

Effects of Historical Selective Logging on Anuran Communities in a Wet Evergreen Forest, South India

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ABSTRACT

Vast areas of tropical evergreen forests have been selectively logged in the past, and many areas continue to be logged. The impacts of such logging on amphibians are poorly understood. I examined the response of anuran communities to historical selective logging in a wet evergreen forest in south India. Anuran assemblages in unlogged forest were compared with assemblages in selectively logged forest. Forty 10 m × 10 m quadrats in forest, riparian zones, and streams of unlogged and selectively logged forests were searched at night for anurans. Species richness did not appear to be affected by logging. However, anuran density varied significantly and was 42 percent lower in selectively logged forests compared to unlogged forests. Anuran densities also varied significantly across microhabitats, with highest densities in streams of both selectively logged and unlogged forests. Patterns of niche overlap varied with selective logging as niche breadth either expanded, contracted, or remained neutral for different species. Ordination analysis explained 95 percent of the variation in species assemblage across selectively logged and unlogged forests. The assemblage in selectively logged forest was nested within unlogged forest. Among the habitat characteristics, litter thickness and water depth had the highest influence on the assemblage. This was followed by litter/water temperature, air temperature, and lastly relative humidity. It appears that species richness and composition of anurans in selectively logged forests is converging with unlogged forests, but the effects of historical logging seem to persist on anuran densities and their niche characteristics even *ca* 40 yr since logging ceased.

Key words: anuran assemblage; habitat modification; Kalakad Mundanthurai Tiger Reserve; persistence; recovery; Western Ghats.

TROPICAL EVERGREEN FORESTS ARE INCREASINGLY BEING SELECTIVELY LOGGED FOR TIMBER (Johns 1992, Asner *et al.* 2005, Gibson *et al.* 2011). Given drastic declines in forest cover, strategies for sustainable timber trade and biodiversity conservation in secondary forests are becoming increasingly important (Vallan *et al.* 2004, Asner *et al.* 2005, Peters *et al.* 2006, and Wilcove *et al.* 2013). Although selective logging is considered to be relatively less impactful than clear felling (Hartshorn 1995), it alters vegetation composition, microclimate, and resource availability (Fredericksen & Fredericksen 2004). Such changes can increase disease susceptibility and reduce breeding success in animal populations, as well as result in the loss or degradation of habitat (Johns 1985, Sodhi *et al.* 2010, and Wilcove *et al.* 2013). Such impacts are known to persist from a few years to several decades following the cessation of logging activities (Chapman *et al.* 2000, Ernst *et al.* 2006). Despite increasing rates of logging in the tropics, there is a limited understanding of both the extent of impacts on biodiversity, and the means for effective mitigation for conservation (Asner *et al.* 2005). Thus, how such logging activities affect forests, wildlife populations in them, and how best to manage logging to facilitate biodiversity conservation are among many critical questions in conservation science (*e.g.*, Ernst *et al.* 2006, Peters *et al.* 2006, Broadbent *et al.* 2008, Hillers *et al.* 2008, and Gardner *et al.* 2009).

Amphibians are sensitive to environmental perturbations and can be severely affected by habitat modification (Alford & Richards 1999, Bickford *et al.* 2010). Amphibian populations are undergoing an unprecedented decline globally, but particularly in the tropics (Stuart *et al.* 2004). Increase in prevalence of diseases, UV-B irradiation, environmental variability (Ernst & Rödel 2005, Kiesecker 2010), and loss or modification of habitat appear to be important causal factors leading to such drastic declines.

Only a few studies have investigated the impacts of selective logging activities and habitat loss or modification on amphibians, and most report negative responses with species richness, density, and community composition as a measure of impact (*e.g.*, Fredericksen & Fredericksen 2004, Vallan *et al.* 2004, Gardner *et al.* 2007 and citations there in, Broadbent *et al.* 2008, Bickford *et al.* 2010, Ofori-Boateng *et al.* 2012). However, effects of modified habitats on niche breadth and overlap of amphibians persisting in modified habitats are not well understood. While species richness and densities serve as a good measure of impact, examining niche breadth can provide insights into the ability of a species to persist in modified habitats (Swihart *et al.* 2003). Changes to niche breadth and subsequent overlap are also indicative of species-specific responses to logging (Vázquez & Simberloff 2002). Thus, using niche breadth based on microhabitat use and overlap as a species-specific measure of the response would provide a nuanced insight into the effects of selective logging.

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The Western Ghats, along with the hill ranges in Sri Lanka, are a global biodiversity hotspot with exceptionally high amphibian diversity and endemism (Duellman & Trueb 1994). The Western Ghats harbor about 185 species of anurans, over 80 percent of which are endemic, 37 percent threatened and 44 percent are data deficient (Dinesh *et al.* 2013). As with the tropical rain forests of Asia, forests of the Western Ghats are rapidly declining. While large areas of forests are legally protected by legislation, the Western Ghats have continued to be affected by anthropogenic forces (Chandran 1997, Cincotta *et al.* 2000). Large areas of forest land are being diverted and/or used for mineral mining, construction of reservoirs, conversion to agriculture/urbanization, fuel wood collection, and for other such developmental activities (*e.g.*, Bhat *et al.* 2001). Studies on the recovery of forests after such land-use changes report noticeable changes in vegetation composition even after 10–15 yr (Pelissier *et al.* 1998). Only few studies have investigated the consequence of logging in the Western Ghats and Sri Lanka and, consistent with patterns from other regions, these studies report negative responses (Vasudevan *et al.* 2001, Gururaja 2002, Krishnamurthy 2003, Kudavidanage *et al.* 2012). Some of these negative responses include local extinction of amphibians in Sri Lanka (Meegaskumbura *et al.* 2007). However, such extinctions are not recorded from India, possibly be due to inadequate studies.

