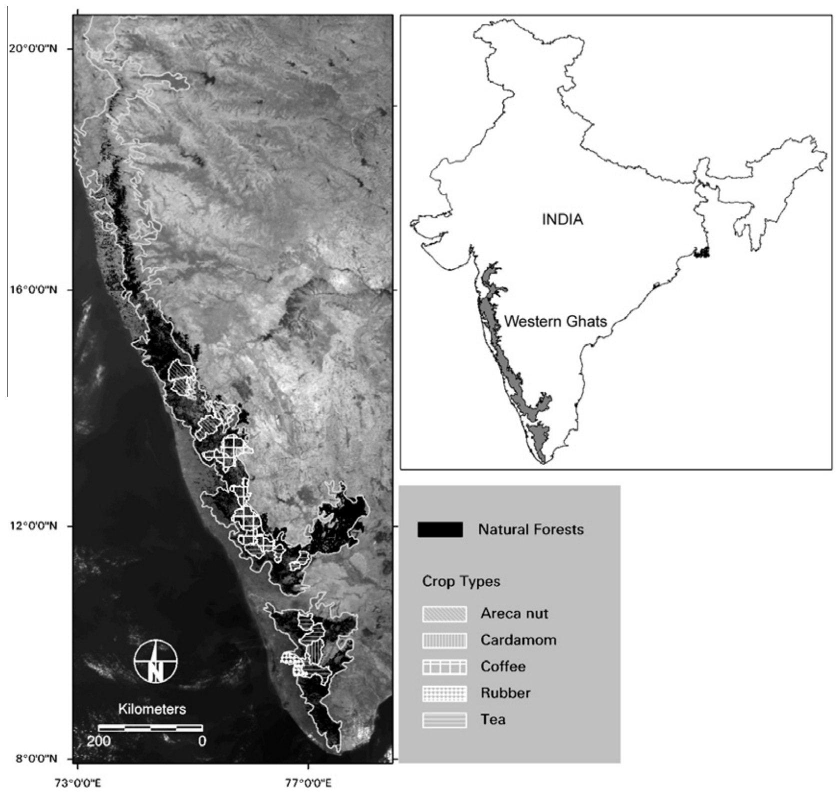

Fig. 1. Map of the Western Ghats (white outline) showing distribution of areas under natural forest. Important Taluks (administrative units) for various agroecosystems and crops are highlighted. Source: Eco-informatics Center, ATREE

biodiversity in such landscapes is influenced by local- and landscape-level factors is crucial to developing strategies for biodiversity conservation.

Human-modified landscapes in the Western Ghats typically feature greater habitat heterogeneity and structural complexity while retaining considerable native forest cover, when compared to other tropical human-modified landscapes e.g. Mexico: Greenberg et al. (1997), Columbia: Armbrecht et al. (2005), Dominican Republic: Wunderle (1999). This juxtaposition of natural and modified areas warrants an approach which accounts not just for the type of land use at a local scale but also for landscape-scale characteristics such as the extent, configuration and proximity of remnants forests within the landscape. Given this spatial configuration, forested and human-modified landscapes interact in several ways. A number of wild species that otherwise reside within continuous forest landscapes frequently occur in the human-used matrix either while foraging for resources e.g. wild bees residing in forest fragments and foraging within coffee plantations (Ghazoul, 2007), or to disperse between patches of suitable habitat e.g. wild elephants dispersing across tea-growing landscapes (Kumar et al., 2004). This matrix may also support viable populations of many generalist species (Bali et al., 2007).

For the purpose of this review, we define a human-modified landscape as one which has been significantly, but not completely converted from native vegetation to other types of land use such as agriculture, forestry, urbanization, and extractive use of forest resources, following Gardner et al. (2009). We provide a brief review of the importance of human-modified landscapes to conservation in the Western Ghats, and then analyze data from existing literature using analysis of covariance within a linear modelling framework (Crawley, 2007) to address the question: What are the local and landscape-level factors that influence the biodiversity of human-modified landscapes in the Western Ghats? Finally, we discuss the gaps in ecological knowledge that need to be addressed for conserving biodiversity in the Western Ghats at broad landscape scales.

1.1. History of human-modification of the Western Ghats

Human activity in the Western Ghats, mostly in the form of hunting and gathering, dates back over 12,000 years before present (Chandran, 1997), and agricultural landscapes were established over 2000 years before present (Ranganathan et al., 2008). The last 200 years have witnessed widespread logging and clear felling for plantations of timber, tea, coffee, fibre and agriculture (Chandran, 1997; Prabhakar, 1994); in contrast much of tropical Asia was forest-dominated even in the 1950s (Kummer and Turner, 1994). The Western Ghats are among the oldest human-modified tropical forest landscapes existing today, therefore providing an opportunity to understand well-established biodiversity patterns in response to long-term habitat changes. Although clear felling and logging were stopped in the early 1980s, most of the forest areas, including those in PAs continue to be under various extractive and non-extractive uses by human communities living within and close to the forest (Daniels et al., 1995; Karanth et al., 2006; Madhusudan, 2004).

By comparing maps from the 1920s and 1990s of over 80,000 km^2 in the central and southern Western Ghats, Menon and Bawa (1997) concluded that this period of 70 years witnessed a 40% decline in forest cover, predominantly due to conversion to open/cultivated lands (76%) or coffee plantations (16%). During this time, there was also a four-fold increase in the number of forest patches, and an 83% reduction in average patch area, both clear indicators of extensive forest loss and fragmentation. In addition to the outright loss of forest cover, there has been widespread forest degradation in the form of opened up forest canopies resulting from extractive (e.g. timber) and non-extractive (e.g. livestock grazing, fire) use of forests. Jha et al. (2000) documented a 27%

decline in primary forest in the central and southern Western Ghats between 1973 and 1995, coupled with a proportionate increase in degraded forests (less than 20% canopy cover) resulting from extractive use.

