

The effects of rainforest fragmentation on herpetofauna of the Western Ghats: A tribute to Dr. Ajith Kumar

Background and Introduction

This study of herpetofauna of the Western Ghats in South India was conceived and designed collectively by Dr Ajith Kumar, and two authors of this article (B.R.N. and R.C.) in the mid-1990s. Small mammals were the third taxa that was the focus of this research project, a taxon which was among Dr. Ajith's favourites. We were funded by the United States Fish and Wildlife Service, routed through the Wildlife Institute of India. Our study had three broad objectives:

1. To examine community structure and ecology of herpetofauna in relatively undisturbed rainforests of the Kalakad-Mundanthurai Tiger Reserve, in terms of species richness and relative abundance; and to understand the factors governing their variation.
2. To identify the nature and extent of changes in the herpetofauna community in rainforest fragments of the Anamalai hills, and the habitat correlates of such changes.
3. To identify implications of above findings for conservation, and for future research of herpetofauna in the Southern Western Ghats.

Dr. Ajith Kumar's major intellectual contributions to this rainforest fragmentation study focuses on two main areas, First, is the development of a set of research questions that are grounded in predictions arising from ecological theory. And the second, is an exploration of the utility of novel sampling designs to estimate the abundance and distribution of rare species of reptiles and amphibians.

Research questions grounded in ecological theory can provide insights into key mechanisms underlying the distribution and abundance of species in ecological systems (Twombly & Hastings 2022). Such knowledge can help managers address complex conservation challenges. The application of novel sampling designs is key because the empirical data required for unbiased estimates of distribution and abundance of rare species are poorly served by traditional sampling methods.

In this article, we focus and reflect primarily on research findings relevant to the abundance, distribution and species richness of forest floor amphibians (see Vasudevan et al. 2001, 2008) and reptiles (see Ishwar et al. 2001). Both these studies estimated two state variables: the density (or abundance scaled by sampled area) and species richness, of amphibians and reptiles. Our discussion in this article focuses primarily on the estimation of species richness patterns derived from the sampling of forest floor environments in intact rainforests of the Kalakad-Mundanthurai Tiger Reserve (henceforth, KMTR) and the rainforest fragments in the Anamalai hills.

Ecological theory underlying diversity in forest fragments

Forest fragmentation theories address how species richness, abundance and population viability are affected by habitat amount and spatial structure. The major theories relevant to the distribution and abundance of wildlife species were well known by Dr. Kumar. Based on his guidance, these theories formed the framework of our research in the rainforest fragmentation project.

The dominant theoretical frameworks relevant to habitat fragmentation at the time -- and ones that influenced our a priori hypotheses -- were the theory of island biogeography (TIB; MacArthur & Wilson 1967) and the related species-area relationship (SAR). The SAR predicts that the relationship between species richness (S) and habitat area (A) is defined by the power function. The TIB includes the monotonic increase in species richness with area, but it also predicts how S decreases with isolation, when habitats are similar (MacArthur & Wilson 1967). One explanation for the positive species-area relationship is based on the habitat heterogeneity hypothesis—that is, larger areas provide more habitat types (Rosenzweig 1995).

A second explanation, based on population viability analyses, is that larger populations are less extinction prone than smaller, more isolated populations (Noon et al. 1999).

We hypothesised that forest fragmentation is an ultimate causal factor leading to the eventual and proximate declines in species richness and local abundances of species. For this, we relied on a typology that distinguishes between two broad classes of stressors (Lawton 1994).

Factors that result in populations being rare and isolated in the first place are called “the ultimate causes of extinction” (Simberloff & Abele 1976) or collectively referred to as the “declining population paradigm” (Caughley 1994). A second set of factors that result in eventual extinction once populations have become small and disjunct, represent the “proximate causes of extinction” (Simberloff & Abele 1976), or what Caughley (1994) grouped together as consequences of the “small population paradigm”. It is useful to qualify these two sets of threats, wherein ultimate factors are the deterministic events that initially put the population at risk, and proximate factors are the stochastic events that lead to eventual extinction.

Regardless of the chosen theoretical framework, it is important to recognize that all scientific theories are conditional on our understanding of causation, and subject to the limits of current knowledge and empirical data.

Methods

We used a suite of sampling methods, including 5 × 5 m quadrats for sampling amphibians and reptiles on the forest floor, line transects for arboreal reptiles, and stream surveys for stream-dwelling amphibians and reptiles.