This study examines the impacts of selective logging on amphibian assemblages in the southern Western Ghats. In present day, Kalakad Mundanthurai Tiger Reserve (KMTR), a large extent of mid-elevation evergreen forests (1200–1500 m asl) was selectively logged about 40 yr ago; following protection these forests have since regenerated. However, the vegetation structure of dominant tree species in selectively logged forests show noticeable differences (Ganesan & Davidar 2003). To determine potential impacts of selective logging, I compared species richness, density, niche breadth, and niche overlap of anuran assemblages in selectively logged areas with those of unlogged forests and addressed these questions: (1) does long-term protection following cessation of logging lead to convergence of anuran assemblage with unlogged forests? (2) What habitat characteristics influence the persistence of anuran assemblages in selectively logged forests and how do they differ from unlogged forests?

METHODS

STUDY AREA.—The Kalakad Mundanthurai Tiger Reserve (KMTR, 895 km²) located between 8°25' to 8°53' N and 77°10' to 77°35' E (Fig. S1) forms the southern extreme of the Western Ghats of India. It encompasses a range of forest types ranging from scrub in lower elevations to wet evergreen forests at higher elevations and is known for high species diversity and endemism (Johnsingh 2001). I carried out this study in mid-elevation wet evergreen forests of Upper Kodayar (1300 m asl). The region receives a mean annual rainfall of 3500 mm spread across two rainy seasons (Ganesh & Davidar 1999). In some areas of this reserve, the forest has been selectively logged since 1870s for reservoir construction, commercial plantations, softwood industries,

and road building (Ganesan 2000). The forests have not experienced any intermittent disturbances since moderate logging activity ceased in the early 1970s (Devy & Davidar 2001). I chose the selectively logged and unlogged forests within Upper Kodayar range (*ca* 6 km²) in reference to previous studies carried out by Devy and Davidar (2001) on butterflies, and Ganesan and Davidar (2003) on vegetation. Sampling was conducted at the end of the rainy season from December 2010 to February 2011.

ANURAN SAMPLING.—I sampled anurans in quadrats stratified in selectively logged and unlogged forests and within these into microhabitats of 'stream' (on the stream); 'riparian' (10 m from stream edge); and 'forest' (beyond 10 m from stream edge). A total of 40, 10 m × 10 m quadrats were laid and permanently marked with ribbon tags and co-ordinates recorded using a handheld GPS (Etrex Hc Garmin®, Garmin International Inc., Olathe, Kansas, USA). I maintained a minimum of 50–100 m between quadrats (to ensure spatial independence) and from the only road passing through this habitat (to avoid edge effects). I laid 20 quadrats in both selectively logged and unlogged forest over an area of 0.4 ha. Selectively logged quadrats were within *ca* 2 km on either side of the road and the unlogged forest quadrats were between *ca* 3–5 km away from the road. I avoided sampling quadrats in the interface of selectively logged and unlogged forest as it would dilute treatment effect. Further, quadrats were stratified within each microhabitat with 10 in forest, five in riparian zone, and five on the stream in both selectively logged and unlogged forests. I sampled between 1800 and 2100 h corresponding with peak activity periods of anurans (Marsh & Pearman 1997). I searched each quadrat for 20 min using an 'all out area based search' method (Krishnamurthy 2003) where three observers searched the forest floor by scraping litter with a search stick 2.5 m in length and thoroughly scanned the vegetation up to 2 m height. I limited the search to litter and did not dig up the soil, thus limiting detection of some fossorial species. Unidentified species were caught and we measured the snout to vent length (SVL) using Mitutoyo® (Mitutoyo corporation, Kawasaki, Japan) digital slide caliper to the nearest 0.1 mm. Subsequently, we photographed species using a Canon Powershot S5IS® (Canon Inc., Tokyo, Japan) and released them in the same quadrat within 30 min of capture. No voucher specimens were collected during the study. Those individuals with uncertain identity were assigned to the closest resembling congener and indicated with 'aff.' and treated as taxonomically distinct units.

The resource states or stratum on which each anuran was encountered was listed in six categories based on which I computed niche breadth and niche overlap. 'Leaf litter' (LL); 'Understory': shrubs of up to 2 m (US); 'In water': water flowing in streams (IW); 'On stones' in water: rocks and pebbles in streams (OSW); 'Rocks adjacent to stream' (RAS) and 'Pools adjacent to stream': water stagnation adjacent to streams (PAS).

MEASUREMENT OF HABITAT CHARACTERISTICS.—We obtained soil and water temperature using a standard 110°C alcohol thermometer. We measured substrate thickness (leaf litter depth for terrestrial

and water depth for aquatic habitats respectively) using a 30 cm steel scale, and measured air temperature and humidity using Kestrel[®] 4500 pocket weather tracker (Nielsen-Kellerman Co., Boothwyn, Pennsylvania, USA). These measurements were taken immediately after searching for anurans and at three points within each quadrat. The mid-point was used for analysis. I estimated the percentile of canopy openness using a modified method by Englebrect and Herz (2001) carried out after approximately 2 wk after sampling was completed. Daylight photographs from below the canopy were taken using an 18–105 mm lens mounted on a Nikon D90[®] digital camera (Nikon Corp. Tokyo, Japan) kept 30 cm above ground. Images were converted to gray scale, brightness reduced to –100 and contrast increased to +100 before obtaining the percentile canopy cover using the ‘Histogram’ option in Adobe Photoshop[®] v. 7.0 (Adobe Systems, San Jose, California, USA).

DATA ANALYSIS.—I carried out all data analysis and statistical tests using Microsoft Excel[®], PAST[®] (Hammer *et al.* 2001), EstimateS[®] (Colwell 2006), and Graphpad Instat[®] (v. 5.04 for Windows, La Jolla, California, U.S.A., www.graphpad.com). I used Shannon H' index as a measure of diversity and compared it between sites using a diversity χ^2 test between two samples of abundance data (Poole 1974). I also used second-order Jackknife for species rarefaction (Colwell 2006). Mean density across habitat (selectively logged and unlogged) and microhabitats (stream, riparian, and forest) were log-transformed for normality and compared using one-way ANOVA followed by Tukey’s pair wise comparison test within microhabitats. I used Mann–Whitney U -test for testing differences among habitat characteristics and for comparing abundance of each amphibian species between selectively logged and unlogged forests. I computed niche breadth of each species using Shannon index and the H' values were used for comparison

$$H' = - \sum p_i \log p_i$$

where p_i is the proportion of individuals of a species found in i th resource state.