1.2. Current land use

In the present day, natural habitats cover close to one-third of the over 160,000 km^2 extent of the Western Ghats, with the PA network comprising 58 parks spanning 13,595 km^2 (Critical Ecosystem Partnership Fund, 2007). The remaining land area is diverse land use including human inhabitations, artificial reservoirs, open agriculture such as paddy (*Oryza spp.*) and vegetables, and plantations of coffee (*Coffea spp.*), tea (*Camellia sinensis*), rubber (*Hevea brasiliensis*) and cardamom (*Elettaria cardamomum*) interspersed with a variety of other cash crops (Daniels et al., 1990). While these plantations of commodity crops spanning over 10,000 km^2 are predominantly in the central and southern reaches of the Western Ghats (Fig. 1), forestry plantations of acacia (*Acacia spp.*) and bluegum (*Eucalyptus spp.*) are more widely distributed. Altogether these plantations account for a large proportion of the area under human use across the landscape. Coffee plantations cover over 3000 km^2 with an output of nearly 270,000 metric tonnes annually (Coffee Board of India, 2009). Coffee, which is almost entirely shade-grown in the Western Ghats, is intercropped with pepper (*Piper nigrum*), citrus (*Citrus spp.*), areca nut (*Areca catechu*) and vanilla (*Vanilla spp.*) and mainly occupies the moist-deciduous and wet-evergreen forest zone between 500 m and1500 m ASL. Recent years have seen a major shift in the shade canopy from one that largely resembled traditional polycultures to monocultures of silver oak (*Grevillea robusta*), primarily for economic benefits derived from harvesting the silver oak for timber (Damodaran, 2002).

Tea plantations occupy over 1100 km^2 in the mid-elevation high rainfall zone and produce more than 219,000 metric tonnes annually (Tea Board of India, 2009). Tea cultivation requires minimal or no shade, and, as a consequence, plantations are markedly different from surrounding forests, in terms of structure and ecology. Rubber plantations span 5000 km^2 in area, primarily in the west-facing valleys, producing over 700,000 metric tonnes annually (Rubber Board of India, 2003). Rubber saplings are frequently intercropped with banana (*Musa spp.*), pineapple (*Ananus comosus*), ginger (*Zingiber officinale*), turmeric (*Curcuma longa*), vegetables and medicinal plants. Cardamom plantations occupy over 730 km^2 between 600 m and 1200 m ASL and produce in excess of 11,000 metric tonnes annually. More so than coffee, cardamom is traditionally grown under a diverse canopy of native shade trees and as a result, cardamom plantations closely resemble natural forests in structure and floristic composition (Kumar et al., 1995; Raman, 2006).

1.3. Conservation importance of human-modified areas

The PA network in the Western Ghats is highly fragmented and embedded in a heterogeneous matrix of human land use. In fact, many PAs resemble doughnuts, with human land use within (e.g. hydro-electric projects, tea and coffee plantations) and around them. In this scenario, such human-used lands become relevant to conservation for several reasons. First of all, connectivity across the fragmented PA network is through the human-modified landscapes. Wild animals from PAs disperse into areas of human use, for food and water, as well as while moving between PAs (or even between one part of a PA and another). Moreover, large resident populations of several species including endangered and endemic mammals occur in human-modified landscapes e.g. lion-tailed macaque, *Macaca silenus* (Singh et al., 2002). In some taxa such as trees, amphibians and reptiles, high species richness and endemism is attributed to highly restricted distributions, and a high species turnover at small scales, such as across hill ranges or drainages (Pascal, 1988; Vasudevan et al., 2006). A few recently-discovered species of frogs e.g. *Philautus dubois* (Biju and Bossuyt, 2006) are presently known to occur only at locations in human-modified landscapes. This pattern may partly be an artefact of inadequate sampling of potential natural habitats of the species. Such a pattern may also arise out of complete conversion to human use of a species' entire distributional range, which is not difficult to imagine, given the inherently restricted and patchy distributions of several amphibian species in the Western Ghats (Vasudevan et al., 2001). Finally, in the face of predicted and documented shifts in species distribution in response to global climate change (Parmesan and Yohe, 2003) lands between PAs may take on increased importance as potential paths for migration of flora and fauna (Donald and Evans, 2006).

2. Data sources and methods

Online and print resources were searched for studies pertaining to biodiversity in human-modified landscapes in the Western Ghats. A 'study' in this case refers to a single document output from a piece of work. For the quantitative review, in cases where one piece of work resulted in more than one output (e.g. two published papers, or a thesis report and a published paper) only one of these was considered in the review. Data were obtained by searching for the keyword 'Western Ghats' from published literature (using ISI Web of Science), unpublished dissertations, reports and websites (using internet search engines and accessing copies at university and institutional libraries). The literature search was not restricted to any time period. All studies that addressed some aspect of biodiversity within human-modified systems were included in the review. The following information was collated from all relevant documents: (1) type of document, (2) whether the study focused on a single-taxonomic group or multiple taxa, (3) whether the study focused on a single land-use type, or multiple land-use types, (4) taxa studied, (5) land-use type(s) of the human-modified system studied, (6) metric used to report biodiversity, (7) whether the study included biodiversity assessment within forest control sites in addition to the human land use being assessed, and (8) descriptive conclusions of the study in terms of biodiversity conservation value of the human-modified landscape studied.

3. Literature summary

The literature survey resulted in the compilation of 35 studies: 27 peer-reviewed articles, seven postgraduate theses and one technical report (Appendix A). Although the search was not restricted to any time period, a majority of the relevant studies were obtained from between 1990 and 2008. Birds (nine studies) were the most-commonly studied taxonomic group and fragments of forest within human use matrix (10 studies) were the most widely studied human land use (Table 1).