Classical sampling theory lacks the flexibility to adjust sampling location based on the spatial patterns of animal abundance. These deficiencies were addressed by the work of Thompson (1990, 1991), and Thompson & Seber (1996). A number of sampling designs emerged, collectively referred to as adaptive sampling. Adaptive designs have proven to be particularly useful for sampling rare species, or species with patchy spatial distributions as well; this was the case for many forest-floor reptiles and amphibians in the Western Ghats.

In our study, quadrat sampling designs complemented simple random sampling (SRS) with adaptive cluster sampling methods (ACS; Thompson & Seber 1996; Christman 2000). We adopted an ACS design because sampling efficiency would be greater when sampling rare species with aggregated spatial distributions. We expected key environmental variables on the forest floor to be spatially correlated, resulting in aggregated spatial distributions of most reptiles and amphibians. ACS allows the inclusion of additional sampling units (e.g., quadrats) in the immediate neighbourhood of any quadrat in which the focal taxonomic groups are found.

In our ACS sampling design, whenever ≥ 1 individual of a forest floor amphibian or reptile was detected within the quadrat, additional units -- called secondary units -- sharing a common

boundary with the original unit were added to the sample (Thompson & Seber 1996). The process continued until the cluster of neighbouring quadrats was surrounded by quadrats with no animals (see Noon et al. 2006 for additional details).

The sampling design for amphibians also included longitudinal surveys of montane streams (Vasudevan et al. 2006). Counts of the number of amphibian species detected within a given stream provided an estimate of alpha diversity. Among stream comparisons allow estimates of the degree of change in species diversity from one stream to another, i.e., beta diversity. And gamma diversity was estimated as the number of different species across all surveyed streams within the study region (Magurran 2004). An important limitation of our study design was that it did not provide estimates of species' detectabilities (Thompson & Seber 1994). As a consequence, estimates of abundance and density based on our counts reflect indices of abundance and density, and not absolute measures.

Estimates of species richness based on survey data are generally biased low because of heterogeneity in species detectabilities, and their imperfect detection ($p < 1$) (Boulinier et al. 1998; Williams et al. 2002). To address limitations of adaptive sampling design, the survey data collected by Drs. Ishwar and Vasudevan, were reanalysed (Noon et al. 2006) using two methods to compute an asymptotic estimate of species richness (Colwell 1997) from the reptile and amphibian quadrat data sets. The first was based on interpolated estimates of species richness using rarefaction (Coleman 1981; Coleman et al. 1982). Rarefaction methods estimate species richness as a function of sample size n (where n is the number of quadrats in the sample) by taking repeated random samples of size k ($k = 1, 2, \dots, n$), without replacement, from the collection of all sampled quadrats. Interpolated estimates fall within the range of known sample estimates.

Because of imperfect detectability, we also explored an extrapolation method to compute an asymptotic estimate of species richness. Extrapolation methods estimate species richness by including species believed to be present in the survey area but unobserved in the sample because of imperfect detectability and/or rarity. Extrapolated estimates fall outside of the range of sample estimates.

Results and Discussion

Test of fragmentation theory: reptiles

Results from our study for reptiles were generally consistent with a priori predictions based on theoretical expectations, namely, that species richness declined with declining patch size and increasing isolation. For example, the overall species richness of reptiles in rainforest fragments of the Anamalais was considerably lower (40 species) than in the contiguous rainforest in KMTR (54 species). However, the density of reptiles on the forest floor -- overall, as well as that of individual taxon -- showed no correlation with fragment area. The density of reptiles was related to different habitat features instead.

The species accumulation curves and species richness estimates based on both SRS and ACS sampling methods were similar, but ACS estimates were lower for both the interpolation estimator and the extrapolation estimator. Thus, information on the true number of reptilian species in KMTR was accumulating less quickly with ACS.

Test of fragmentation theory: amphibians

In the case of amphibians, in contrast to theoretical predictions, more species were recorded from the rainforest fragments of Anamalai Hills (40 species) than in the continuous forests of KMTR (32 species). This finding was attributed to the patchy distribution of amphibians and turnover of species across different streams (high beta diversity). Despite an overall increase in species richness with fragment area, however, the large and medium sized fragments had

more species than the largest fragment. Thus, the fragment area effect seems to be greater in reptiles than in the amphibians, especially in the case of endemics.

As in the case of reptiles, the density of amphibians too showed no association with fragment area; instead, the occurrence or abundance of many taxa was associated with specific habitat features. It should therefore be possible, from a management perspective, to maintain the vegetation structure and composition of fragments regardless of size in order to retain

populations. Specific measures would depend on the taxa and their conservation importance.