I calculated niche overlap between species pairs using Pianka’s Niche overlap Index (Inger *et al.* 1987)

$$O_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where p_{ij} and p_{ik} are proportions of j th and k th species in the i th resource states.

I only used those species encountered more than five times for computing niche breadth and overlaps to avoid biases from singletons. I tested the relationship of habitat characteristics on anuran assemblage using a canonical correspondence analysis (CCA) followed by a permutation test (Legendre & Legendre 1998). I used a matrix listing samples in rows and corresponding habitat variables in columns followed by abundance of all species for CCA. Data were $\log(x + 1)$ transformed for this analysis.

Canopy cover values were in percentages and hence were arc-sine transformed before $\log(x + 1)$ transformation (McDonald 2009).

RESULTS

SPECIES RICHNESS AND DIVERSITY.—I recorded a total of 12 anuran species belonging to seven families. Only three species were unique to unlogged forests and all twelve species were endemic to Western Ghats (Appendix S1). There was only a marginal difference between observed and rarefied species richness (second order jackknife estimate) in both unlogged (observed: 12 vs. rarefied: 13.8) and selectively logged forests (observed: 9 vs. rarefied: 13.7). Diversity was significantly higher in unlogged compared to selectively logged forests (Shannon $H' = 2.0$ and 1.7 respectively; diversity χ^2 test = 3.022, $df = 198.24$, $P = 0.002$).

CHANGES IN ANURAN DENSITY ACROSS DISTURBANCE GRADIENT AND MICROHABITATS.—A total of 257 individuals were encountered in an area of 0.4 ha with an average of 6.4 individuals/100 m². Mean anuran density (\pm SE) was significantly higher in unlogged forests ($8.15 \pm 2.5/100$ m²) compared to selectively logged forests ($4.7 \pm 0.8/100$ m²; $F = 6.443$, $df = 5$, $P < 0.005$). Among three microhabitats, anuran densities were highest in streams followed by riparian zones and were the least in forest microhabitat of both unlogged and selectively logged forests (Fig. 1). The densities differed significantly between stream ($N = 10$) and riparian ($N = 5$) microhabitats of unlogged forests (Tukey’s HSD $Q = 5.27$, $P < 0.001$). However in selectively logged forests, densities differed significantly between forest ($N = 5$) and stream ($N = 10$) microhabitats (Tukey’s HSD $Q = 4.65$, $P < 0.005$).

SPECIES-WISE COMPARISON.—Among the 12 species encountered, *Micrixalus kodayari* had the highest density ($2.2 \pm 1.3/100$ m²) in unlogged forest and *Raorchestes* aff. *graminirupes* had the highest density in selectively logged forest ($2 \pm 0.3/100$ m²). Further, in unlogged forest, *R.* aff. *graminirupes*, *Nyctibatrachus aliciae*, and

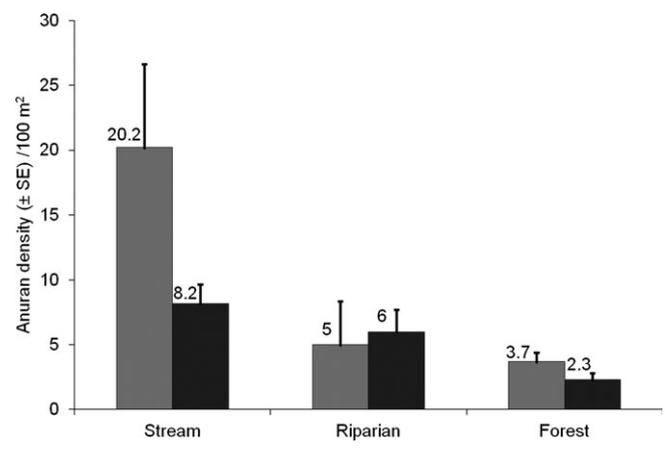


FIGURE 1. Anuran densities (mean \pm SE) across microhabitats in selectively logged and unlogged forests. Light gray bars indicate unlogged and black bars indicate selectively logged.

Racophorus calcadensis were found in densities greater than one individual/100 m², while all other species had lower than one individual/100 m². All species except *R. aff. graminirupes* were found in densities lower than one individual/100 m² in selectively logged forest. However, pair wise comparison of densities for each species between selectively logged and unlogged was not significantly different for any species (Fig. S2; Appendix S1 for densities of species across microhabitats in unlogged and selectively logged forests).

EFFECT ON NICHE BREADTH.—Anurans were encountered in six microhabitats and information on resource state was available for a total of 235 anuran encounters across eight species. Overall, in unlogged forest, the highest number of individuals were found in the understory ($N = 56$) and the least on rocks adjacent to streams ($N = 9$). In selectively logged forests, the highest number of individuals were found in the understory ($N = 39$) and the least in pools adjacent to streams ($N = 2$).

When only those species encountered more than five times were considered, the highest number of individuals in unlogged forest were found on leaf litter ($N = 5$), while the least individuals were found on stones in water and rocks adjacent to streams ($N = 1$ each). However, in selectively logged forest, the highest number of individuals was found in understory ($N = 2$) and no frogs were found in pools adjacent to streams ($N = 0$). Niche breadth index varied from 0 to 0.69 for seven species in unlogged forests and from 0 to 0.95 for five species in selectively logged forests (Fig. 2). In unlogged forests, niche breadth was widest for *Nyctibatrachus aff. vasanthi*; wide for *N. aliciae* and *R. aff. graminirupes*; narrow for *M. kodayari* and narrowest for *Hylarana temporalis*, *R. agasthyaensis*, and *R. calcadensis*. In contrast, niche breadth of species in selectively logged forests was widest for *Ramanella montana*; wide for *Pseudophilautus aff. kani*, *N. aliciae*, *M. kodayari*, and *R. aff. graminirupes*; and was narrowest for *R. calcadensis*. Further, comparison of niche breadth values between unlogged and selectively logged forests showed that niche breadth for *M. kodayari*, *N. aliciae*, and *R. aff. graminirupes* increased, but that of *R. calcadensis* did not change with selective logging.