In the 35 studies reviewed, the most commonly-reported biodiversity metric was overall species richness within the taxon (30 times), followed by measures of community composition (18), species diversity (14) and species richness among taxa of conservation priority (e.g. endemic species, threatened species, forest-dependant species: 11 times). All but six studies (which assessed tea plantations and rice fields) in the review focussed on tree-covered human land use; the "Others" category included studies on the effects of edges, pollution, livestock-grazing, pastures and human settlements. There was a strong bias towards single taxon (83% of all studies) and single human land use (63%) studies. The

Table 1
Land-use-taxa matrix with numbers within cells indicating the number of studies carried out on a given biodiversity group in that particular land-use type.

Taxonomic group	Birds	Trees	Butterflies	Mammals	Amphibians	Lianas	Ants	Earthworms	Fish	Beetles	Spiders	Macrofungi	Reptiles	Epiphytes	Total
Land-use type															
Fragmented forest	2	3	2	3	1	2	0	0	0	0	1	1	1	1	17
Diverse shade coffee plantation	4	1	2	1	0	0	0	0	0	1	1	1	0	0	11
Monoculture shade coffee plantation	3	1	1	1	0	0	0	0	0	1	0	0	0	0	7
Logged forest	1	2	1	0	0	1	0	0	0	0	0	0	0	0	5
Used forest	1	2	0	1	0	1	0	0	0	0	0	0	0	0	5
Teak plantation	1	0	1	0	1	0	1	0	0	0	0	0	0	0	4
Arecanut plantation	2	0	0	0	0	0	1	0	0	0	0	0	0	0	3
Acacia plantation	1	0	0	0	1	0	0	1	0	0	0	0	0	0	3
Paddy cultivation	1	1	1	0	0	0	0	0	0	0	0	0	0	0	3
Eucalyptus plantation	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2
Tea plantation	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2
Cardamom plantation	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Cashew nut plantation	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Regenerating forest	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Others	3	1	1	0	1	0	0	2	2	0	0	0	0	0	10
Total	22	12	9	7	5	4	3	3	2	2	2	2	1	1	

number of taxonomic groups assessed by any study ranged from one to three (mean = 1.3, mode = 1) and the number of land-use types covered by any study ranged from one to four (mean = 1.7, mode = 1). A large proportion (83%, see Appendix A) of the studies compared biodiversity measures of one or more forms of human use to that of forests within the study site e.g. birds, trees and macrofungi (Bhagwat et al., 2005b), butterflies (Devy and Davidar, 2001), spiders (Kapoor, 2008), amphibians (Krishnamurthy, 2003), earthworms (Blanchart and Julka, 1997) and mammals (Sridhar et al., 2008).

Studies in the Western Ghats have focussed on assessing biodiversity in various land-use types, in order to both identify the determinants of biodiversity within these landscapes, as well as assess the conservation value of such landscapes by contrasting their biodiversity to that of native forest sites. These studies report species richness, particularly of forest species to be negatively affected by factors such as decreasing area and increased disturbance of forest fragments (Kumar et al., 2002; Muthuramkumar et al., 2006), reduced floristic diversity (Anand et al., 2008), simplified habitat structure of land-use types (Raman, 2006), and at increasing distances to native forests (Anand et al., 2008; Bali et al., 2007; Dolia et al., 2008). Bhagwat et al. (2005a) demonstrate that tree cover within human-modified landscapes in the Western Ghats may have a buffering impact on biodiversity loss, by reducing the influence of patch area or isolation on species richness. Additionally, rare, large-bodied (Raman and Sukumar, 2002) and endemic species (Muthuramkumar et al., 2006) are relatively scarcer in man-modified habitats than in natural habitats. These findings are largely consistent with those of other studies from across the tropics (see Gardner et al. (2009)).

The extent of and proximity to natural habitats have a strong influence on biodiversity in human-modified landscapes across the world (Horner-Devine et al., 2003; Ricketts et al., 2001). The concept of countryside biogeography (Daily et al., 2001) and the 'halo effect' (Horner-Devine et al., 2003; Tubelis et al., 2004) emphasize the importance of natural habitats in facilitating biodiversity within adjacent modified areas. Although similar patterns have been illustrated by some recent work in the Western Ghats (Anand et al., 2008; Bali et al., 2007; Dolia et al., 2008; Raman and Sukumar, 2002; Ranganathan et al., 2008), the role played by native forest fragments in maintaining patterns of biodiversity across human-use areas has received surprisingly little attention.

4. Analysis

Studies which compared land-use types most commonly reported counts or estimates of overall species richness within the treatments. A number of these studies also reported species richness from control forest sites within the study area. For each of these 18 studies, we calculated a log response ratio (Hedges et al., 1999), defined as the natural logarithm of the ratio of species richness within human land use (experimental treatment) to species richness within a forest site (control treatment). The ratio was log transformed in order to linearize the metric and to normalize its otherwise skewed distribution (Hedges et al., 1999). We interpret this ratio as a measure of biodiversity in the human-modified landscape. This index takes on a value of zero when the human land use and forest control have the same species richness, increasingly negative values as the species richness in forest sites exceeds that within human land use, and positive values in case where species richness in human land use was greater than control forest sites.