Reconciling fragmentation theory with our findings

Failure to find strong support for predicted fragmentation effects on species richness based on the theory of island biogeography, is not a refutation of the theory. Several factors may have contributed to variable results. Most significant may have been variable detection probabilities among species in each of these communities.



Figure 1 (clockwise, from top-left): (A) Metamorph of venated gliding frog taken in Andiparai Shola, Anamalais before its description to science. The distinctive patterns on the back of the metamorph froglet prompted the taxonomic investigation. (B) The survey team spent extensive periods in the field including in Kakkachi in Kalakad-Mundanthurai Tiger Reserve. The Kakkachi Fern House offered only a single room accommodation for the entire team to stay and the team performed the surveys from here. (C) Ajith Kumar and Barry Noon interacting with students in the field at Sengaltheri in Kalakad-Mundanthurai Tiger Reserve where the project had its first base camp. (D) The first camera trap image of a Brown Palm Civet *Paradoxurus jerdoni*, a flagship species that was studied in the project. The camera trap was fabricated by converting a point-and-shoot camera to trigger a photo when an animal walked on the pressure pad; the pressure pad itself was made by lining the inside of an air pillow with aluminium foil. Some attractive baits were placed carefully on top of the pressure pad. The camera trap was fabricated in Coimbatore by someone that Ajith knew. It worked!

At the time of conducting this study (1990s), the importance of variable detection probabilities among species was not fully appreciated, and survey methods to estimate p-values were not well developed.

In addition, estimates of abundance generally involve repeated sampling of populations, for which the identity of individuals is often required—for example, mark-recapture studies (White & Burnham 1999). These were the constraints under which the project operated and tried to come up with findings that are useful to inform conservation.

Test of alternative sampling designs: ACS versus SRS

For a fixed sampling effort, adaptive cluster sampling (ACS) resulted in higher estimates of species richness than simple random sampling (SRS). Both reptiles and amphibians in KMTR showed evidence of spatial clustering: they were more likely to occur in adjacent quadrats than expected at random. However, the estimates of reptile and amphibian density from the SRS and ACS sampling protocols were similar with overlapping 95% confidence intervals occurring in all cases (Noon et al. 2006).

Species richness of reptiles – measured through species accumulation curves and as species richness estimates –from the two re-sampling methods was similar. ACS estimates were lower than SRS for both the interpolation and extrapolation estimators. Thus, information on the true number of reptilian species accumulated less quickly with ACS than with SRS.

For amphibians, the SRS method detected only 10 species based on 87 individuals. Both the interpolated and extrapolated species accumulation curves for ACS were consistently above those for SRS, indicating a faster rate of encountering new species with ACS. For fixed sampling effort, ACS resulted in higher estimates of species richness than SRS.

Reanalysis of the reptile and amphibian quadrat sampling data from KMTR suggests that ACS was marginally more efficient than SRS in: 1) estimating species richness, because rare species were more likely to be detected, particularly evident for amphibian species, 2) providing larger sample sizes for habitat studies of focal taxa, and 3) documenting the degree of spatial aggregation, in terms of both multi-species assemblages and multi-individual aggregations.

The Linnean Shortfall

At the initiation of the project, 75 species of anurans were known from the Western Ghats, with most species described in the early 1900s, or earlier. Initially, knowledge of the species' taxonomic relationships was poorly known. This was a major hindrance for our research as several morphologically or acoustically distinct anurans were just labelled as species 1, 2 and so on. However, at the conclusion of our project, there was a steep rise in taxonomic descriptions and the number of amphibian species documented within the bounds of our study area. As of 2020, the number of anurans in the Western Ghats was thrice as high (226 species), and is likely to be even higher today (Dahanukar & Molur 2020).

Dr. Ajith Kumar was worried about the gap between the species detected and documented in our study and the greater number of species that were being described more broadly. However, there was little we could do beyond waiting for new descriptions to be available and updating our species designations with new binomial names as appropriate.

Our study resulted in rediscoveries of species not observed and documented for over 100 years. These species were *Melanobatrachus indicus*, *Rhacophorus calcadensis*, and *Walkerana phrynoderma*. It was reassuring to discuss these findings with Dr. Ajith Kumar: he was appreciative of the effort put into taxonomic identification of anurans, given the limitations in taxonomic capacity in



Figure 2: Photo of the poster of key herpetofauna from the project, entitled Living Treasure. © the authors.