EFFECT ON NICHE OVERLAP.—Niche overlap values ranged from 0.0 (no overlap) to 1 (complete overlap). Overall, patterns in which niches of arboreal, semi-aquatic, and aquatic species overlapped, changed only marginally with selective logging (Table 1). In general, niche of aquatic and semi-aquatic species; arboreal and semi-arboreal species; and semi-aquatic and terrestrial species showed varying degree of overlaps in both selectively logged and unlogged forests.

INFLUENCE OF HABITAT CHARACTERISTICS.—Ordination analysis did not show distinct clustering of unlogged and selectively logged quadrats, but selectively logged forests were nested within unlogged forests. Among the variables measured to characterize habitat, only air temperature (median: unlogged = 21.4°C; selectively logged = 16.7°C; $U = 58$, $N = 40$, $P < 0.001$); relative humidity (median: unlogged = 76.3%; selectively logged = 92.5%; $U = 72$, $N = 40$, $P < 0.001$); and litter/water temperature

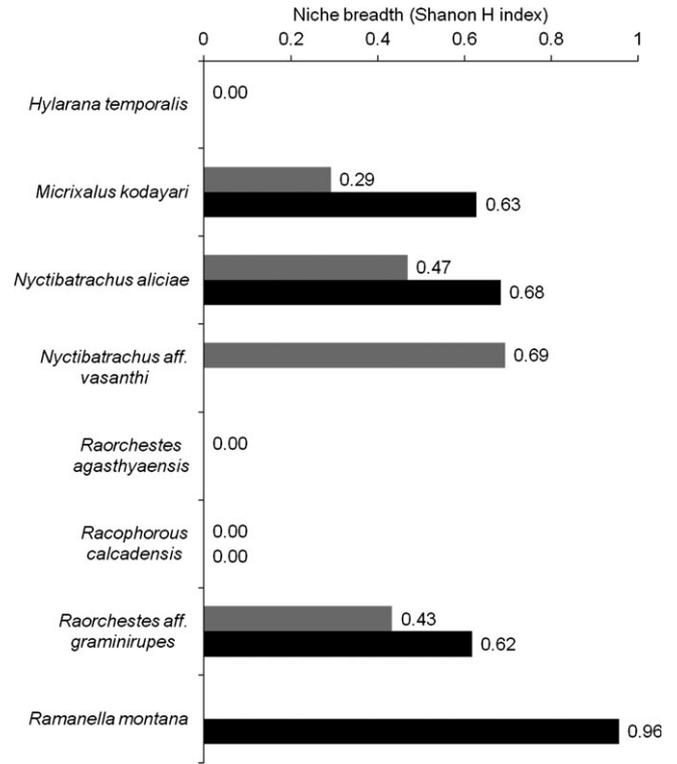


FIGURE 2. Niche breadth (Shannon H' index) comparison between unlogged and selectively logged forests. Species encountered on more than five occasions are used (0.0 indicates narrow niche breadth and 1 indicates wide niche breadth). Light gray bars indicate unlogged and black bars indicate selectively logged.

(median: unlogged = 19°C; selectively logged = 14.9°C; $U = 71.5$, $N = 40$, $P < 0.001$) varied significantly between unlogged and selectively logged forests, but not canopy cover (median: unlogged = selectively logged = 1.1; $U = 180$, $N = 40$, $P > 0.005$) and litter thickness/water depth (median: unlogged = 4.75 cm; selectively logged = 5 cm; $U = 194$, $N = 40$, $P > 0.005$).

The canonical correspondence ordination, using pooled data of selectively logged and unlogged forests, significantly explained 95 percent of variance along the first three components (Fig. 3; CCA permutation test, $N = 40$; $P = 0.03$). The first component explained 56 percent ($P < 0.05$) of variation with strong contribution of litter thickness/water depth (71%); second component explained 25 percent ($P > 0.05$) of variation with contributions of both litter/water and air temperatures (46% and 38% respectively) and third component explained 14 percent ($P > 0.05$) of variation with contribution from relative humidity (25%).

Anurans found in first quadrant *viz.*, *M. kodayari*, *N. aliciae*, *N. aff. vasanthi*, and *R. calcadensis*, were positively influenced by litter thickness/water depth. *Duttaphrynus beddomeii*, *R. montana*, and *H. temporalis* found in second quadrant were negatively influenced by litter thickness/water depth and relative humidity; *R. aff. graminirupes* and *Indirana diplosticta* found in third quadrant were negatively influenced by canopy cover and *P. aff. kani*, *R. agasthyaensis*, and *M. aff. phyllophilus* found in the fourth quadrant

TABLE 1. Niche overlap values for different species encountered on more than five occasions.