Our assumptions in using this ratio in the analysis were: (1) all the observed variation was accounted for by fixed effects, with no random effects i.e. there were no between-study effects independent of the type of land use being studied, (2) within studies, samples were representative of local communities, and (3) there were no differences between the land-use types in species detection probabilities. We have tried to ensure comparability of data across studies in our dataset by focussing on only one type of response variable (overall species richness) that has been measured using any standard prescribed procedure. Standardized approaches to comparing communities are relatively new (Gotelli and Colwell, 2001), and were not practiced in several studies reviewed here. We assume that biases were not unidirectional to the extent of affecting the conclusions of the study. This is a conservative assumption, as standard sampling techniques are believed to inadequately sample forest specialist species, thereby underestimating species richness in the control site and differences in species richness between primary and modified habitats (Gardner et al., 2007).

We analyzed the response of the log-ratios (species richness in human land use/species richness in forest) across studies with respect to three independent covariates: (1) biodiversity group (categorical variable), (2) human land-use type (categorical variable) and (3) percentage of forest within 10-km radius of the centre of the study site (continuous variable). This was done using a linear multiple regression model framework with a Gaussian error distribution. Data for the two categorical variables were recorded from the respective studies. Percentage forest cover was derived from a map of forest cover in the Western Ghats created by combining three sources of information. First, three scenes from the Indian Remote Sensing (IRS) satellite WiFs sensor (pixel resolution 188 m) from dates between December 2000 and March 2003 were classified following Krishnaswamy et al. (2004). Areas classified as forest by this method were verified using and combined with data from existing forest cover maps prepared by the French Institute, Pondicherry (Pascal and Ramesh, 1995) and the Forest Survey of India, Dehradun. This combination of methods ensured a true representation of forest cover even from areas outside administrative forest boundaries, while distinguishing true forest cover from other tree-covered lands such as coffee and cardamom plantations. The time period from which these forest cover data were available correspond well with the time period within which most of the reviewed studies were conducted. The centre of the study site was approximated from the geographic coordinates of the boundaries of the study, either provided in the study site description or map. While it is accepted that the scale of a landscape varies widely with taxa, we used a standard 10-km radius buffer for all studies. We did this because based on our assessment of the sizes of study sites this buffer would best approximate the forest cover within the study sites. Percentage forest cover within the study sites ranged in value from 17% to 79% across all studies included in the analysis.

A total of 17 studies contributed 30 data points in all to the meta-analysis. The four categories of the land-use type variable were (1) diverse tree plantations such as polyculture shade coffee plantations, (2) monoculture tree plantations such as monoculture shade coffee and *Areca* plantations, (3) logged forest, being blocks of forest with a documented history of logging and (4) forest fragments embedded in a matrix of human use. Such fragments, in addition to having been selectively logged up to few decades back, are subject to various disturbances such as removal of foliage, timber and fallen wood and non-timber forest products. In contrast, logged forests are often a part of large stretches of forests which had been logged up to a few decades ago, but since then have received protection from most forms of human disturbance. Land-use categories were assigned following the study site description of each of the documents reviewed. In instances where land-use type in a study did not exactly match any of the four defined categories (e.g. abandoned cardamom plantation), they were assigned to the category that most suitably described them, based on our interpretation of the study site description.

Three groups comprised the biodiversity group variable: (1) vegetation, (2) invertebrates and (3) vertebrates. These broad biodiversity groups were used in order to make available adequate replicates within the biodiversity group category to permit meta-analysis. The justification for this grouping is that, all else being equal, responses of species within the group are likely to be more similar than across groups, based on similarities in body size and life history. All statistical computing was performed using the statistical package R (R Development Core Team, 2007).

We used an information-theoretic model selection approach to identify the most plausible model for explaining the observed log response ratio as the response variable and the three covariates described above as independent variables in a linear regression model. This approach, which optimizes not only goodness of fit of models but also their complexity, is increasingly favored in ecological analyses over conventional null hypothesis testing (Anderson et al., 2000; Burnham and Anderson, 1998; Hobbs and Hilborn, 2006; Johnson and Omland, 2004). This approach leads to selection of regression models with the best fit to the data that are also parsimonious in the number of parameters or covariates.

Small sample corrected Akaike Information Criteria (AIC_c) values were used to rank the models and the likelihood of models was assessed based on their Akaike weights (Johnson and Omland, 2004). The parameters (slopes and intercepts) of the selected model were compared to assess the magnitude and direction of covariate effects on the model intercepts and of interaction terms on the slopes. Models considered in the analysis included all three covariates, singly and in all possible combinations (17 in total) with the most complex model comprising three covariate terms, three two-way interactions and one three-way interaction term. There is ample ecological justification to include two-way interaction terms: biodiversity groups are known to differ in their response to land use (e.g. (Schulze et al. (2004)) and their forest cover in the landscape (because the scale of perception of landscapes by organisms varies widely depending on their body size and dispersal ability). Similarly, one may also expect three-way interaction terms characterizing the mediation by forest cover in the landscape of the interaction between biodiversity group and land use.

Finally it is acknowledged that species richness itself is neither the best measure of biodiversity value – because of the presence of species of lower conservation importance (Kerr, 1997), nor the most suitable measure for comparing communities, because of species replacement and community turnover. Species replacement across habitats may result in two sites with very dissimilar communities having similar species richness values, thereby reducing response ratios computed on species richness data. To assess the influence of species composition and turnover on species richness and the response ratio, and hence the validity of our analyses, we computed Pearson's correlation coefficient to test the association between the response ratio and community turnover from forest to human-used sites. We hypothesize that a positive correlation between response ratio and community dissimilarity would reflect the limited influence of species replacement on the response ratio – thereby making our analyses valid – whereas no correlation between the two would indicate that the response ratio is not adequately capturing changes in the community across land-use types. When dissimilarity scores were not reported in studies but species-site matrixes were provided, we estimated Jaccard's Index of community dissimilarity based on data in these matrices. Community dissimilarity and response ratio were preferred to other means of enquiry such as nested subset analysis, as the former provided more data points for analysis. Thirteen studies contributed 22 data points to this analysis.