Karthikeyan Vasudevan

Dr. Ajith was a mentor with a personal touch -- he cared for his students, as if they were his friends. This friendliness between a mentor and the student has many positives; among them, the bonhomie causing a contagion. It is striking that several young and mid-career ecologists are now following this tradition in India.

Barry Noon

Dr. Ajith Kumar was an accomplished researcher and an outstanding mentor and guide for all his students. His enthusiasm for the natural world, his outstanding sense of humour and his value as a friend cannot be overstated. I feel fortunate to have known him and for the opportunity to collaborate with him in our Western Ghats fragmentation study.

Ravi Chellam

Ajith was a force of nature. He genuinely cared for everyone he interacted with. His deep knowledge, amazing curiosity and zest for life are legendary. Despite all his achievements, he remained humble. I was fortunate to have worked closely with him for several years. We had tremendous fun, especially while doing fieldwork and playing cricket.

India. Our project also contributed to a broader understanding of the diversity of anuran species in India. In addition, we examined specimens collected from the Western Ghats study area at the Field Museum of Natural History at Chicago, USA. This resulted in the description of the Venated Gliding Frog *Rhacophorus pseudomalabaricus* (Vasudevan & Dutta 2000). *R. pseudomalabaricus* is now a flagship species that is driving an Amphibian Recovery Program in the southern Western Ghats (<https://www.wti.org.in/projects/amphibian-recovery-project/>).

Implications for anuran community assemblage in the Western Ghats

Despite taxonomic limitations, we were able to identify several key drivers of amphibian diversity in the southern Western Ghats. A significant finding was the discovery of beta-diversity in river basins and mountain ranges that act as the important spatial units, contributing to landscape scale (gamma) diversity of anurans in the southern Western Ghats (Vasudevan et al. 2006). For example, we documented a strong turnover of species from one river basin to another—at any given river basin there were only 30–40 species of anurans, even though we documented many more species across the Western Ghats.

This study was followed by studies on the diversity of anurans along the elevation gradient (Naniwadekar & Vasudevan 2007), and the impact of large dams on anuran community (Naniwadekar & Vasudevan 2014) in KMTR. Dr. Ajith Kumar was available for discussions and feedback on all these studies, and his mentoring played a pivotal role in building confidence of young researchers; these young researchers went on to establish successful careers in conservation biology.

Broad implications of this study for conservation of herpetofauna

The project was able to reveal for the first time, some fundamental knowledge about the species richness, abundance and distribution of

amphibians and reptiles in the Western Ghats. The distribution of both amphibians and reptiles in the Western Ghats is very irregular. Turnover in species composition from site to site arises from many factors, including the natural heterogeneity of the landscape resulting from steep topographical gradients, and human-induced fragmentation of otherwise continuous habitats. The combination of inherent heterogeneity and human induced fragmentation emphasises the necessity of landscape connectivity to facilitate species' movement and successful dispersal.

The patchy distribution of herpetofauna has important conservation implications. For example, protected areas in the Western Ghats need to enclose ecological gradients and continuous drainage systems. Conservation must also emphasise mature or old-growth rainforest fragments that are rare in the Western Ghats, and are of particular importance to arboreal reptiles.

Matrix habitats between forest fragments are also critical and in need of management and protection to facilitate movement of herpetofauna. This importance arises from the critical need of species with metapopulation structures to successfully disperse among habitat fragments by traveling through matrix habitats. Finally, it was proposed that conservation efforts should focus first on the largest patches that remain in the landscape, because sufficiently large forest patches support large, persistent populations (average birth rates exceed average death rates), thus providing potential colonists to smaller, neighbouring patches (Source-sink theory, Pulliam 1988).

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Barry R. Noon¹, Karthikeyan Vasudevan² & Ravi Chellam³

¹Department of Fish, Wildlife and Conservation Biology
Colorado State University, Fort Collins, CO 80521, USA
barry.noon@colostate.edu

²Laboratory for the Conservation of Endangered Species (LaCONES), CSIR-Centre for Cellular and Molecular Biology, Hyderabad, Hyderabad, Telangana 500048 India
karthik@ccmb.res.in

³Professor, Coexistence Studies Group
The University of Trans-Disciplinary Health Sciences and Technology, 74/2, Jarakabande Kaval, Post Attur via Yelahanka, Bengaluru, Karnataka 560064
India dr.ravichellam@tdu.edu.in

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