Unlogged	<i>Hylarana temporalis</i>	<i>Micrixalus kodayari</i>	<i>Nyctibatrachus aliciae</i>	<i>Nyctibatrachus aff. vasanthi</i>	<i>Raorchestes agasthyaensis</i>	<i>Racophorous calcadensis</i>	<i>Raorchestes aff. graminirupes</i>
<i>Hylarana temporalis</i>	1						
<i>Micrixalus kodayari</i>	0	1					
<i>Nyctibatrachus aliciae</i>	0	0.48	1				
<i>Nyctibatrachus aff. vasanthi</i>	0	0.48	1	1			
<i>Raorchestes agasthyaensis</i>	0	0	0	0	1		
<i>Racophorous calcadensis</i>	0	0	0	0	1	1	
<i>Raorchestes aff. graminirupes</i>	0	0.19	0	0	0.55	0.55	1

Selectively logged	<i>Micrixalus kodayari</i>	<i>Nyctibatrachus aliciae</i>	<i>Racophorous calcadensis</i>	<i>Ramanella montana</i>	<i>Raorchestes aff. graminirupes</i>
<i>Micrixalus kodayari</i>	1				
<i>Nyctibatrachus aliciae</i>	0.48	1			
<i>Racophorous calcadensis</i>	0	0	1		
<i>Ramanella montana</i>	0.13	0.4	0	1	
<i>Raorchestes aff. graminirupes</i>	0.19	0	0.554	0.19	1

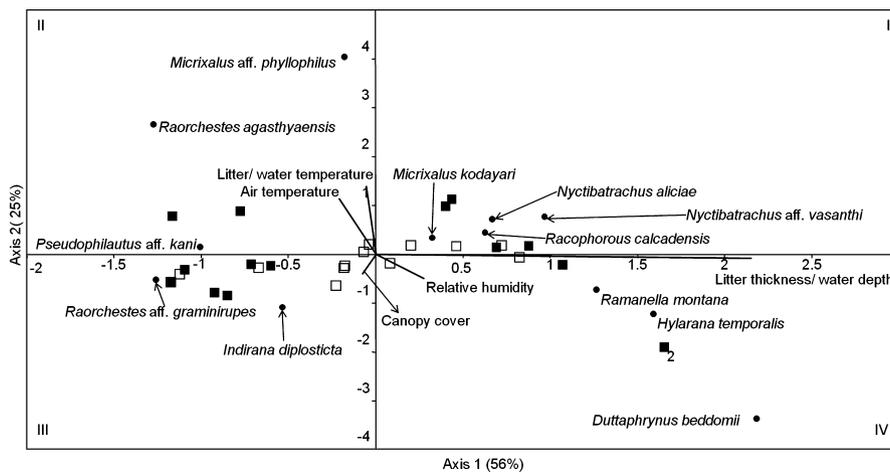


FIGURE 3. Ordination tri-plot of canonical correspondence analysis using environmental variables with abundance of each encountered species in respective sampling quadrats. Closed circles indicate species; closed box indicates unlogged forests and open box indicate selectively logged forests and; Dark lines originating from center indicate environmental variables. Roman numerals I-IV indicates quadrants.

were negatively influenced by air temperature and litter/water temperature (Fig. 3).

DISCUSSION

This study examined effects of selective logging activity on anuran assemblages in wet evergreen forests of the Western Ghats. Anuran assemblages—compared using species richness, density, niche breadth, and overlap as measures of impact—differed considerably between selectively logged and unlogged forests. These changes were evident even at the species level, where niche breadth and overlap were affected in logged habitats, thus

indicating species-specific responses. Anuran assemblage of selectively logged forest did not form a distinct cluster, but was nested within patterns observed in unlogged forests. My findings suggest that despite cessation of logging *ca* 40 yr ago, the effects of selective logging on anurans appear to have persisted. Air temperature, relative humidity, leaf litter thickness, water temperature, and water depth—but not canopy cover—emerged as primary factors explaining variation observed in assemblages.

Previous studies have documented negative impacts of such logging activities on species composition and densities (*e.g.*, Gardner *et al.* 2007, Ofori-Boateng *et al.* 2012). Persistent impact of selective logging has also been documented, and appears to

depend on both the nature and extent of logging (*e.g.*, primates: Chapman *et al.* 2000, birds: Robinson & Robinson 2001, forest vegetation: Brown & Gurevitch 2004, Butterflies: Devy & Davidar 2001, and trees: Ganesan & Davidar 2003). The findings reported here suggest that effects of moderate selective logging are negative and persist even *ca* 40 yr post-logging. The marked difference of anuran densities in selectively logged forests could be due to several factors, including alteration of microclimate, changes in availability of moisture, increased sedimentation resulting in turbid streams, and the reduction in leaf litter. It could also be due to the reduction of canopy cover creating increased insolation rates and fluctuations in local temperature leading to desiccation, as suggested by Fredericksen and Fredericksen (2004). The marginally lower species richness in selectively logged forest compared to unlogged, however, could be due to re-colonization events owing to proximity of unlogged forest (*e.g.*, Schulze *et al.* 2004). Higher anuran density in stream and riparian zones, even in selectively logged forests, suggest that riparian areas serve as important *refugia* and sustain amphibian assemblages by maintaining atmospheric moisture, especially in extreme cold or dry weather.

EFFECTS ON NICHE BREADTH AND OVERLAP.—Species with narrow niche breadths occurred in both unlogged and selectively logged forests. For some species, niche breadth appeared to expand while for some it reduced. The niche breadth of only one species (*R. calcadensis*), remained neutral to selective logging. Expansion of niche breadth (*R. aff. graminirupes*) and neutrality in (*R. calcadensis*) is possibly due to increased availability of understory vegetation in selectively logged forests (Ganesan & Davidar 2003). It appears that selectively logging trees could facilitate ‘ecological release’ (Bolnick *et al.* 2010) and increase the persistence of generalist species. *Rachophorus calcadensis* is an arboreal frog that needs slow flowing water pools for tadpoles to drop from overhanging foam nests and metamorphose. Aquatic and semi-aquatic frogs such as *M. kodayari* and *N. aliciae* were found in lower densities compared to unlogged forests, but had a wider niche breadth. Species with wider niche breadths are often considered to be resilient to habitat alterations (Swihart *et al.* 2003). In this study, niche breadth of a few species increased (*e.g.*, *M. kodayari*, *N. aliciae*, *R. aff. graminirupes*, *R. montana*) in selectively logged forests, whereas a few species were completely absent (*e.g.*, *R. agasthyaensis*, *N. aff. vasantbi*). The species absent in selectively logged forests may have been specialists that were negatively affected; it could also be assumed that the niches of all species were detrimentally affected immediately following selective logging activity and have since then recovered.