5. Results

The log response ratio of species richness within human land use to that within forest control sites was found to vary widely, but on average was small in magnitude and not significantly different from zero for individual biodiversity groups (vegetation: mean ± 1 SD = −0.07 ± 0.19; invertebrates: 0.02 ± 0.24; vertebrates: −0.02 ± 0.17) and land-use types (diverse tree plantations: 0.06 ± 0.16, monoculture tree plantations: −0.19 ± 0.18, forest fragments: −0.07 ± 0.19, logged forests: 0.08 ± 0.14). Monoculture plantations (−0.19 ± 0.18) were the only exception to this, having a negative effect size. These results reflect the observed variation in studies: for example while Bhagwat et al. (2005b) documented higher tree species richness within forest fragments than large forest reserves at one location, Muthuramkumar et al. (2006) reported declines in tree species richness within fragments at another site within the Western Ghats. Such heterogeneity in the response suggests the influence of factors other than land-use type *per se* on the response of biodiversity to human land use.

The percentage forest cover within a 10 km radius appeared in each of three most probable models explaining the data (Table 2). Models comprising percent forest, land-use type and an interaction term between the two variables in the first model, percentage forest cover and biodiversity group and their interaction term in the second model, and a third model with the three variables and two interaction terms each had comparable likelihoods and combined for an Akaike weight of 0.75 (Table 2). According to these models, under conditions of low forest cover in the landscape, forest control sites had significantly higher species richness than human land use for vegetation and vertebrates. On the other hand, no apparent pattern emerged for invertebrates (Table 3). According to model 3, within biodiversity groups, intercepts were different from zero ($p < 0.05$) across all land-use types for vertebrates and in two land-use types for vegetation, while there were no differences between intercepts across land-use type for invertebrates. For vegetation and vertebrates, across land-use types, a positive (intercept = −0.3, slope = 0.005, $p = 0.001$) relationship was noted between the response ratio and percentage forest cover within 10 km (Fig. 2).

The species richness in vegetation and vertebrates appeared not to be influenced as much by the type of land use *per se* as they were by percentage forest cover in the landscape (with the exception of land-use type monoculture plantations, which had a consistently negative response across the percentage forest gradient). Slopes of the model did not vary significantly across land-use types, with respect to percentage forest cover, suggesting the overriding influence of forest cover within the landscape on the response of these groups.

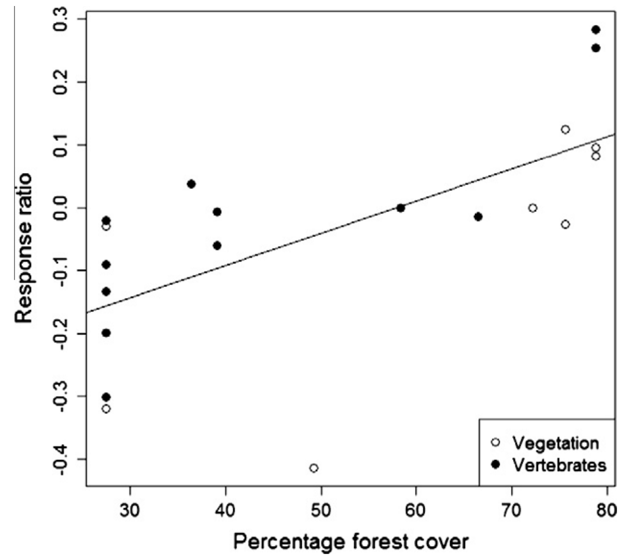

Fig. 2. Plot of log response ratio (of species richness in human use to species richness in forest control site) for vegetation and vertebrates along a gradient of increasing percent forest cover. Fitted line represents the single covariate model [percent forest cover] ($p < 0.001$).

Community dissimilarity between forest control and human land use sites was on average 55%, and did not vary across land-use type (Fig. 3). Dissimilarity was positively and significantly related to the magnitude of the species richness response ratio (Pearson's $R = 0.45$, $p = 0.04$). These results indicate that while there are differences in biological communities between forested and human-use sites, species turnover had limited impact on the response ratio, and smaller differences in species richness typically corresponded with lower dissimilarity between the two communities.

6. Discussion

Human-modified landscapes in the Western Ghats feature a variety of land-use types that are structurally and compositionally somewhat similar to native forests (e.g. shade coffee and cardamom plantations). As is the case elsewhere in the tropics e.g. Atlantic forest (Faria et al., 2006) and Costa Rica (Harvey and González

Table 2
List of ΔAIC values and AIC weights of the most probable models identified by model selection in the ANCOVA. ΔAIC values of smaller magnitude and larger AIC weights indicate more probable models.

Covariate model	ΔAIC_c	AIC_c weight
Land use + percent forest + land use: percent forest	0.0	0.26
Biodiversity group + percent forest + biodiversity group: percent forest	0.06	0.25
Land use + biodiversity group + percent forest + land use: biodiversity group + biodiversity group: percent forest	0.16	0.24

Table 3
Intercepts of the model [land use + taxon group + percent forest + land use: taxon group + taxon group: percent forest]. This model, along with the models [land use + percent forest + land use: percent forest] and [biodiversity group + percent forest + biodiversity group: percent forest] was identified as the most probable model, given the data.

	Vegetation	Invertebrates	Vertebrates
Diverse plantations	−0.31 ($p > 0.15$, $n = 1$)	0.47 ($p > 0.15$, $n = 3$)	−0.35 ($p = 0.009$, $n = 4$)
Monoculture plantations	−0.66 ($p = 0.003$, $n = 1$)	0.39 ($p > 0.15$, $n = 2$)	−0.36 ($p = 0.001$, $n = 2$)
Forest fragments	−0.30 ($p = 0.04$, $n = 4$)	0.48 ($p = 0.02$, $n = 1$)	−0.52 ($p = 0.01$, $n = 5$)
Logged forest	−0.34 ($p = 0.14$, $n = 3$)	0.20 ($p > 0.15$, $n = 1$)	−0.30 ($p = 0.02$, $n = 1$)

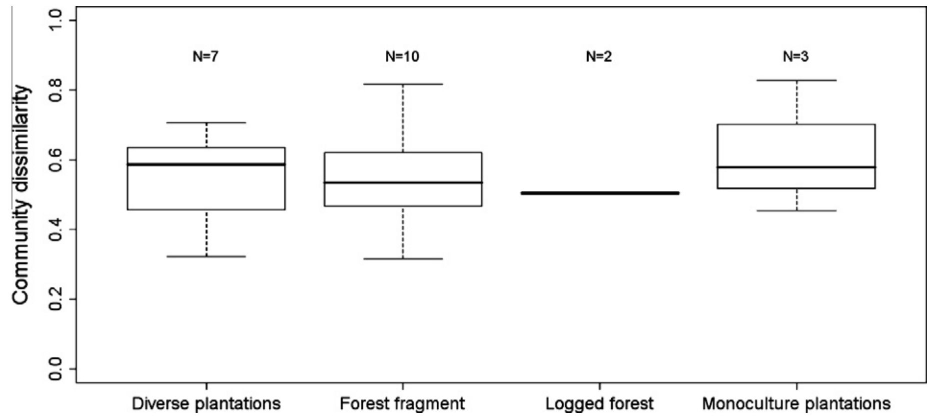

Fig. 3. Community dissimilarity (when not reported, computed using Jaccard's index) across land-use types.

Villalobos, 2007; McNeely and Schroth, 2006), these landscapes harbor substantial biodiversity, although on their own not adequately conserving a number of forest-dependant species.

Although not comparable in volume to work from Southeast Asia and central and southern America, there has been substantial research focus on biodiversity in human-modified landscapes in the Western Ghats. Yet, due to large research biases in taxonomic and land-use focus in the Western Ghats, and the availability of very few multi-taxa or multi-land use comparisons, there is still much to be understood with regard to landscape structure and composition that favour biodiversity within these landscapes. There are also significant gaps in the published literature in spatial coverage across the region: a majority of publications are based on studies in the central and southern Western Ghats (roughly 15.8°N–8.1°N) with relatively little work emerging from the northern parts of the landscape (roughly 21.1°N–15.8°N). More studies are therefore required, especially from the variety of open agriculture that is prevalent in parts of the Western Ghats, to reliably generalize these results to the entire region and potentially even beyond. Studies that report other biodiversity metrics apart from species richness (e.g. community composition, endemics species richness) are also urgently needed. Research elsewhere has shown that measures of community composition and turnover are likely to not only bring out stronger differences between forested and non-forested habitats, but also show more consistent patterns in responses across taxonomic groups (Barlow et al., 2007). It is these responses, more so than overall species richness that are likely to illustrate the true impacts and potential of human-modified landscapes for biodiversity.

Whereas a majority of the studies reviewed (83%) compared biodiversity within human land use to that of control forest sites in the same landscape, very few investigated the influence of the extent and configuration of these forests in contributing to the biodiversity within these landscapes. This is potentially an important issue, as the few studies that have looked at the role of forests in the surrounding landscape, either by comparing biodiversity at sites that are connected to forests to those that are not (Raman, 2006), or by assessing biodiversity value along a gradient of increasing distance from the forest (e.g. Anand et al. (2008), Bali et al. (2007), Dolia et al. (2008)) have found forest cover to positively influence the biodiversity value of human-modified landscapes, especially for many forest-dependant species.

Land-use type *per se* did not appear to have a large effect on the biodiversity response, except in the case of monoculture plantations, which are not only compositionally but also structurally highly dissimilar from natural habitat. These patterns might have resulted partly due to the influence of landscape-scale variables such as forest cover in surrounding landscape, but some of the unaccounted variation may also have resulted from the scale of sampling. Sampling scale – which varied widely across studies – can significantly affect the results of such analyses (Hill and Hamer, 2004), but the type of impact is neither clear nor uniform, varying in direction and magnitude across sites and taxonomic groups (Gardner et al., 2007; Hill and Hamer, 2004).

6.1. Halo effect of remnant forests in human-modified landscapes

The strong influence of remnant natural forests on biodiversity in the human-modified landscapes is reflected in the results of our analysis. Local land management practices (e.g. polyculture vs. monoculture shade coffee) may only have a secondary or localized effect on the biodiversity response, which appears to be most strongly influenced by the extent of forest cover in the landscape.

These results suggest the prevalence of a halo effect (Tubelis et al., 2004) of remnant forests within the Western Ghats landscape on the land under human use. Local-scale effects may be strongest in land-use types that are more different structurally (e.g. monoculture shade plantations, tea) from native forests. From a conservation perspective, our results emphasize that it is important to ensure the conservation and restoration of remnant forests not only for the species they currently harbor but for biodiversity in surrounding areas of human land use as well, thereby in the Western Ghats as a landscape.

6.2. Land-management for conservation in human-modified landscapes

The matrix surrounding the PA network in the Western Ghats supports a wide variety of human-use systems which not only harbor significant biodiversity value (Das et al., 2006) but also serve as an important source of livelihood. Sustainable conservation here will only result from reconciling ecological and economic ambitions for these landscapes (Gardner et al., 2009), which can be achieved through collaboration between the various stakeholder groups – the State, non-government organizations and private land-owners.