Four species had a high niche overlap (>40%), and two pairs of species had complete overlap in unlogged forest. In contrast, in selectively logged forests only three species had a high overlap (>40%) and none of the species had a complete niche overlap of their niches. This could be due to two untested possibilities. First, niches overlapped to a high degree in unlogged forests because of high anuran density. Second, it is possible that there were enough resources in unlogged forests to support a high density

of anurans, such that they could therefore afford to have overlapping niches. In contrast, in selectively logged forests, none of the species had high degree of overlap perhaps because resources were limited and anuran density was lower. Observational and experimental data could help resolve among these hypotheses.

INFLUENCE OF HABITAT CHARACTERISTICS.—Among the factors investigated, the thickness/quantity of leaf litter in the case of semi-aquatic or terrestrial species, and water depth in the case of aquatic species, significantly influenced anuran densities in both unlogged and selectively logged forests. The quantity of leaf litter is hypothesized to be an important factor influencing anuran assemblages (Scott 1976, Whitfield *et al.* 2007, Hillers *et al.* 2008). The amount of litter could influence food resource availability, as anurans are primarily arthropodivorous. It might also directly affect some fossorial species. Reduced litter fall rates have been documented in recently selectively logged forests by Villela *et al.* (2006), but the present study documents the absence of any such changes in leaf litter between selectively logged and unlogged forests.

Litter thickness/water depth emerged as an important variable explaining a large proportion of observed variance in this study, even at a species level. For instance, aquatic/semi-aquatic species such as *M. kodayari* require torrential streams, whereas *R. calcadensis*, *N. aliciae*, and *N. aff. vasantbi* require shallow, slow flowing natural pools in streams for breeding. The terrestrial species *R. montana*, *H. temporalis*, *M. aff. phyllophilus*, and *D. beddomeii* are dependent on litter thickness/water depth, relative humidity, and air temperature, and *Micrixalus aff. phyllophilus*—a small semi-terrestrial species—dwells in swampy areas. Increased temperatures resulting from loss of canopy cover could lead to desiccation of swamps, which might negatively influence on their densities.

Nevertheless, other environmental factors also have species-specific effects. Arboreal species (*e.g.*, *R. agasthyaensis*, *P. aff. Kam*) were influenced by litter and air temperature; alterations in air temperature could influence anuran vocalization and subsequently breeding success. Finally, two species were influenced by canopy cover: *R. aff. graminirupes* and *I. diplosticta*. While the former is an arboreal species, the latter dwells in leaf litter. Canopy cover may increase with increasing shrub density and understory growth following logging, and increased litter fall may be positively influencing these species. However, in a pan-tropical comparison that included data from stream and riparian areas of this study site, Vasudevan *et al.* (2008) rejected the role of litter on anuran assemblages. Instead, they proposed a relationship with the availability of moisture in streams and riparian areas. Moisture availability is critical to amphibians, as they are biphasic and critically depend on availability of moisture for breeding and development (Crump 2010). Selective logging can lead to increased rate of drying in water sources and is known to increase the content of ammonia in water and such fluctuations could result in a cascading effect on amphibian food resources (Fredericksen & Fredericksen 2004). In this study, the highest density of anurans was in streams, which are serving as *refugia* and therefore important for conservation.

CAVEATS.—The findings discussed here should be treated with caution owing to the proximity of selectively logged with unlogged forests and the longtime period since logging ceased. Furthermore, the study itself was carried out over a short period at the end of the rainy season. In understanding the influence of habitat characteristics on anurans, it has to be noted that there may have been several other physicochemical factors I did not measure that could have played a role, as well as road and edge effects that could influence the anuran assemblages in selectively logged forests. Monitoring of the physicochemical parameters in relation to anuran assemblages is necessary to better understanding of their influence, as are studies conducted over longer periods—particularly sampling coinciding with the monsoon season, when amphibians tend to be most active. Finally, rigorous investigations on the niche requirements that consider resources used at a finer scale could further elucidate my findings.

CONSERVATION IMPLICATIONS.—The recovery of human altered forests, especially in the tropics, can be a slow process (*e.g.*, Terborgh 1992, Guariguata & Ostertag 2001, Chazdon 2003). In spite of drastic changes in vegetation, however, modified habitats can be important for sustaining biodiversity (Chazdon *et al.* 2009, Woods & DeWalt 2013). The findings reported here provide the first evidence from the Western Ghats that anuran assemblages in selectively logged areas, which are largely dependent on habitat, do not show convergence with those in unlogged forests, despite 40 yrs since logging ceased and forests were protected. These findings emphasize the importance of logged forests in harboring anuran assemblages, and also suggest that microhabitats such as riparian regions are important for the conservation of several endemic anuran species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

APPENDIX S1. List of anurans encountered in unlogged and selectively logged forests during October 2010 to March 2011 and their respective densities.

FIGURE S1. Thematic map showing study area.

FIGURE S2. Species-wise density comparison between unlogged and selectively logged forests.