Two fundamentally different approaches to wildlife conservation in human-modified landscapes are in practice across the world: (1) wildlife friendly farming practices and (2) sparing land from human use for the purpose of conservation (Benton, 2007;

Green et al., 2005). While the former typically advocates lowered farming intensity and increased floristic and structural and compositional diversity of farmed areas, the latter places less emphasis on farming practices themselves and more on setting aside lands within farmed areas for conservation. As these practices are commonly associated with reduced agricultural yield in the short term (Perfecto et al., 2005), a common practice in recent years has been to provide economic incentives to offset the costs of biodiversity-friendly agriculture. This is widely gaining popularity and recent years have seen the influx of international certifying agencies into production landscapes in the Western Ghats.

The efficacy of these two strategies in achieving conservation is likely to vary widely. Biodiversity-friendly farming practices are likely to be most effective in landscapes where natural habitats are highly depleted and degraded (Moguel and Toledo, 1999), or where the conventional farming options result in drastically different habitat from traditional or biodiversity-friendly ones e.g. shade coffee vs. sun coffee (Rice and McLean, 1999). In more complex and heterogeneous landscapes, however, where characteristics of the broader landscape (particularly the extent and configuration of remnant forests) strongly influence biodiversity (Bennett et al., 2006; Radford and Bennett, 2007), prioritizing the conservation of these natural habitats by setting them aside from human use is likely to be the most efficacious conservation strategy.

While a combination of biodiversity-friendly farming and set-aside conservation are required, our review suggests that the latter strategy needs to be prioritized in the Western Ghats. Conserving remnant forests will not only secure their ability to harbor biodiversity, but also enhance the effectiveness of biodiversity-friendly farming practices, which although important, by themselves cannot sustain many components of biodiversity in the long term.

While a major proportion of forest cover in the Western Ghats is presently within State-administered PAs and as such does not face immediate threats of conversion, large areas of forest are still found outside the PA network and within human-modified landscapes. Examples of these are corporate- or privately-owned forests in the Anamalai hills of the southern Western Ghats and in the Sahyadris of the northern Western Ghats, and community-managed forests in Kodagu and Uttara Kannada districts in the central Western Ghats, all of which have high documented biodiversity value (Bhagwat et al., 2005b; Raman, 2006; Shastri et al., 2002). While some of these forests have been protected by religious and cultural ethics that date back several centuries (Gadgil and Vartak, 1976; Pandey, 2007), at present they all face pressures of timber and fuel-wood extraction, livestock grazing and clearing for development and agricultural expansion. In evergreen forests of the Western Ghats, these activities have been shown to open up habitats and facilitate the growth of deciduous and secondary vegetation (Daniels et al., 1995). In addition to these anthropogenic stresses, remnant forests also face numerous other biotic (e.g. weed invasions) and abiotic (e.g. soil desiccation) stresses resulting from increased exposure to habitat edges (Fahrig, 2003). Several sensitive species in fragmented landscapes face greater risks to survival from demographic stochasticity, and long-lived species with presently low probabilities of reproduction remain as 'living dead' organisms (Sodhi et al., 2010) in these modified landscapes. A variety of interventions are needed to restore and sustain the conservation value of these landscapes.

6.3. Future direction

Building on the outcomes of this review, we propose an agenda for future research aimed at strengthening biodiversity conservation efforts in human-modified landscapes in the Western Ghats. Several substantial gaps have been identified in taxonomic, geographic, land-use coverage, and study methodologies, which need to be covered. While a meta-analysis of this nature may not be ideally suited to infer causes of observed biodiversity patterns, given the variety and complexity of influential processes as well as the nature of data used and the scale at which questions have been asked, it certainly does generate several testable hypothesis regarding the observed biodiversity responses (Fernandez-Duque and Valeggia, 1994). Importantly, future studies need to explicitly investigate the influence of specific landscape properties, such as extent and configuration of remnant forests, on observed biodiversity patterns in human-modified landscapes. With improving technology and access to remotely-sensed and geographic information, such investigations are far more achievable today than ever before.

Finally, outcomes of such research should go into defining the role of human-modified landscapes in biodiversity conservation. Characteristics of human-modified landscapes that favour biodiversity conservation need to be identified and this understanding must be used to refine land-use policies. Our review suggests that this would involve greater focus on prioritizing the conservation of remnant forests in human-modified landscapes and maintaining landscape connectivity: factors which appear to be the reason for much of the biodiversity value of these landscapes. A dedicated effort involving diverse stakeholders is urgently required to restore and conserve these threatened habitats in the Western Ghats and the biodiversity within them (Raman and Mudappa, 2003). As these habitats presently do not have high protected status, are often on private lands and are embedded in landscapes geared towards production, conservation solutions need to not only maintain biodiversity but also sustain livelihoods. Across tropical human-modified landscapes, payments for ecosystem services (Engel et al., 2008; Jack et al., 2008) are being viewed as an important mechanism to sustain conservation in the long-term (deClerck et al., 2010; Norris et al., 2010; Sodhi et al., 2010). State-sponsored initiatives along these lines are already being developed in the Western Ghats (http://beta.thehindu.com/news/national/article31350.ece accessed 8th January 2010) and will hopefully contribute to better management of mixed landscapes for biodiversity conservation and ecosystem services.

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Appendix A

See Table 4.

Table 4
List of studies on biodiversity in human-modified landscapes in the Western Ghats.

Sl no.	Reference	Nature of study			Taxonomic group	Land use	Percentage forest cover	Biodiversity metric
		Taxonomic coverage	Land-use coverage	Forest control				
1	Anand et al. (2008)[a]	Single	Multiple	No[*,b]	Birds	Diverse shade coffee plantation, Monoculture shade coffee plantation	39.1	Overall species richness, Restricted species richness
2	Babu (2000)[a]	Single	Single	Yes[b]	Butterflies	Forest fragments	27.4	Overall species richness, Restricted species richness, Species diversity, Community composition
3	Bali et al. (2007)[a]	Single	Multiple	No	Mammals	Diverse shade coffee plantation, Monoculture shade coffee plantation		Overall species richness, Restricted species richness
4	Badrinarayanan et al. (2001)[a,+]	Single	Multiple	Yes[c]	Beetles	Diverse shade coffee plantation, Monoculture shade coffee plantation	46.3	Overall species richness, Restricted species richness, Community composition
5	Bhagwat et al. (2005b)[a]	Multiple	Multiple	Yes[b]	Birds, Trees, Lianas	Diverse shade coffee plantation	78.8	Overall species richness, Restricted species richness, Community composition
6	Bhat (2004)	Single	Single	Yes	Fish	Polluted streams		Overall species richness, Species diversity, Community composition
7	Blanchart and Julka (1997)[a]	Single	Multiple	Yes[c]	Earthworms	Acacia plantation, Pasture, Thicket	40	Overall species richness, Species diversity
8	Daniels et al. (1990)	Single	Multiple	Yes	Birds	Eucalyptus plantation, Teak plantation, Arecanut plantation		Overall species richness, Restricted species richness, Species diversity, Community composition
9	Daniels (2003)	Single	Single	No	Amphibians	Tea plantation		Overall species richness
10	Devy and Davidar (2001)[a]	Single	Single	Yes[b]	Butterflies	Logged forest	17.4	Overall species richness, Restricted species richness, Species diversity
11	Dolia et al. (2008)[a]	Single	Multiple	No[b]	Butterflies	Diverse shade coffee plantation, Monoculture shade coffee plantation	39.1	Overall species richness
12	Gadagkar et al. (1993)	Single	Multiple	Yes	Ants	Eucalyptus plantation, Teak plantation, Arecanut plantation		Overall species richness, Species diversity, Community composition
13	Kapoor (2008)[a]	Single	Multiple	Yes[b]	Spiders	Diverse shade coffee plantation	27.4	Overall species richness, Community composition
14	Krishnamurthy (2003)	Single	Single	Yes	Amphibians	Acacia plantation, Human habitation		Overall species richness, Species diversity, Community composition
15	Kumar et al. (1995)[a]	Single	Single	Yes	Trees	Cardamom plantation		Overall species richness, Species diversity
16	Kumar et al. (2002)[a]	Multiple	Single	Yes[b]	Mammals, Amphibians, Reptiles	Forest fragments	27.4	Overall species richness, Species diversity, Community composition
17	Kumara et al. (2004)	Single	Single	No	Mammals	Tea plantation		Overall species richness
18	Kunte et al. (1999)	Multiple	Multiple	Yes	Birds, Butterflies, Trees	Monoculture shade coffee plantation, Rice cultivation, Scrub		Overall species richness, Species diversity, Community composition
19	Madhusudan (2004)	Single	Single	Yes	Mammals	Livestock grazed forest		
20	Mehta et al. (2008)	Single	Single	Yes	Trees	Used forest		Species diversity, Community composition
21	Muthuramkumar et al. (2006)[a]	Multiple	Single	Yes[b]	Trees, Lianas	Forest fragments	27.4	Overall species richness, Restricted species richness, Species diversity, Community composition
22	Nair (1997)	Single	Single	Yes	Fish	Teak plantation		
23	Page (2007)	Multiple	Single	Yes	Trees, Lianas, Epiphytes	Forest fragments		Overall species richness, Species diversity, Community composition
24	Parthasarathy (1999)[a]	Multiple	Single	Yes[b]	Trees, Lianas	Logged forest, Used forest	75.6	Overall species richness, Species diversity, Community composition
25	Pélissier et al. (1998)[a]	Single	Single	Yes[b]	Trees	Logged forest	72.1	Overall species richness, Community composition
26	Premdas (1990)	Single	Single	Yes	Birds	Acacia plantation		Overall species richness
27	Raman (2006)[a]	Single	Multiple	Yes[b]	Birds	Diverse shade coffee plantation, Monoculture shade coffee plantation, Forest fragments	27.4	Overall species richness, Restricted species richness, Community composition
28	Raman and Sukumar (2002)[a]	Single	Multiple	Yes[b]	Birds	Regenerating forest, Logged forest, Edge habitat	66.4	Overall species richness
29	Ranganathan et al. (2008)[a]	Single	Multiple	Yes[b]	Birds	Arecanut plantation, Cashewnut plantation, Used forest, Scrub	36.4	Overall species richness, Restricted species richness, Community composition
30	Saravanakumar (1995)	Single	Single	Yes	Amphibians	Teak plantation		
31	Shahabuddin (1997)[a]	Single	Single	Yes[c]	Birds	Diverse shade coffee plantation	58.4	Overall species richness, Community composition
32	Sreekantha et al. (2007)	Single	Single	Yes	Fish	Human habitation		Overall species richness, Restricted species richness

(*continued on next page*)

Table 4 (*continued*)

Sl no.	Reference	Nature of study			Taxonomic group	Land use	Percentage forest cover	Biodiversity metric
		Taxonomic coverage	Land-use coverage	Forest control				
33	Sridhar et al. (2008)[a]	Single	Single	Yes[b]	Mammals	Forest fragments	27.4	Overall species richness
34	Umapathy and Kumar (2000)	Single	Single	Yes	Mammals	Forest fragments		
35	Veena (2008)	Single	Multiple	No	Butterflies	Diverse shade coffee plantation, Forest fragments		Overall species richness

Data for forest control site in * obtained from Anand (2006). Data for + obtained from Badrinarayanan (2001).
[a] Indicates those studies that were included in the meta-analysis.
[b] Control forest sites were large, contiguous intact reserves.
[c] Control forest sites were disturbed forests.

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