LITERATURE CITED

- ALFORD, R. A., AND S. J. RICHARDS. 1999. Global amphibian declines: A problem in applied ecology. *Annu. Rev. Ecol. Syst.* 30: 133–165.
- ASNER, G. P., D. E. KNAPP, E. N. BROADBENT, P. J. C. OLIVEIRA, M. KELLER, AND J. N. SILVA. 2005. Selective logging in the Brazilian amazon. *Science* 310: 480–482.
- BHAT, D. M., K. S. MURALI, AND N. H. RAVINDRANATH. 2001. Formation and recovery of secondary forests in India: A particular reference to Western Ghats in South India. *J. Trop. Forest Sci.* 13: 601–620.
- BICKFORD, D., S. D. HOWARD, D. J. NG, AND J. A. SHERIDAN. 2010. Impacts of climate change on the amphibians and reptiles of Southeast Asia. *Biodivers. Conserv.* 19: 1043–1062.
- BOLNICK, D. I., T. INGRAM, W. E. STUTZ, L. K. SNOWBERG, O. L. LAU, AND J. S. PAUL. 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proc. R. Soc. Lond. B Biol. Sci.* 277: 1789–1797.
- BROADBENT, E. N., G. P. ASNER, M. KELLER, D. E. KNAPP, P. J. C. OLIVEIRA, AND J. N. SILVA. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv.* 141: 1745–1757.
- BROWN, K. A., AND J. GUREVITCH. 2004. Long-term impacts of logging on forest diversity in Madagascar. *Proc. Natl Acad. Sci. USA* 101: 6045–6049.
- CHANDRAN, M. D. S. 1997. On the ecological history of the Western Ghats. *Curr. Sci.* 73: 146–155.
- CHAPMAN, C. A., S. R. BALCOMB, T. R. GILLESPIE, J. P. SKORUPA, AND T. T. STRUSHSAKER. 2000. Long-term effects of logging on african primate communities: A 28-year comparison from Kibale National Park, Uganda. *Conserv. Biol.* 14: 207–217.
- CHAZDON, R. L. 2003. Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* 6: 51–71.
- CHAZDON, R. L., C. A. PERES, D. DENT, D. SHEIL, A. E. LUGO, D. LAMB, N. E. STORK, AND S. E. MILLER. 2009. The potential for species conservation in tropical secondary forests. *Conserv. Biol.* 23: 1406–1417.
- CINCOTTA, R. P., J. WISNEWSKI, AND R. ENGELMAN. 2000. Human Populations in the biodiversity hotspots. *Science* 404: 990–992.
- COLWELL, R. K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8. Persistent URL: <http://purl.oclc.org/estimates>.
- CRUMP, M. L. 2010. Amphibian diversity and life history. *In* K. C. Dodd Jr. (Ed.). *Amphibian ecology and conservation a handbook of techniques*, pp. 1–19. Oxford University Press, Oxford, U.K.
- DEVY, M. S., AND P. DAVIDAR. 2001. Response of wet forest butterflies to selective logging in Kalakad-Mundanthurai Tiger Reserve: Implications for conservation. *Curr. Sci.* 80: 400–405.
- DINESH, K. P., C. RADHAKRISHNAN, K. V. GURURAJA, K. DEUTI, AND G. BHATTA. 2013. A checklist of Amphibia of India with IUCN Red list status. http://zsi.gov.in/checklist/Amphibia_final.pdf. Accessed 15 August 2013.

- DUPELLMAN, W. E., AND L. TRUEB. 1994. *Biology of amphibians*. The John Hopkins University Press, Baltimore, Maryland.
- ENGBRECHT, B. M., AND H. M. HERZ. 2001. Evaluation of different methods to estimate understorey light conditions in tropical forests. *J. Trop. Ecol.* 17: 207–224.
- ERNST, R., K. E. LINSEMAIR, AND M. O. RÖDEL. 2006. Diversity erosion beyond the species level: Dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biol. Conserv.* 133: 143–155.
- ERNST, R., AND M. O. RÖDEL. 2005. Anthropogenically induced changes of predictability in tropical anuran assemblage. *Ecology* 86: 3111–3118.
- FREDERICKSEN, N. J., AND T. S. FREDERICKSEN. 2004. Impacts of selective logging on amphibians in a Bolivian tropical humid forest. *For. Ecol. Manage.* 191: 275–282.
- GANESAN, R. 2000. Tree diversity and regeneration in logged wet evergreen forests of the Agasthyamalai range in south Western Ghats, India. PhD dissertation, Madras Christian College, Chennai, India.
- GANESAN, R., AND P. DAVIDAR. 2003. Effect of logging on the structure and regeneration of important fruit bearing trees in a wet evergreen forest, southern Western Ghats, India. *J. Trop. Forest Sci.* 15: 12–25.
- GANESH, T., AND P. DAVIDAR. 1999. Fruit biomass and relative abundance of frugivores in a rain forest of southern Western Ghats, India. *J. Trop. Ecol.* 15: 399–413.
- GARDNER, T. A., J. BARLOW, R. CHAZDON, R. M. EWERS, C. A. HARVEY, C. A. PERES, AND N. S. SODHI. 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecol. Lett.* 12: 561–582.
- GARDNER, T. A., J. BARLOW, AND C. A. PERES. 2007. Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles. *Biol. Conserv.* 138: 166–179.
- GIBSON, L., T. M. LEE, L. P. KOH, B. W. BROOK, T. A. GARDNER, J. BARLOW, C. A. PERES, C. J. A. BRADSHAW, W. F. LAURANCE, T. E. LOVEJOY, AND N. S. SODHI. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478: 378–381.
- GUARIGUATA, M. R., AND R. OSTERTAG. 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. *For. Ecol. Manage.* 148: 185–206.
- GURURAJA, K. V. 2002. Effect of habitat fragmentation on distribution and ecology of anurans in some parts of central Western Ghats. PhD Dissertation, Kuvempu University, Karnataka, India.
- HAMMER, Ø., D. A. T. HARPER, AND P. D. RYAN. 2001. PAST-Paleontological statistics. www.uv.es/~pardomv/pe/2001_1/past/pastprog/past.pdf. Accessed 20 March 2013.
- HARTSHORN, G. S. 1995. Ecological basis for sustainable development in tropical forests. *Annu. Rev. Ecol. Syst.* 26: 155–175.
- HILLERS, A., M. VEITH, AND M. O. RÖDEL. 2008. Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. *Conserv. Biol.* 22: 762–772.
- INGER, R. F., H. B. SHAFFER, M. KOSHY, AND R. BAKDE. 1987. Ecological structure of a herpetological assemblage in South India. *Amphibia-Reptilia* 8: 189–202.
- JOHNS, A. D. 1985. Selective logging and wildlife conservation in tropical rain-forest: Problems and recommendations. *Biol. Conserv.* 31: 355–375.
- JOHNS, A. D. 1992. Vertebrate responses to selective logging: Implications for the design of logging systems. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 335: 437–442.
- JOHNSINGH, A. J. T. 2001. The Kalakad–Mundanthurai tiger reserve: A global heritage of biological diversity. *Curr. Sci.* 80: 378–388.
- KIESECKER, J. M. 2010. Global stressors and the global decline of amphibians: Tipping the stress immunocompetency axis. *Ecol. Res.* 26: 897–908.
- KRISHNAMURTHY, S. V. 2003. Amphibian assemblages in undisturbed and disturbed areas of Kudremukh National Park, central Western Ghats, India. *Environ. Conserv.* 30: 274–282.
- KUDAVIDANAGE, E. P., T. C. WANGER, C. ALWIS, S. SANJEEWA, AND S. W. KOTAGAMA. 2012. Amphibian and butterfly diversity across a tropical land-use gradient in Sri Lanka; implications for conservation decision making. *Anim. Conserv.* 15: 253–265.
- LEGENDRE, P., AND L. LEGENDRE. 1998. *Numerical ecology* (2nd English edition). Elsevier Science B. V., Amsterdam, The Netherlands, pp. 853.
- MARSH, D. M., AND P. B. PEARMAN. 1997. Effects of habitat fragmentation on the abundance of two species of Leptodactylid frogs in an Andean montane forest. *Conserv. Biol.* 11: 1323–1328.
- MCDONALD, J. H. 2009. *Handbook of biological statistics* (2nd edition). Sparky House Publishing, Baltimore, Maryland. <http://udel.edu/~mcdonald/stattransform.html>. Accessed 20 March 2014.
- MEEGASKUMBURA, M., K. MANAMENDRA-ARCHICHI, C. J. SCHNEIDER, AND R. PETHIYAGODA. 2007. New species amongst Sri Lanka's extinct shrub frogs (Amphibia: Rhacophoridae: Philautus). *Zootaxa* 1397: 1–15.
- OFORI-BOATENG, C., W. ODURO, A. HILLERS, K. NORRIS, S. K. OPPONG, G. B. ADUM, AND M. O. RÖDEL. 2012. Differences in the effects of selective logging on amphibian assemblages in three West African forest types. *Biotropica* 1: 1–8.
- PELISSIER, R., J. P. PASCAL, F. HOULLIER, AND H. LABORDE. 1998. Impact of selective logging on the dynamics of a low elevation dense moist evergreen forest in the Western Ghats (South India). *For. Ecol. Manage.* 105: 107–119.
- PETERS, S. L., J. R. MALCOM, AND B. L. ZIMMERMAN. 2006. Effect of selective logging on bat communities in the southeastern Amazon. *Conserv. Biol.* 20: 1410–1421.
- POOLE, R. W. 1974. *An introduction to quantitative ecology*. McGraw-Hill, New York.
- ROBINSON, W. D., AND S. K. ROBINSON. 2001. Effects of selective logging on forest bird populations in a fragmented landscape. *Conserv. Biol.* 13: 58–66.
- SCHULZE, C. H., M. WALTERT, P. J. A. KESSLER, R. PITOPANG, D. VEDDELER, M. MÜHLENBERG, S. R. GRADSTEIN, C. LEUSCHNER, I. STEFFAN-DEWENTER, AND T. TSCHARNTKE. 2004. Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. *Ecol. Appl.* 14: 1321–1333.
- SCOTT, N. J. JR. 1976. The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* 1: 41–58.
- SODHI, N. S., M. R. C. POSA, T. M. LEE, D. BICKFORD, L. P. KOH, AND B. W. BROOK. 2010. The state and conservation of Southeast Asian biodiversity. *Biodivers. Conserv.* 19: 317–328.
- STUART, S. N., J. S. CHANSON, N. A. COX, B. E. YOUNG, A. S. L. RODRIGUES, D. L. FISCHMAN, AND R. W. WALLER. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306: 1783–1786.
- SWIHART, R. K., T. M. GEHRING, AND M. B. KOLOZSVARY. 2003. Response of 'resistant' vertebrates to habitat loss and fragmentation: The importance of niche breadth and range boundaries. *Divers. Distrib.* 9: 1–18.
- TERBORGH, J. 1992. Maintenance of diversity in tropical forests. *Biotropica* 24: 283–292.
- VALLAN, D., F. ANDREONE, V. H. RAHERISOA, AND R. DOLCH. 2004. Does selective wood exploitation affect amphibian diversity? The case of An'Ala, a tropical rainforest in eastern Madagascar. *Oryx* 38: 410–417.
- VASUDEVAN, K., A. KUMAR, AND R. CHELLAM. 2001. Structure and composition of rainforest floor amphibian communities in Kalakad-Mundanthurai Tiger Reserve. *Curr. Sci.* 80: 406–412.
- VASUDEVAN, K., A. KUMAR, B. R. NOON, AND R. CHELLAM. 2008. Density and diversity of forest floor anurans in the rain forests of southern Western Ghats, India. *Herpetologica* 64: 207–215.
- VÁZQUEZ, D. P., AND D. SIMBERLOFF. 2002. Ecological specialization and susceptibility to disturbance: Conjectures and refutations. *Am. Nat.* 159: 606–623.
- VILLELA, D. M., M. T. NASCIMENTO, L. E. O. ARAGÃO, AND D. M. DA GAMA. 2006. Effect of selective logging on forest structure and nutrient

- cycling in a seasonally dry Brazilian Atlantic forest. *J. Biogeogr.* 33: 506–516.
- WHITFIELD, S. M., K. E. BELL, T. PHILIPPI, M. SASA, F. BOLAÑOS, G. CHAVES, J. M. SAVAGE, AND M. A. DONNELLY. 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proc. Natl Acad. Sci.* 104: 8352–8356.
- WILCOVE, D. S., X. GIAM, D. P. EDWARDS, B. FISHER, AND L. P. KOH. 2013. Navjot's nightmare revisited: Logging, agriculture, and biodiversity in Southeast Asia. *Trends Ecol. Evol.* 28: 531–540.
- WOODS, C. L., AND S. J. DEWALT. 2013. The conservation value of secondary forests for vascular epiphytes in central panama. *Biotropica* 45: 119–127.